DANIELA SCHMITZ

ECOLOGICAL DRIVERS OF PLANT COMMUNITIES DIVERSITY AND STRUCTURE ALONG PEDOENVIRONMENTAL GRADIENTS IN MARITIME ANTARCTICA

Tese apresentada a Universidade Federal de Viçosa, como parte das exigências do Programa de Pós-Graduação em Botânica, para obtenção do título de *Doctor Scientiae.*

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SUMÁRIO

RESUMO

SCHMITZ, Daniela, D.Sc., Universidade Federal de Viçosa, julho de 2019. **Modeladores ecológicos da diversidade e estrutura de comunidades vegetais ao longo de gradientes pedoambientais na Antártica Marítima**. Orientador: Carlos Ernesto Gonçalves Reynaud Schaefer. Coorientador: Jair Putzke.

Na escala de paisagem, a disponibilidade de áreas livres de gelo determina a distribuição da vegetação terrestre na Antártica. A vegetação é composta predominantemente por briófitas e liquens que se estabelece em planícies, terraços, encostas, sobre rochas e solos em diferentes estádios de desenvolvimento, nas ilhas e regiões costeiras da Antártica. A distribuição e estrutura da vegetação na Antártica Marítima se dá por fatores ainda pouco elucidados. As características do solo podem ser um importante fator na montagem das comunidades vegetais, bem como sua dinâmica e desenvolvimento. Alterações na paisagem e nas comunidades vegetais são respostas às mudanças climaticas nessas áreas extremamente sensíveis. O objetivo do presente estudo foi analisar as mudanças na riqueza, composição e cobertura vegetal ao longo de um gradiente pedoambiental em três distintas ilhas da Antártica Marítima, avaliando os padrões ecológicos da diversidade de espécies de plantas não vasculares. E ainda, analisar as mudanças nos regimes térmicos da camada ativa, em três criossolos com contrastantes comunidades vegetais e diferentes padrões de cobertura. Essa avaliação foi realizada em três distintas ilhas do Arquipélago das Shetland do Sul: Nelson, Half Moon e Elefante. Para tanto, a amostragem da vegetação foi realizada em áreas distintas que formam um gradiente pedoambiental. As comunidades vegetais de cada pedoambiente foram amostradas utilizando-se em torno de 20 parcelas através do método fitossociológico de Braun-Blanquet. Em cada parcela foi coletada uma amostra de solo superficial para análise química e física. Para analisar o regime térmico da camada ativa, foram selecionadas três áreas na ilha Elefante, com coberturas vegetais distintas e abertos perfis de solo para instalação de sensores de temperatura e umidade do solo em diferentes profundidades e ainda, um sensor de temperatura do ar. A coleta de dados foi feita a cada hora e armazenada em um datalogger CR3000 por um período de dois anos. Nossos resultados mostram que a riqueza e composição de espécies, bem como a cobertura vegetal variou ao longo do gradiente pedoambiental. No entanto, diferenças na composição de espécies não foram tão acentuadas quanto o esperado, mostrando altos graus de similaridade entre diferentes pedoambientes. Nossos modelos, mostraram que diferentes preditores tem efeitos sobre a composição de espécies, nas diferentes ilhas estudadas, presumindo que não há um padrão especifico para a distribuição de espécies moldadas por um gradiente pedoambiental. Nos permitindo concluir que a filtragem pedoambiental pode determinar diferentes padrões de diversidade e estrutura de comunidades de plantas não vasculares através de diferentes processos em cada uma das ilhas. E ainda, que houve diferenças significativas entre a temperatura do ar e do solo, pelo efeito da cobertura vegetal, porém, não foi observado efeito na umidade do solo.

ABSTRACT

SCHMITZ, Daniela, D.Sc., Universidade Federal de Viçosa, July, 2019. **Ecological drivers of plant communities diversity and structure along pedoenvironmental gradients in Maritime Antarctica**. Adviser: Carlos Ernesto Gonçalves Reynaud Schaefer. Co-adviser: Jair Putzke.

In landscape scale, the availability of ice-free areas determines the distribution of terrestrial vegetation in Antarctica. The vegetation is predominantly composed of bryophytes and lichens that develops in plains, terraces, slopes, on rocks and soils at different stages of development, in the islands and coastal regions of Antarctica. The distribution and structure of vegetation in Antarctic Maritime is due to factors still little elucidated. Soil characteristics can be an important factor in the assembly of plant communities, as well as their dynamics and development. Changes in landscape and plant communities are responses to climate change in these extremely sensitive areas. The study aimed was to analyze the changes in richness, composition and vegetation cover along a pedoenvironmental gradient in three distinct islands of Maritime Antarctica, evaluating the ecological standards of the diversity of species of non vascular plants. Also, analyzing the changes in the thermal regimes of the active layer in three criossolos with contrasting plant communities and different coverage patterns. This evaluation was conducted in three distinct islands of the South Shetland archipelago: Nelson, Half Moon and Elephant. For this, vegetation sampling was performed in distinct areas that form a pedoenvironmental gradient. The vegetation communities of each pedoambiente were sampled using around 20 plots using the phytosociological method of Braun-Blanquet. In each plot a soil sample was collected for chemical and physical analysis. In order to analyze the thermal regime of the active layer, three areas were selected on Elefante Island, with different vegetation cover and open soil profiles for the installation of temperature and moisture soil sensors at different depths, as well as an air temperature sensor. Data collection was done every hour and stored in a CR3000 datalogger for a period of two years. Our results show that the richness and composition of species as well as the vegetation cover varied along the pedoenvironmental gradient. However, differences in species composition were not as marked as expected, showing high degrees of similarity between different pedoenvironments. Our models have shown that different predictors have effects on species composition in the different islands studied, presuming that there is no specific pattern for the distribution of species molded by a pedoenvironmental gradient. It allows us to conclude that pedoenvironmental filtering can determine different patterns of diversity and structure of non-vascular plant communities through different processes in each of the islands. Also, there were significant differences between air and soil temperature, due to the vegetation cover effect, but no effect was observed on soil moisture.

INTRODUÇÃO GERAL

A Antártica é o principal ecossistema terrestre dominado por comunidades de plantas não-vasculares (Poelking et al., 2015; Rodriguez et al., 2018), as quais estão restritas às poucas áreas livres de gelo, que constituem menos de 2% do continente (Robinson et al., 2003). A maioria destas áreas são representadas por regiões costeiras, e afloramentos rochosos íngremes de difícil acesso (Ochyra et al., 2008). Os ecossistemas das áreas livres de gelo da Antártica Marítima são fortemente condicionados pelo clima, é por isso sua relevância como indicadores para o monitoramento das mudanças climáticas (e.g. Robinson et al., 2018). Assim, as condições de crescimento para as plantas não vasculares na Antártica são extremas, como temperatura média anual do ar de -2.5°C, predomínio de fortes ventos e baixa radiação solar incidente (Beyer, 2000; Øvstedal e Smith, 2001).

A flora da Antártica é composta principalmente por briófitas e espécies de líquens adaptados a verões curtos e a baixas temperaturas (Putzke & Pereira, 2001). Há apenas duas espécies de angiospermas nativas na Antártica, a Poaceae, *Deschampsia antarctica* Desv. e a Caryophyllaceae, *Colobanthus quitensis* (Kunth.) Bartl.. As briófitas estão divididas em dois grupos taxonômicos: as hepáticas, com 27 espécies (Bednarek-Ochyra et al., 2000), e os musgos, dos quais existem 111 espécies descritas (Ochyra et al., 2008). Para fungos liquenizados, segundo Øvstedal & Lewis-Smith (2001), são conhecidas 386 espécies, sendo que trabalhos mais recentes sugerem que este número pode chegar a aproximadamente 500 espécies (Øvstedal & Schaefer, 2013).

Hábitats recentemente criados, resultantes da recessão do gelo, são escassamente colonizados nos estágios iniciais de sucessão, mas, com o tempo podem tornar-se amplamente cobertos pela vegetação, e, em áreas de escoamento do degelo, por tapetes de cianobactérias (Riffenburgh, 2007). Com o desenvolvimento e estabilização dos terrenos, diferentes tipos de comunidades vegetais podem ser encontradas ao longo de gradientes ambientais (e.x., Pereira and Putzke, 2013; Thomazini et al., 2018). Assim, hábitats úmidos sustentam comunidades dominadas por musgos, enquanto hábitats secos são tipicamente ocupados por diferentes comunidades de líquens (Schaefer et al., 2004). Uma vez que as comunidades vegetais se encontrem estabelecidas, tornam-se vulneráveis a sofrer modificações em sua estrutura (e.x. cobertura vegetal), e composição de espécies, depois de novos eventos de perturbação, (Lindsay, 1971; Longton, 1988), e é por isso sua importância como indicadores de monitoramento das mudanças climáticas (Robinson et al., 2018).

Nas áreas em que ocorreu degelo recente na Antártica Marítima, e consequente formação de lagos, as aves desempenham um papel importante na modificação dos solos da região costeira da Antártica (Poelking, et al., 2015). As aves marinhas, especialmente seus pontos de nidificação, constituem fator dominante no aporte de nutrientes e de carbono orgânico nos solos (COS) da Antártica (Beyer, 2000; Beyer et al., 2000; Park et al., 2007). A ocorrência de avifauna favorece a biodiversidade e a disponibilidade de nutrientes em alguns locais, proporcionando a formação de solos ornitogênicos (Tatur & Myrcha, 1993) e tornando-o suscetível ao aparecimento de espécies vegetais (Bockheim & Haus, 2014; Bockheim, 2015). Nestes solos observa-se a ocorrência de diversos minerais de argila fosfatados incomuns em solos de outros ambientes naturais do planeta (Tatur & Myrcha, 1993; Sun et al., 2002). Todos estes processos ambientais, desde a dinâmica do degelo até os processos de formação dos solos, também têm efeitos importantes sobre a geomorfologia (Michel et al., 2006; Francelino et al., 2011), o que pode ser determinante na diferenciação de hábitats e comunidades vegetais ao longo de gradientes pedoambientais (Schmitz et al., 2018; Schmitz et al., *in press*).

A estruturação das comunidades vegetais pode ser conduzida por diferentes processos em diferentes escalas espacias, selecionando espécies de um conjunto regional de espécies em um habitat local, ou seja, por filtragem ambiental (Kraft & Ackerly, 2010). Condições ambientais podem ser os principais modeladores da estruturação das comunidades, resultando no estabelecimento de determinadas espécies funcionalmente semelhantes sob a influência da filtragem do hábitat (Götzenberger et al., 2012; Kraft et al., 2015). Por exemplo, as propriedades do solo podem ser um filtro ambiental importante em pequenas escalas espaciais (Laliberté et al., 2014; Conti et al., 2017; Scherrer et al., 2018). Assim, mesmo em pequena escala, os mesmos padrões das comunidades vegetais (e.x., diversidade e estrutura) podem ser o resultado de diferentes processos e apenas testando a dependência da heterogeneidade abiótica dentro da comunidade, é possível diferenciá-los (Kraft et al., 2015).

Por tanto, é importante analisar a dinâmica temporal e espacial com as relações ecológicas na Antártica, como por exemplo, como as propriedades do solo, formas de relevo e microclima (Schaefer et al., 2004), podem determinar variações da diversidade e estrutura das comunidades vegetais (Conti et al., 2017). Espécies de plantas não vasculares, e particularmente as comunidades formadas por grupos específicos de associações, podem estar relacionadas a diferentes propriedades físicas (e.x., textura, profundidade) e químicas (e.x., pH, capacidade de troca cationica, matéria orgânica) do solo (Poelking, et al., 2015). Dessa forma, a transição de uma comunidade para outra é muitas vezes abrupta, criando um mosaico de pequenas, mas nitidamente contrastantes comunidades vegetais (Lewis Smith, 1988; Victoria et al., 2013; Schmitz et al., 2018).

No verão, a temperatura que controla a quantidade de água disponível para formação do solo e existência da biota, fica em torno de 0°C nas Shetland do Sul (Bockheim, 2015). As condições no nível da planta parecem estar influenciadas pela profundidade da cobertura de neve, bem como pela temperatura do ar e pelo metabolismo microbiano (Longton & Holdgate, 1967). Contudo, as temperaturas da cobertura vegetal ao nível do solo, são muitas vezes superiores às registradas no ar (Longton, 1967; Francelino, 2004; Almeida et al., 2014). Desta forma, a vegetação também tem uma influência sobre o equilíbrio energético do solo e, portanto, mudanças na vegetação podem resultar em alterações na espessura da camada ativa, nos ciclos de congelamento-descongelamento, na temperatura do permafrost subjacente, disponibilidade de água e influenciar nas características químicas do solo (Cannone et al., 2008, Guglielmin et al., 2014). A espessura da camada ativa também está relacionada a outros fatores como a presença de vegetação, a intensidade do frio e o tipo de solo, e pode ser estimada através das medições diárias da temperatura do solo (Campbell e Claridge, 1987; French, 2007; Guglielmin et al., 2014).

Na Antártica, a vegetação fornece um efeito isolante na temperatura da superfície do solo apesar de ter uma cobertura dispersa (Cannone e Guglielmin, 2009). O grau de resfriamento varia de acordo com as diferenças no tipo, estrutura, cobertura e espessura da vegetação (Cannone e Guglielmin, 2009; Almeida et al., 2014). Fatores que influenciam os processos de transferência de calor na camada ativa do solo, são as propriedades térmicas, tais como a temperatura e umidade do solo, e a textura (Michel et al., 2006). Contudo, os processos de transferência de energia entre o solo e o ar são mais efetivos em ambientes com ausência tanto da neve como da vegetação (Salamene, 2013). Por estes motivos, mais pesquisas ainda são necessárias para entender as variações térmicas e higrométricas na camada ativa em diferentes tipos de pedoambientes com diferentes coberturas vegetais de comunidades na Antártida, como base fundamental para o monitoramento de mudanças climáticas.

O Núcleo de pesquisas nos ecossistemas terrestres da Antártica (Terrantar) vem desenvolvendo atividades na Antártica desde 2002. No ano de 2015, os trabalhos relacionados a dinâmica e estrutura da vegetação se intensificaram nas ilhas Shetland do Sul. Com isso, um banco de informações esta sendo gerado, auxiliando no monitoramento da vegetação e no entendimento dos fatores que moldam a sua distribuição, principalmente relacionados ao solo, em uma escala fina e local.

Diante disso, o presente trabalho teve como objetivo analisar as mudanças na riqueza, composição de espécies e cobertura vegetal ao longo de um gradiente pedoambiental em três distintas ilhas da Antártica Marítima. Desta forma, avaliou-se os efeitos relativos de diferentes modeladores abióticos (propriedades físicas e químicas do solo, altitude) e bióticos (cobertura vegetal) sobre os padrões de riqueza e composição de espécies ao logo de gradientes pedoambientais. Além disso, analisou-se as mudanças nos regimes térmicos da camada ativa, em três criossolos com contrastantes comunidades vegetais e diferentes padrões de cobertura. Desta forma, esse trabalho foi dividido em duas partes, a primeira com três capítulos, referentes ao estudo da estrutura e diversidade das comunidades de plantas não vasculares e sua relação com os fatores edáficos em cada uma das três áreas de estudo, Península Stansbury, na Ilha Nelson; Ilha Half Moon; e Stinker Point, na Ilha Elefante. A segunda parte, com um capítulo referente à descrição e análise do microclima, solo e vegetação em três pedoambientes da Ilha Elefante. Intitulados da seguinte forma:

Parte I

- Capítulo 1: “Pedoenvironmental gradient shapes non-vascular species assemblage and community structure in Maritime Antarctica”

- Capítulo 2: “Plant community diversity and coverage pattern along a pedoenvironmental gradient in Maritime Antarctica”
- Capítulo 3: “Fertilidade do solo determina variações na composição de espécies, mas não na riqueza de plantas não vasculares ao longo de um gradiente pedoambiental na Antártica Marítima”

Parte II

- Capítulo 4: “Fine scale active layer thermal and hygrometrical regime in three cryosols with different plant community coverage from Elephant Island, Antarctica”.

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CAPÍTULO I:
Pedoenvironmental gradient shapes non-vascular species assemblage and community structure in Maritime Antarctica

*Submetido em **Ecological Indicator** (sob revisão)*

Abstract

SCHMITZ, Daniela, D.Sc., Universidade Federal de Viçosa, July, 2019. **Pedoenvironmental gradient shapes non-vascular species assemblage and community structure in Maritime Antarctica**. Adviser: Carlos Ernesto G.R. Schaefer. Co-adviser: Jair Putzke.

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. Based on the gradient analysis, soil texture and nutrient contents were important pedoenvironmental filters for non-vascular plants assemblages, clay content was particularly important for species composition, although there was high similarity between different pedoenvironments. Plant coverage, soil chemistry, soil texture and soil variables did not affect species richness and species composition, with the exception of clay content. High pedoenvironmental heterogeneity apparently did not promote species richness divergence among the pedoenvironments but determined high beta diversity. Pedoenvironmental filtering determines changes in species composition supporting a deterministic pattern. 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.

Keys words: lichens; pedoenvironmental filtering; microsite conditions; mosses; non-vascular plants; plant coverage.

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)[1]. 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 (Lundholm, 2009; Liu et al., 2014). Environmental heterogeneity may affect abiotic resources such as soil nutrients, which in turn strongly affect species diversity and community structure (Clarke et al., 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 (Amorin 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; Amorin 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 (Putzke and Pereira, 2001). In these areas, the vegetation shows a patchy spatial distribution as a consequence of multiple ecological conditions (Kappen et al., 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 soil 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; Amorin et al., 2017; Peñaloza-Bojacá et al., 2018); we hypothesized that soil characteristics (e.g. soil texture, soil chemistry) and coverage drive the community assembly. 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 (Sanaei et al., 2018a, 2018b); 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

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 to -1.0 ºC (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).

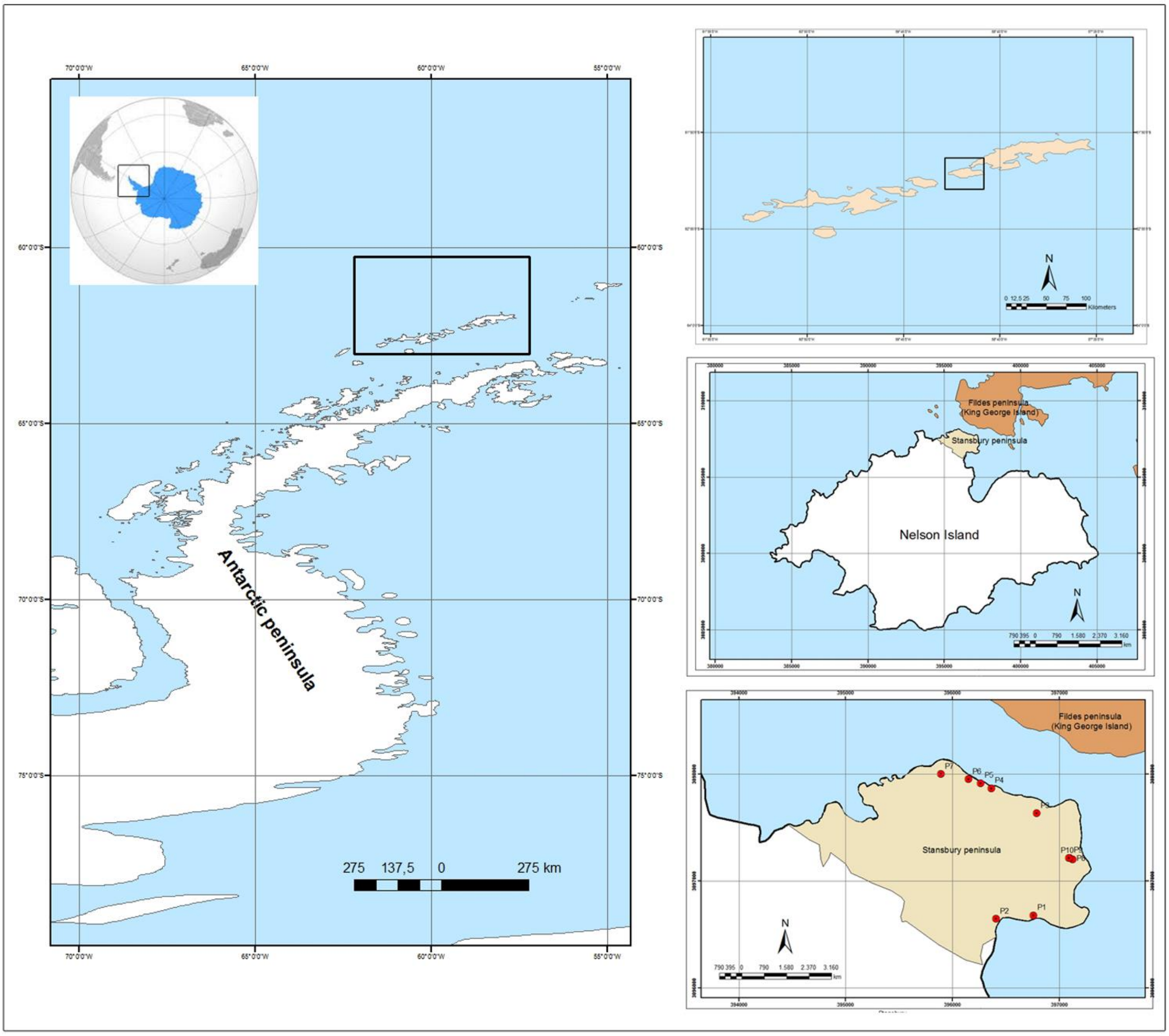

Fig. 1. Localization of the study area. Localization of the study area in relation to Antarctica (A), South Shetlands Islands (B), Nelson Island (C), Stansbury peninsula with the ten pedoenvironments (D).

Selection of different pedoenvironments

We selected ten pedoenvironments based on a geological approach (Figs. A.1 to 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, Subaquatic, Arenic and Protosodic, but differ from each other because P1 is Oligeoeutric and P2 is Orthoeutric and Akrofluvic. This also occurs for P3 and P4 which are Hyperskeletic, but P3 is Protic (shows no development), Reductaquic (has a saturated layer of water during the period of defrost) and Turbic (presents cryoturbation characteristics), while P4 is Leptic (rock continues above 100cm) and Tidalic (it is affected by tidal water). P6 and P7 differ still further from those cited above as being Protic Relictiturbic and Orthoskeletic (Table 1).

Table 1. Description of the ten sampling pedoenvironments (P).

P	Plots	Species number	Geographical coordinates	Landform	Geology	Geomorphology	Pedoenvironment	Plant community
1	20	10	62°14’50.52”S 58°59’15.19”W	Relatively flat with 5º of slope	Basaltic-andesitic	Marine terrace (2nd level)	Akroskeletic Protosalic Subaquatic Turbic Cryosols (Oligeoeutric. Arenic. Protosodic)	Moss carpet *Sanionia georgicouncinata-Warnstorfia fontinaliopsis.*
2	15	2	62°14’51.19”S 58°59’39.24”W	Flat	Basaltic-andesitic	Marine terrace (2nd level)	Akroskeletic Protosalic Subaquatic Cryosols (Orthoeutric. Arenic. Akrofluvic. Protosodic)	Moss carpet Sanionia uncinata
3	30	13	62°14’19.60”S 58°59’11.14”W	High declivity with striated pattern	Basaltic surrounded by andesitic boulders	Scree slope	Hyperskeletic Protosalic Protic Reductaquic Turbic Cryosols (Hypereutric. Clayic. Protosodic)	Moss carpet *Warnstorfia sarmentosa- Sanionia* spp.
4	20	14	62°14’11.70”S 58°59’40.54”W	Intermediate area between the beach and scree slope	Andesitic material deposited	Marine terrace (2nd level)	Hyperskeletic Protosalic Leptic Tidalic Cryosols (Hypereutric. Arenic. Protosodic)	Moss carpet *Sanionia* spp
5	20	9	62°14’09.90”S 58°59’46.46”W	High declivity with drainage lines	Basaltic-andesitic	Marine terrace (2nd level)	Akroskeletic Subaquatic Turbic Cryosols (Hypereutric. Loamic. Sodic)	Moss carpet *Sanionia* spp
6	20	16	62°14’08.26” S 58°59’52.85”W	Flat	Basaltic-andesitic	Scree slope	Protic Relictiturbic Cryosols (Hypereutric. Loamic. Ornithic)	Moss carpet *Sanionia georgicouncinata-Hennediela*
7	20	19	62°14’06.96”S 59° 0’11.82”W	flat	Basaltic-andesitic	Raised marine plataform	Orthoskeletic Subaquatic Turbic Cryosols (Orthodystric. Loamic. Hyperhumic)	Moss carpet *Warnstorfia Sanionia georgicouncinata*
8	20	19	62°14’34.56”S 58°58’48.88”W	Flat	Basaltic-andesitic	Marine terrace (3rd level)	Akroskeletic Subaquatic Turbic Cryosols (Orthoeutric. Loamic. Protosodic)	Moss carpet *Sanionia uncinata-Bryum argenteum*
9	20	17	62°14’33.68”S 58°58’50.11”W	soft wavy	Basaltic-andesitic	Marine terrace (3rd level)	Akroskeletic Turbic Cryosols (Hypereutric. Arenic))	Moss carpet *Sanionia georgicouncinata-Syntrichia-Hennediela*
10	21	18	62°14’33.59”S 58°58’51.36”W	soft wavy	Basaltic-andesitic	Marine terrace (3rd level)	Akroskeletic Turbic Cryosols (Orthoeutric. Loamic)	Moss carpet *Sanionia georgicouncinata*

Vegetation sampling

During the austral summer of 2017, 15 to 30 plots of 20 × 20 cm (Fig. A.11) were established for the sampling of non-vascular plants (lichens, mosses and alga) 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.

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 (H_2O), 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_t), clay and silt contents.

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:

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

$$F = 100x/n \qquad (2)$$

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:

$$C= \sum(ci)/x \qquad (3)$$

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 codominant species or by restricted occurrence in more specific habitats (Longton, 1988, Poelking et al., 2015).

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, βsne represents nestedness-resultant dissimilarity, which measures how dissimilar the sites are due to a nested pattern (Baselga et al. 2010). βsne was calculated as the difference between βsor and βsim (Baselga, 2010, 2012).

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 (βsor, βsim, βsne), and coverage 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 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., 2013). 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 *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; 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 (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 18 analysed parameters (see above), as well as further soil parameters such as sand, silt, clay, SB, OM and pH. 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., 2018). 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. 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., 2018). 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).

3. Results

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.

Table 2. Descriptive statistics of soil attributes for the ten sampled areas in the ice-free areas of Rip Point, Nelson Island, Maritime Antarctica.

	P1	**P2**	**P3**	**P4**	**P5**	**P6**	**P7**	**P8**	**P9**	**P10**
pH H_2O	6.52 ± 0.20a	6.38 ± 0.15a	6.10 ± 0.21bc	6.38 ± 0.15ab	6.40 ± 0.17a	6.17 ± 0.76b	5.68 ± 0.50c	6.34 ± 0.17ab	6.40 ± 0.17ab	5.99 ± 0.15c
P (mg/dm^3)	58.64 ± 8.30d	109.3 ± 40.73c	112.8 ± 64.92c	76.06 ± 32.87	178.36 ± 114.21c	455.9 ± 104.32b	881.6 ± 174.99a	263.1 ± 127.1c	68.7 ± 16.97d	40.78 ± 9.20e
K (mg/dm^3)	209.2 ± 51.09a	269.6 ± 58.09a	154.0 ± 23.70	253.6 ± 52.60a	185.2 ± 25.40bc	169.6 ±25.39c	163.6 ± 63.03c	148.8 ± 4.81c	116.8 ± 5.40d	124.0 ± 12.88d
Na (mg/dm^3)	614.32 ± 186.18a	706.06 ± 217.08a	484.72± 156.9b	622.32 ± 201.37ab	394.96 ± 131.96b	323.1 ± 43.80bc	309.2 ± 117.83cd	287.2 ± 36.6cd	247.4 ± 29.08de	229.4 ± 27.66e
Ca^{2+} (cmol$_c$/dm^3)	13.52 ± 2.76b	6.33 ± 0.95c	29.28 ± 5.54a	15.88 ± 3.04b	25.31 ± 4.56 a	30.14 ± 7.09 a	12.68 ± 7.76 b	12.72 ± 2.39 b	25.08 ± 5.96 a	16.86 ± 2.71 b
Mg^{2+} (cmol$_c$/dm^3)	10.37 ± 2.82b	6.94 ± 1.21d	19.68 ±4.66a	11.60 ± 1.62b	15.54 ± 2.56a	13.19 ± 5.70bc	8.97 ± 5.17c	4.16 ± 0.40d	8.70 ± 1.2c	6.93 ± 1.54cd
H + Al (cmol$_c$/dm^3)	2.76 ± 1.06d	2.64 ± 0.51d	4.2 ± 0.69b	2.92 ± 0.96d	3.6 ± 0.34c	8.34 ± 6.72a	10.86 ± 5.37a	3.8 ± 0.95c	3.22 ± 0.57c	4.0 ± 0.91b
SB (cmol$_c$/dm^3)	27.11 ± 6.10b	17.04 ± 1.88c	51.46 ± 6.35a	30.84 ±2.80b	43.05 ± 6.32a	45.17 ± 29.46ab	23.42 ± 13.21bc	18.51 ± 2.65c	35.17 ± 7.17b	25.11 ± 4.06b
(t) (cmol$_c$/dm^3)	27.54 ± 5.75b	17.31 ± 1.73c	51.54 ± 6.45a	31.08 ±2.77b	43.09 ± 6.30a	46.44 ± 27.91ab	23.80 ± 13.04bc	18.51 ± 2.65c	35.19 ± 7.15b	25.13 ± 4.03b
OM (dag/kg)	0.36 ± 0.32d	0.70 ± 0.57d	1.35 ± 0.39c	1.2 ± 0.83c	1.93 ± 1.66c	2.45 ± 2.35bc	14.29 ± 12.91a	4.85 ± 3.24b	1.30 ± 0.49c	3.23 ± 1.91b
Cu (mg/dm^3)	6.35 ± 2.20a	5.38 ± 0.74b	5.28 ± 1.58b	7.68 ± 1.13a	5.06 ± 0.92b	5.31 ± 3.55ab	4.18 ± 2.47bc	6.02 ± 1.61a	6.08 ± 2.32a	5.11 ± 0.66b
Mn (mg/dm^3)	74.34 ± 19.51ab	34.7 ± 13.46c	69.54 ± 19.90ab	91.78 ± 33.22a	110.46 ± 15.47a	68.2 ± 51.63ab	43.7 ± 26.17b	46.5 ± 28.58b	62.58 ± 32.36b	53.42 ± 10.16b
Fe (mg/dm^3)	217.0 ± 23.38ab	195.9 ± 34.55b	174.2 ± 47.09b	208.5 ± 47.59ab	170.7 ± 14.56b	187.9 ± 73.39b	189.96 ± 29.33b	277.3 ± 48.3a	238.8 ± 51.1a	216.32 ± 39.55b
Zn (mg/dm^3)	0.86 ± 0.22c	0.96 ± 0.18c	1.33 ± 0.41b	1.48 ± 0.30b	1.30 ± 0.33b	1.08 ± 0.39b	3.00 ± 1.66a	2.30 ± 0.72a	1.38 ± 1.38b	1.59 ± 0.39b
N (dag/kg)	0.032 ± 0.02d	0.063 ± 0.01d	0.122 ± 0.039d	0.085 ± 0.02d	0.138 ± 0.08c	0.193 ± 0.135bc	0.682 ± 0.546a	0.274 ± 0.27bc	0.081 ± 0.016	0.183 ± 0.18c
Coarse sand (g/kg)	0.85 ± 0.04a	0.77 ± 0.08a	0.48 ± 0.06c	0.70 ± 0.05a	0.44 ± 0.17c	0.43 ± 0.02c	0.40 ± 0.08c	0.27 ± 0.06d	0.55 ± 0.05b	0.45 ± 0.10b
Fine sand (g/kg)	0.02 ± 0.009e	0.13 ± 0.10c	0.13 ± 0.01c	0.07 ± 0.03d	0.12 ± 0.06c	0.17 ± 0.04b	0.18 ± 0.02b	0.22 ± 0.05ab	0.17 ± 0.03b	0.16 ± 0.04b
Silt (g/kg)	0.04 ± 0.02e	0.01 ± 0.003e	0.15 ± 0.06d	0.09 ± 0.01d	0.23 ± 0.09b	0.22 ± 0.04b	0.24 ± 0.08b	0.33 ± 0.07a	0.15 ± 0.04c	0.21 ± 0.07b
Clay (g/kg)	0.09 ± 0.01d	0.09 ± 0.03d	0.25 ± 0.02a	0.14 ± 0.01c	0.22 ± 0.03a	0.17 ± 0.007b	0.18 ± 0.05b	0.18 ± 0.04b	0.14 ± 0.005c	0.18 ± 0.04b
Texture	sand	sand	Clay loam	Sandy loam	Clay loam	Sandy loam	Sandy loam	loam	Sandy loam	Sandy loam

pH: H_2O (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.

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 A.1), one flowering plant *D. antarctica* and two macroscopic algae (*Prasiola crispa* and one unidentified green alga). The richest family was the Bryaceae with seven species, followed by the Amblystegiaceae with four species.

The NMDS revealed that species composition varied between pedoenvironments but with a marked overlap among the ten groups (PERMANOVA: $F_{9,195} = 12.17$, $p < 0.01$; Fig. 2).

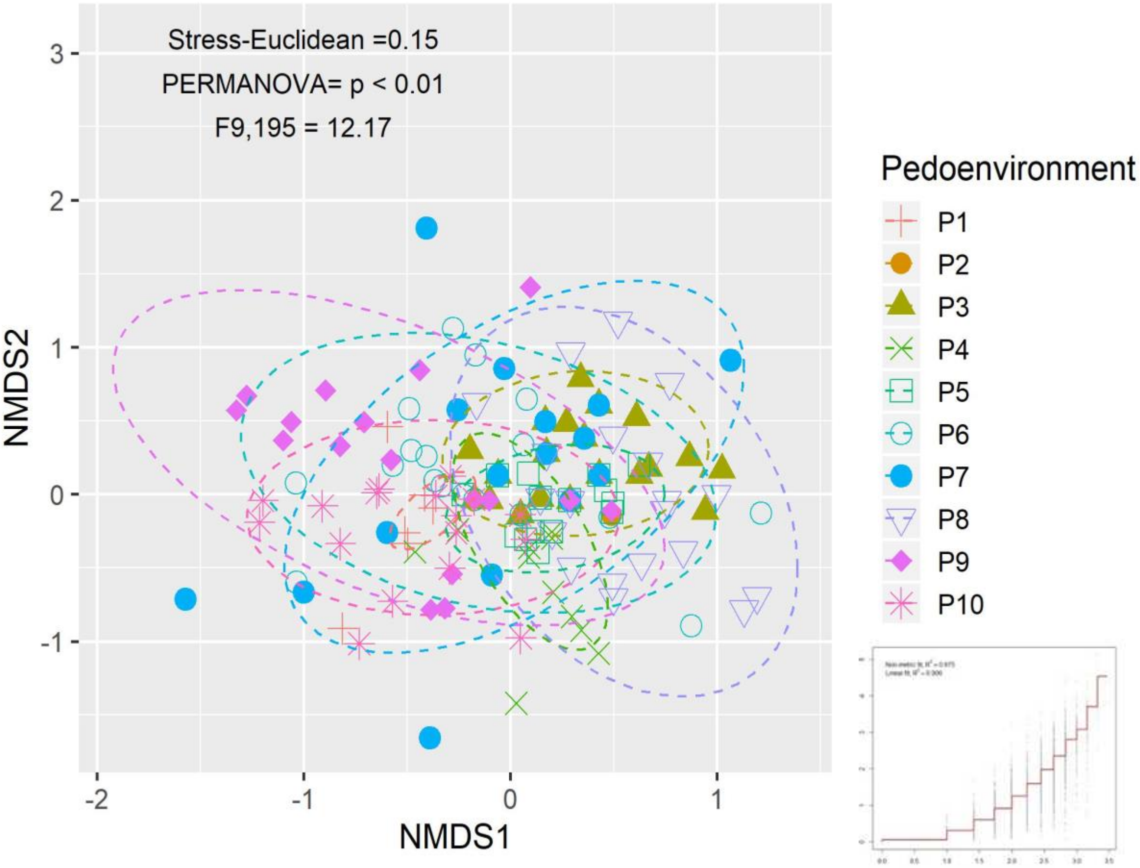

Fig. 2. Non metric multidimensional scaling (NMDS) based on species composition from different pedoenvironment sites.

Pedoenvironments 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, which indicated sampling sufficiency as we noted an asymptote of the extrapolated curves. Between nine and 19 species occurred in each pedoenvironment (except P_2, which presented only two species).

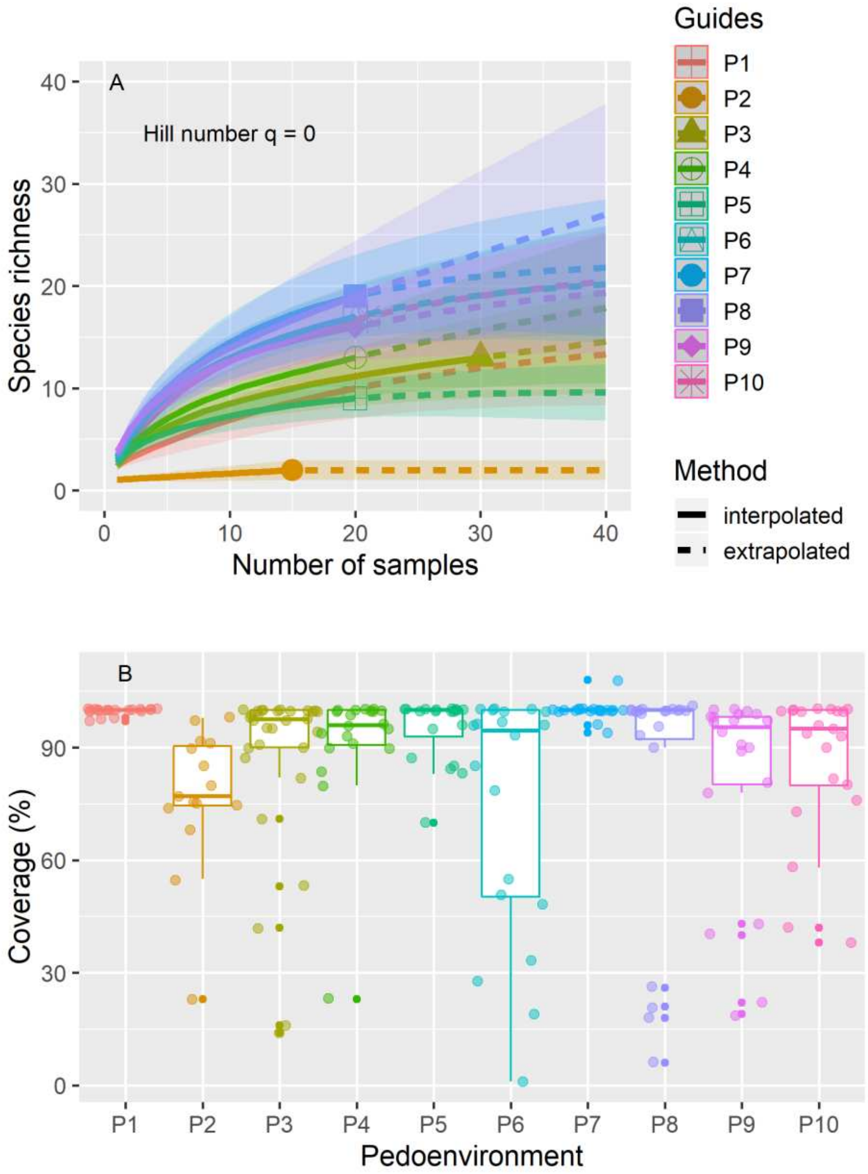

Fig. 3. Sampled-based rarefaction (solid lines) and extrapolation curves (dashed lines) of bryophyte species diversity based on the first Hill numbers (q = 0) for the sampled pedoenvironment (A), and coverage (B) between sampled pedoenvironment. Rarefaction and extrapolation curves present the lines that represent the mean values and the bands the standard deviation with 95% confidence intervals. Differences among the sampled pedoenvironment are indicated in Figure A.1.

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). Pedoenvironments P2 and P8 had *Sanionia uncinata* as the dominant species, but in P8 this species was associated with *Bryum argenteum*. P3 and P7 were very similar, *Warnstorfia sarmentosa* was the dominant species at both sites, followed by *S. georgicouncinata*, but the other species found in these communities differed considerably (Table A.2); 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. uncinata* (IES = 242.50) and *S. georgicouncinata* (IES = 269.5) as co-dominant species. P6 presented a S. *georgicouncinata-Hennediella heimii* association, this pedoenvironment was located near the nests of petrels and was the only one of the study sites where the grass *D. antarctica* occurred, although it was scarce (registered in only one plot; 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).

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 pedoenvironments P2, P5 and P8 and *W. sarmentosa* in pedoenvironments P3 and P7 (Table A.2.).

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 course sand ($R = -0.80$, $p < 0.05$) 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).

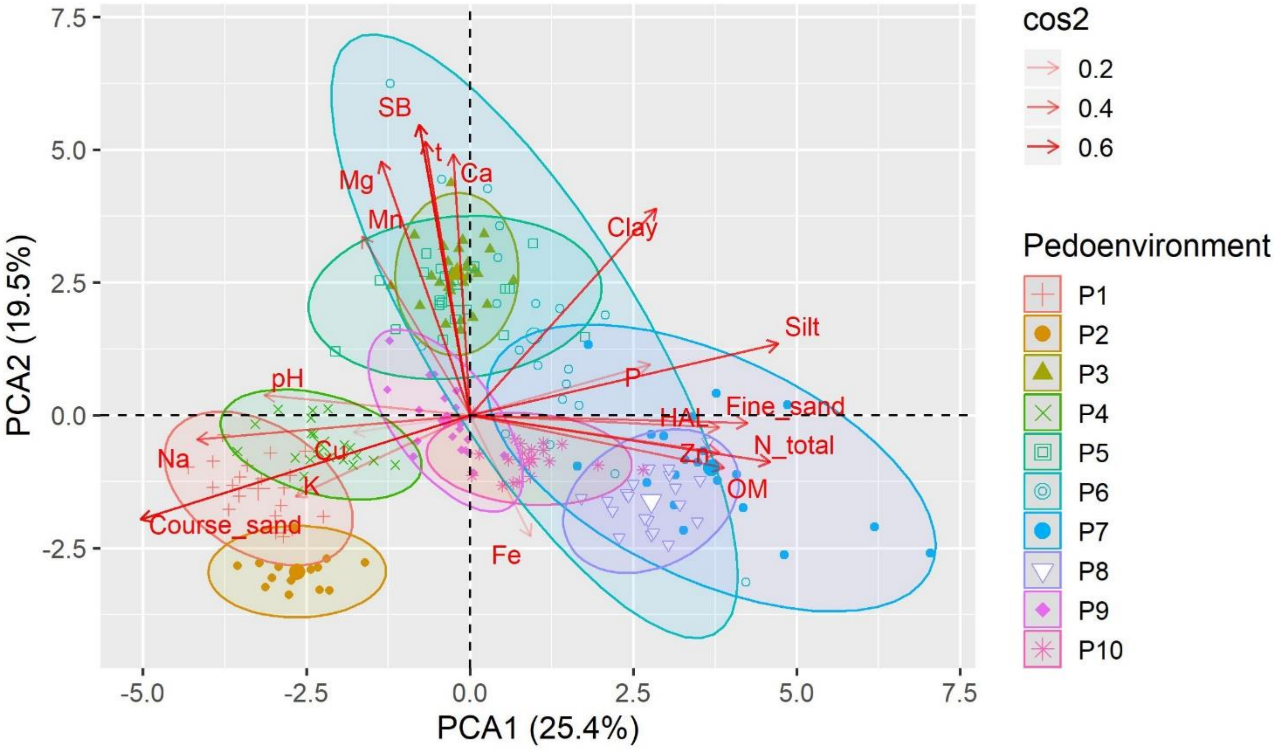

Fig. 4. Principal Component Analysis (PCA) for the soil parameters of different types of pedoenvironment sites. For analysis, available: total N, available P, K, Ca, Na, Mg, Fe, Cu, Mn, Zn, exchangeable acidity (H + Al), pH (H_2O), organic matter (OM), sum of exchangeable bases (SB); effective cation exchange capacity (t), and the soil texture as coarse sand (Sand_c), fine sand (Sand_t), clay and silt contents were included. The level of Pearson correlation of each vector is indicated (cos2).

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, D. antarctica* and *W. fontinaliopsis* were closely associated with pedoenvironments with greater pH and higher sand_c 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).

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: $z = 0.24$, $p < 0.036$), although further models fit species composition equally well without significant differences (Fig. 6; Table A4).

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 P_1, P_2 and P_4, which presented the lowest values (Fig. 7). Taxonomic β-diversity (Beta.SOR) ranged from 0.80 in pedoenvironments P3 to P10, but it was less than 50 in P2. The taxonomic turnover and β-diversity were higher than the nestedness-resultant component (Beta.sne) in the study area, except for P1, P2 and P4, where there was a higher degree of nestedness (Fig. 7).

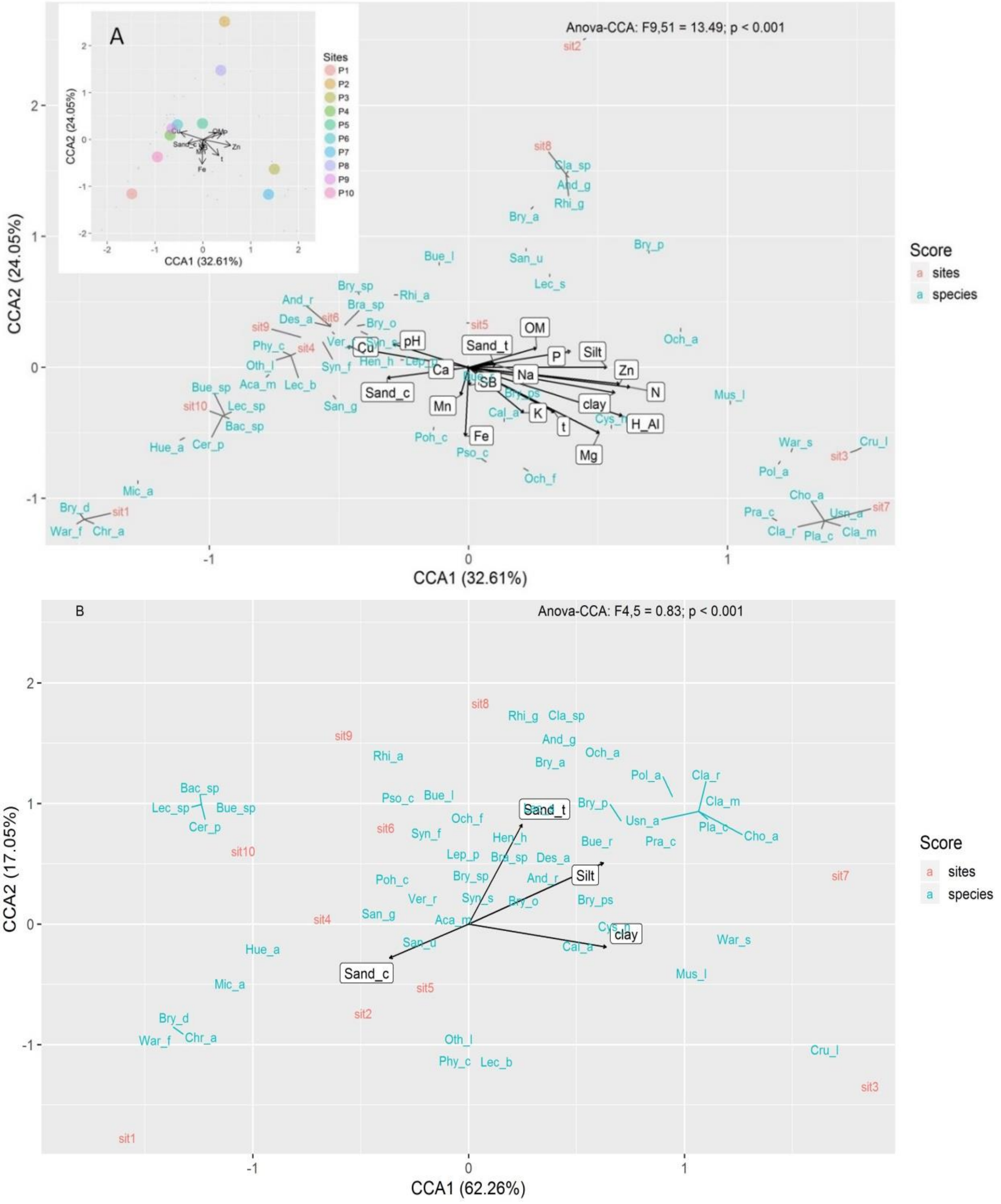

Fig. 5. Canonical correspondence analysis (CCA) showing species and plot scores in function of soil properties sampled within different types of pedoenvironments (A), and CCA only with texture properties (B). For analysis, available Zn, effective cation exchange capacity (t), exchangeable acidity (H+Al), 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.

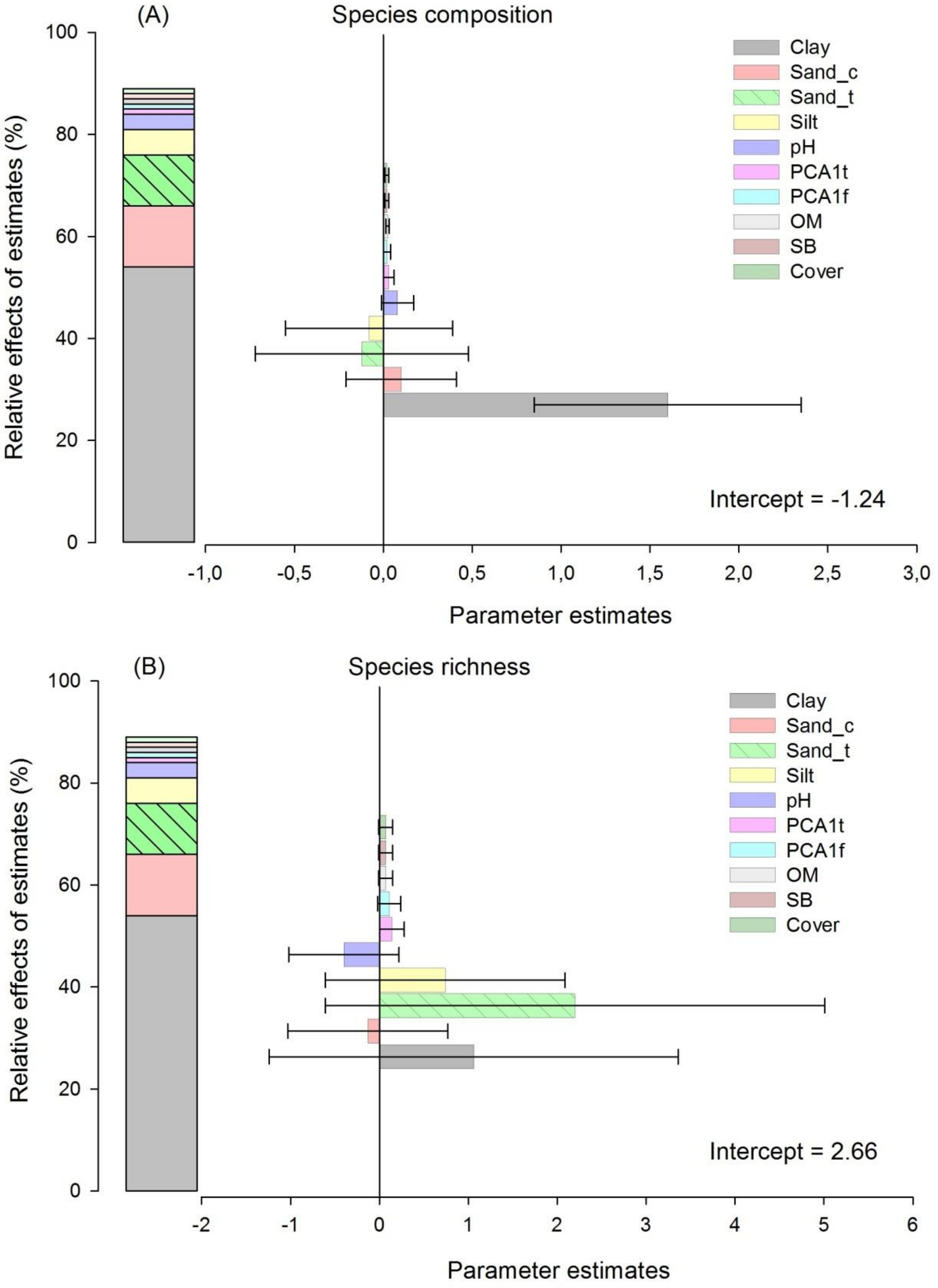

Fig. 6. Effects of multiple predictors on species composition (A) and species richness (B) in Antarctic. Results are presented for the mean distributions. We show the averaged parameter estimates (standardized regression coefficients) of model predictors, the associated 95% confidence intervals and the relative importance of each factor, expressed as the percentage of explained variance. The p-value of each predictor is given as: (.), $p < 0.1$; *, $p < 0.05$; ** $p > 0.01$; *** $p < 0.001$.

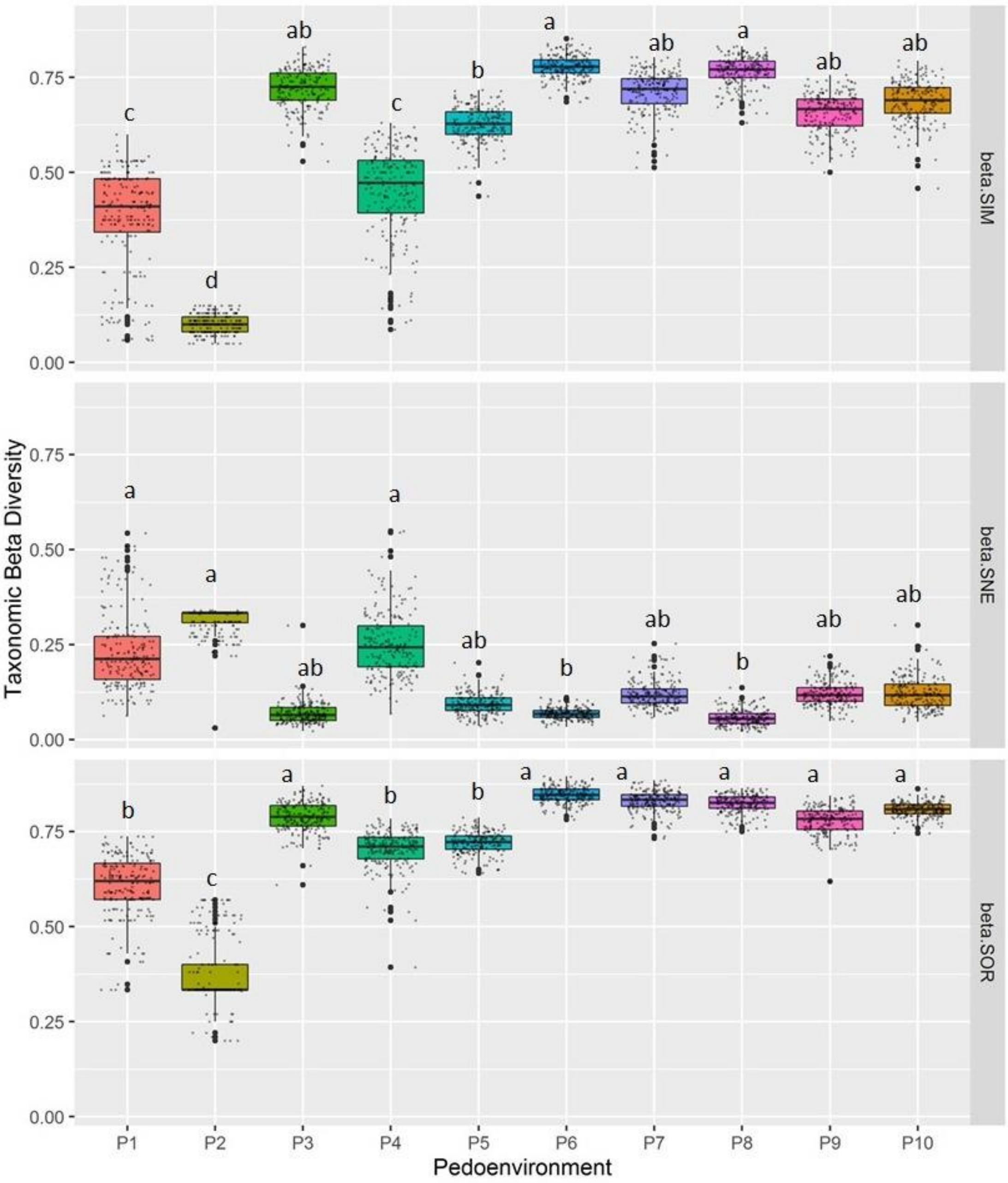

Fig. 7. Differences in the taxonomic beta diversity components of non-vascular species assemblages at different pedoenvironments. Taxonomic beta-diversity (beta.SOR) and its two components, turnover (beta.SIM) and nestedness-resultant (beta.SNE) are indicated. Different letters indicate significant differences at posteriori analyses (Dunn test, $P < 0.05$).

4. Discussion

Changes in diversity and community structure

Our results showed differences in species richness, species composition and plant coverage along the pedoenvironmental gradient, which corroborates our first hypothesis.

Likewise, we observe that the community similarity decreases as the differences in soil properties between the pedoenvironments increases, which supports our hypothesis. These changes in the soil properties along the pedoenvironmental gradient promote a high species turnover between pedoenvironments. The differences observed in the beta diversity could be related to differences in the soil properties evaluated through a direct gradient analysis.

Environmental gradient effects on bryophyte species richness have been reported in previous studies (e.g. Baniya et al., 2012; Batista and Santos, 2016; Amorin 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 (Amorin 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 much 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 Smith, 1996; Victoria et al., 2009a; Park et al., 2018). *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.

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 solifluction. 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 that the texture and chemical properties of soils were important pedoenvironmental filters for non-vascular plant assemblages. The contents of clay, sand_c and OM, as well as base saturation, were the main variables influencing changes in species composition along the gradient. However, only clay had a significant effect on species composition and no predictor (soil texture or fertility) had an effect on species richness. These results allow us to postulate that in non-vascular species assemblages environmental filters should be evaluated both at community and species level. First, at community level, little variation is observed in either species richness or composition along the pedoenvironmental gradient. Second, 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), determine changes in species distribution along the pedoenvironmental gradient.

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, 2018b). 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.

Species associations and types of communities

We observed that pedoenvironments are important filters for species associations at fine scale. For example, the moss carpet *S. georgicouncinata-W. fontinaliopsis* 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 sand_c 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.

Our results indicated that pedoenvironmental filtering not only determined diversity pattern at fine scale but also the type of community and species association along the gradient. For example, 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. However, 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*), 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. A12). 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.

The P9 pedoenvironment was located on a scree slope close to the drainage channel adjacent to the refuge; the area remained waterlogged during the summer and was covered by a moss carpet community of *Sanionia-Syntrichia-Hennediella* association. The abundant occurrence of *S. filaris* may be associated with the presence of alkaline soil, as well as high Ca. Likewise, the P10 pedoenvironment was located on a similar waterlogged zone close to the drainage channel, forming a *S. georgicouncinata* community moss carpet: *Bacidia sp.*, *Ceratodon purpureus* and *Lecidia sp.* were only found in this pedoenvironment, 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 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., 2018).

5. Conclusions

There were differences in non-vascular species richness, species composition and plant coverage along a pedoenvironmental gradient in maritime Antarctica and there was evidence of pedoenvironmental filtering driving non-vascular plant community assemblages. However, differences in species richness and species composition were not as marked as expected, showing high degrees of similarity between different pedoenvironments. Clay content was the only soil variable with a significant effect on species composition, but not on species richness at community level. High pedoenvironmental heterogeneity apparently did not promote species richness divergence among the pedoenvironments but determined high beta diversity. We assumed that pedoenvironmental filtering determined differences in species composition in this island from maritime Antarctica. This study revealed that the fine-scale heterogeneity contributed to typical non-vascular species associations along the pedoenvironmental gradient; thus, the soil filtering not only determined diversity patterns but also community types. Clay, coarse sand and OM content and base saturation levels were the main soil variables affecting species composition changes along the pedoenvironmental gradient.

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Appendix A: Supplementary data

Table A.1. List of species identified in the study areas.

Family	Group	Species	Abbreviation	N. of plots*
Poaceae	angiosperm	*Deschampsia antarctica* Desv.	Des_a	1
Amblystegiaceae	moss	*Sanionia georgicouncinata* (Müll. Hal.) Ochyra & Hedenäs	San_g	127
	moss	*Sanionia uncinata* (Hedw.) Loeske	San_u	91
	moss	*Warnstorfia fontinaliopsis* (Müll. Hal.) Ochyra	War_f	17
	moss	*Warnstorfia sarmentosa* (Wahlenb.) Hedenäs	War_s	54
Andreaeaceae	moss	*Andreaea gainii* Cardot	And_g	3
	moss	*Andreaea regularis* Müll. Hal.	And_r	1
Brachytheciaceae	moss	*Brachythecium* sp. Schimp.	Bra_sp	7
Bryaceae	moss	*Bryum argenteum* Hedw.	Bry_a	11
	moss	*Bryum dichotomum* Hedw.	Bry_d	1
	moss	*Bryum orbiculatifolium* Card. Et Brothv	Bry_o	11
	moss	*Bryum pallescens* Schleich. Ex Scwaegr.	Bry_p	6
	moss	*Bryum pseudotriquetrum* (Hedw.) Gaertn.	Bry_ps	8
	moss	*Bryum* sp Hedw.	Bry_sp	6
	moss	*Pohlia cruda* (Hedw.) Lindb.	Poh_c	3
Ditrichaceae	moss	*Ceratodon purpureus* (Hedw.) Brid.	Cer_p	4
Dicranaceae	moss	*Chorisodontium aciphyllum* (Hook. f. & Wilson) Broth.	Cho_a	3
Pottiaceae	moss	*Hennediella heimii* (Hedw.) R.H. Zander	Hen_h	20
	moss	*Syntrichia filaris* (Müll. Hal.) R.H. Zander	Syn_f	15
	moss	*Syntrichia saxicola* (Cardot) R.H. Zander	Syn_s	11
Polytrichaceae	moss	*Polytrichastrum alpinum* (Hedw.) G.L. Sm.	Pol_a	6
Acarosporaceae	lichen	*Acarospora macrocyclos* Vain.	Aca_m	3
Caliciaceae	lichen	*Buellia latemarginata* Darb.	Bue_l	2
	lichen	*Buellia russa* (Hue) Darb.	Bue_r	2
	lichen	*Buellia* (sp) De Not	Bue_sp	7
Cladoniaceae	Lichen	*Cladonia metacorallifera* Asahina	Cla_m	1
	Lichen	*Cladonia rangiferina* (L.) Weber ex F.H. Wigg.	Cla_r	1
	lichen	*Cladonia* (sp.) P. Browne	Cla_sp	1
Collemataceae	lichen	*Leptogium puberulum* Hue	Lep_p	20

Lecanoraceae	lichen	*Rhizoplaca aspidophora* (Vain.) Redón	Rhi_a	2
Lecideaceae	lichen	*Lecidea sciatropha* Hue	Lec_s	21
	lichen	*Lecidea* (sp) Ach.	Lec_sp	4
Not defined	lichen	*Cystocoleus niger (*Huds.) Har.	Cys_n	26
Ochrolechiaceae	lichen	*Ochrolechia antarctica* (Müll. Arg.) Darb.	Och_a	3
	lichen	*Ochrolechia frigida* (Sw.) Lynge	Och_f	3
Pannariaceae	lichen	*Psoroma cinnamomeum* Malme	Pso_c	4
Parmeliaceae	lichen	*Usnea aurantiacoatra* (Jacq.) Bory	Usn_a	2
Physciaceae	lichen	*Physcia caesia* (Hoffm.) Hampe ex Fürnr.	Phy_c	1
Ramalinaceae	lichen	*Bacidia* (sp.) De Not	Bac_sp	3
	lichen	*Lecania brialmontii* (Vain.) Zahlbr.	Lec_b	1
Rhizocarpaceae	lichen	*Rhizocarpon geographicum* (L.) DC.	Rhi_g	1
Teloschitaceae	lichen	*Caloplaca athallina* Darb.	Cal_a	4
	lichen	*Huea austroshetlandica* (Zahlbr.) C.W. Dodge	Hue_a	10
Thelenellaceae	lichen	*Microglaena antarctica* I.M. Lamb	Mic_a	2
Trapeliaceae	lichen	*Placopsis contortuplicata* I.M. Lamb	Pla_c	2
Verrucariaceae	lichen	*Verrucaria racovitzae* Vain.	Ver_r	10
-	lichen	Crustose lichens	Cru_l	1
-	lichen	Muscicolous lichens	Mus_l	37
-	lichen	Other lichens	Oth_l	1
-	algae	Green algae	Chr_a	1
Prasiolaceae	algae	*Prasiola crispa* (Lightfoot) Kützing	Pra_c	3

*Number of plots for each specie, in a total 206 plots

Table A.2. Where: F = relative frequency of the species; C = coverage*; ESI = Ecological Significance Index **.

Pedoenvironment	Species	F	C	ESI
P1	*Sanionia georgicouncinata*	100	4.45	545
P1	*Warnstorfia fontinaliopsis*	85	1.85	242.25
P1	*Bacidia austroshetlandica*	15	0.25	18.75
P1	*Cystocoleus niger*	10	0.15	11.5
P1	*Prasiola crispa*	10	0.1	11
P1	*Microglaena antarctica*	5	0.4	7
P1	*Chriptomonas antarcticum*	5	0.1	5.5
P1	*Acarospora macrocyclos*	5	0.05	5.25
P1	*Bryum dichotomum*	5	0.05	5.25
P1	*Buellia latermaginata*	5	0.05	5.25
P2	*Sanionia uncinata*	100	4.6	560
P2	*Bryum* sp.	6.66	0.06	7.11
P3	*Warnstorfia sarmentosa*	80	3.06	325.33

P3	*Sanionia georgicouncinata*	53.33	0.76	94.22
P3	*Sanionia uncinata*	40	1.33	93.33
P3	Muscicolous lichens not id	33.33	1.03	67.77
P3	*Cystocoleus niger*	13.33	0.26	16.88
P3	*Bryum pallescens*	10	0.1	11.0
P3	*Leptogium puberulum*	10	0.1	11.0
P3	*Bryum pseudotriquetrum*	6.66	0.33	8.88
P3	*Bryum argenteum*	3.33	0.03	3.44
P3	*Lecidea sciatrapha*	3.33	0.03	3.44
P3	*Liquen crustoso* não id	3.33	0.03	3.44
P3	*Pohlia cruda*	3.33	0.03	3.44
P3	*Syntrichia* sp.	3.33	0.03	3.44
P4	*Sanionia georgicouncinata*	100	4.2	520
P4	*Sanionia uncinata*	85	1.85	242.5
P4	*Lecidia sciatrapha*	25	0.25	31.25
P4	Muscicolous lichens not id	25	0.25	31.25
P4	*Bacidia austroshetlanica*	15	0.15	17.25
P4	*Caloplaca athalina*	15	0.15	17.25
P4	*Verrucaria racovitzie*	15	0.15	17.25
P4	*Bryum argenteum*	5	0.05	5.25
P4	*Cystocoleus niger*	5	0.05	5.25
P4	*Lecania brialmontii*	5	0.05	5.25
P4	Outros liquens muscícolas	5	0.05	5.25
P4	*Physcia caesia*	5	0.05	5.25
P4	*Syntrichia filaris*	5	0.05	5.25
P4	*Verrucaria* sp.	5	0.05	5.25
P5	*Sanionia uncinata*	85	2.55	301.75
P5	*Sanionia georgicouncinata*	70	2.85	269.5
P5	*Warnstorfia sarmentosa*	40	1.05	82
P5	*Bryum orbiculatifolium*	30	0.05	31.5
P5	Muscicolous lichens not id	10	0.15	11.5
P5	*Brachythecium sp*	10	0.1	11
P5	*Syntrichia* sp.	10	0.1	11
P5	*Cystocoleus niger*	5	0.05	5.25
P5	*Verrucaria racovitzie*	5	0.05	5.25
P6	*Sanionia georgicouncinata*	60	2.3	198
P6	*Hennediella heimii*	30	1	60
P6	*Sanionia uncinata*	35	0.55	54.75
P6	*Syntrichia saxicola*	30	0.3	39
P6	*Cystocoleus niger*	25	0.4	35
P6	*Bryum* sp.	25	0.25	31.25
P6	*Bryum orbiculatifolium*	20	0.45	29
P6	Muscicolous lichens not id	10	0.2	12
P6	*Acarospora macrocyclus*	10	0.1	11

P6	*Lecidia sciatrapha*	10	0.1	11
P6	*Verrucaria racovitzie*	10	0.1	11
P6	*Brachythecium* sp.	5	0.15	5.75
P6	*Deschampsia antarctica*	5	0.15	5.75
P6	*Buellia russa*	5	0.05	5.25
P6	*Leptogium puberulum*	5	0.05	5.25
P6	*Warnstorfia sarmentosa*	5	0.05	5.25
P7	*Warnstorfia sarmentosa*	70	2.7	259
P7	*Sanionia georgicouncinata*	55	1.95	162.25
P7	*Cystocoleus niger*	35	0.5	52.5
P7	Muscicolous lichens not id	30	0.5	45
P7	*Polytrichastrum alpinum*	20	0.25	25
P7	*Chorisodontium aciphyllum*	15	0.35	20.25
P7	*Lecidia sciatrapha*	15	0.2	18
P7	*Psoroma cinnamomeum*	15	0.15	17.25
P7	*Sanionia uncinata*	10	0.45	14.5
P7	*Usnea aurantiaco atra*	10	0.3	13
P7	*Hennediella heimii*	10	0.15	11.5
P7	*Ochrolechia antarctica*	10	0.1	11
P7	*Placopsis contortuplicata*	10	0.1	11
P7	*Prasiola crispa*	5	0.15	5.75
P7	*Buellia russa*	5	0.05	5.25
P7	*Caloplaca athalina*	5	0.05	5.25
P7	*Cladonia metacoralifera*	5	0.05	5.25
P7	*Cladonia rangiferina*	5	0.05	5.25
P7	*Ochrolechia frigida*	5	0.05	5.25
P8	*Sanionia uncinata*	70	2.5	245
P8	*Bryum argenteum*	40	0.9	76
P8	Muscicolous lichens not id	45	0.65	74.25
P8	*Sanionia georgicouncinata*	30	1.1	63
P8	*Lecidia sciatrapha*	30	0.55	46.5
P8	*Warnstorfia sarmentosa*	30	0.5	45
P8	*Andreaea gainii*	15	0.25	18.75
P8	*Bryum pallescens*	15	0.2	18
P8	*Leptogium puberulum*	15	0.15	17.25
P8	*Polytrichastrum alpinum*	10	0.1	11
P8	*Buellia latermaginata*	5	0.1	5.5
P8	*Brachythecium* sp	5	0.05	5.25
P8	*Cladonia* sp	5	0.05	5.25
P8	*Microglaena antarctica*	5	0.05	5.25
P8	*Ochrolechia antarctica*	5	0.05	5.25
P8	*Rhizocarpon geographicum*	5	0.05	5.25
P8	*Rhizoplaca aspidophora*	5	0.05	5.25
P8	*Syntrichia saxicola*	5	0.05	5.25

P8	*Verrucaria racovitzae*	5	0.05	5.25
P9	*Sanionia georgicouncinata*	80	2.85	308
P9	*Syntrichia filaris*	65	1.45	159.25
P9	*Hennediella heimii*	55	0.9	104.5
P9	*Leptogium puberulum*	40	0.5	60
P9	*Bryum pseudotriquetrum*	30	0.3	39
P9	*Sanionia uncinata*	20	0.8	36
P9	*Bacidia austroshetlanica*	15	0.2	18
P9	*Brachythecium sp*	15	0.15	17.25
P9	*Liquen muscicola*	10	0.2	12
P9	*Cystocoleus niger*	10	0.15	11.5
P9	*Lecidia sciatrapha*	10	0.1	11
P9	*Bryum argenteum*	5	0.1	5.5
P9	*Bryum orbiculatifolium*	5	0.05	5.25
P9	*Buellia* sp.	5	0.05	5.25
P9	*Lecidia* sp.	5	0.05	5.25
P9	*Verrucaria racovitzae*	5	0.05	5.25
P9	*Warnstorfia sarmentosa*	5	0.05	5.25
P10	*Sanionia georgicouncinata*	100	4.2	528.57
P10	*Buellia* sp	28.57	0.38	39.45
P10	*Leptogium puberulum*	23.80	0.33	31.74
P10	*Sanionia uncinata*	19.04	0.52	29.02
P10	*Ceratodon purpureus*	19.04	0.19	22.67
P10	*Lecidia* sp.	19.04	0.19	22.67
P10	*Bacidia* sp	14.28	0.19	17.0
P10	*Cystocoleus niger*	14.28	0.14	16.32
P10	*Ochrolechia frigida*	9.52	0.09	10.43
P10	*Pohlia cruda*	9.52	0.09	10.43
P10	*Syntrichia saxicola*	9.52	0.04	9.97
P10	Muscicolous lichens not id	4.76	0.42	6.80
P10	*Bacidia* sp.	4.76	0.09	5.21
P10	*Andreaea regularis*	4.76	0.04	4.98
P10	*Lecidia sciatrapha*	4.76	0.04	4.98
P10	*Psoroma cinammomeum*	4.76	0.04	4.98
P10	*Rhizoplaca aspidophora*	4.76	0.04	4.98
P10	*Verrucaria racovitzae*	4.76	0.04	4.98

Values ranging from 0 to 5; ** Values ranging from 0 to 600.

Table A.3. Significance levels are based on Pearson's correlation coefficients between soil parameters and principal components of both texture PCA and fertility PCA from 206 different plots along the pedoenvironmental gradient.

Soil parameters	**PCA1**	**PCA2**
Coarse sand (%)	**-0.80**	-0.31
Fine sand (%)	**0.67**	-0.02
Clay (%)	**0.45**	**0.61**
Silt (%)	**0.74**	0.21
pH	**-0.49**	0.06
OM	**0.61**	-0.15
HAl	**0.60**	-0.03
t	-0.10	**0.81**
SB	-0.12	**0.86**
N	**0.73**	-0.13
P	**0.44**	0.15
K	**-0.42**	-0.24
Mg	-0.21	0.75
Ca	-0.04	**0.78**
Na	**-0.66**	-0.07
Cu	-0.28	-0.05
Mn	-0.26	**0.53**
Fe	0.14	**-0.36**
Zn	**0.60**	-0.11

Factors that significantly correlated with PCA axes are highlighted in bold. For analysis, available Zn, effective cation exchange capacity (CEC), 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.

Table A.4.Candidate mixed effect models predicting the species richness with Poisson error distribution (generalized linear mixed effects model - glmer), species composition and basal area with Gaussian error distribution (linear mixed effects model - lme) from different pedoenvironments from Nelson island, maritime Antarctica. Predictors are: Sand_c, pH, soil texture (PCA1t), soil fertility (PCA1f), OM, SB, coverage. Result of information-theoretic–based model selection is indicated (Akaike criterion corrected for small samples). We consider as best models those with values of ΔAICc < 2.

Response variable	**Predictor**	**df**	**logLik**	**AICc**	**ΔAICc**	**AICw**
Species composition	~ Clay	4	-115.81	239.82	0	0.65
	~ Sand_c	4	-115.98	242.25	2.44	0.19
Gaussian lme	~ Sand_t	4	-118.17	244.54	4.72	0.06
	~ Silt	4	-118.43	245.05	5.24	0.05
	~pH	4	-118.84	245.87	6.06	0.03
	~PCA1t	4	-119.72	247.64	7.82	0.01
	~PCA1f	4	-120.68	249.56	9.74	<0.001
	~OM	4	-121.25	250.70	10.88	<0.001
	~SB	4	-122.16	254.61	14.80	<0.001
	~Cover	4	-123.41	255.02	15.20	<0.001
Response variable	**Predictor**	**df**	**logLik**	**AICc**	**ΔAICc**	**AICw**
Richness	~ Sand_t	4	-347.18	702.57	0	0.51
	~ Clay	4	-348.41	705.02	2.46	0.15
Poisson glmer	~ Sand_c	4	-348.58	705.47	2.90	0.12
	~ Silt	4	-348.91	706.01	3.45	0.09
	~pH	4	-349.45	707.10	4.54	0.05
	~PCA1f	4	-349.63	707.46	4.89	0.04
	~PCA1t	4	-350.77	709.75	7.18	0.01
	~OM	4	-350.79	709.78	7.22	0.01
	~SB	4	-352.80	713.79	11.23	0.01
	~Cover	4	-352.92	714.60	12.03	0.01

Abbreviations: The Akaike information criterion corrected for small samples (AICc), difference between one estimated AICc and the lowest AICc the best model (ΔAICc), and model weights (AICcwt).

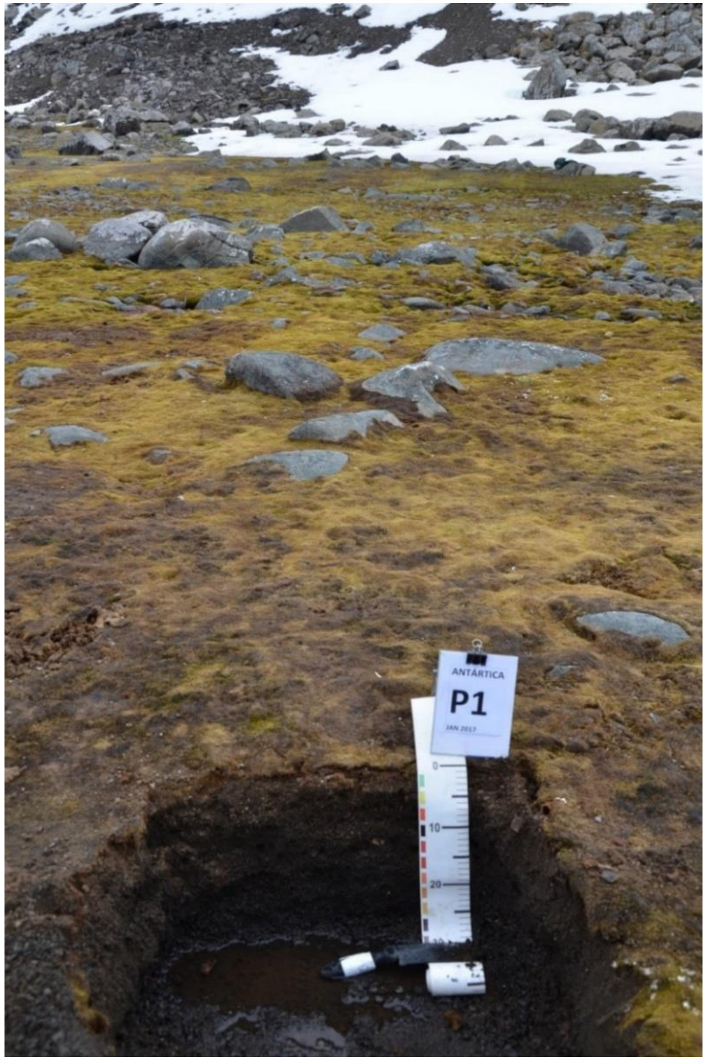


Fig. A.1. P1: Akroskeletic Protosalic Subaquatic Turbic Cryosols (Oligeoeutric. Arenic. Protosodic); Moss carpet community - *Sanionia georgicouncinata-Warnstorfia fontinaliopsis* association.

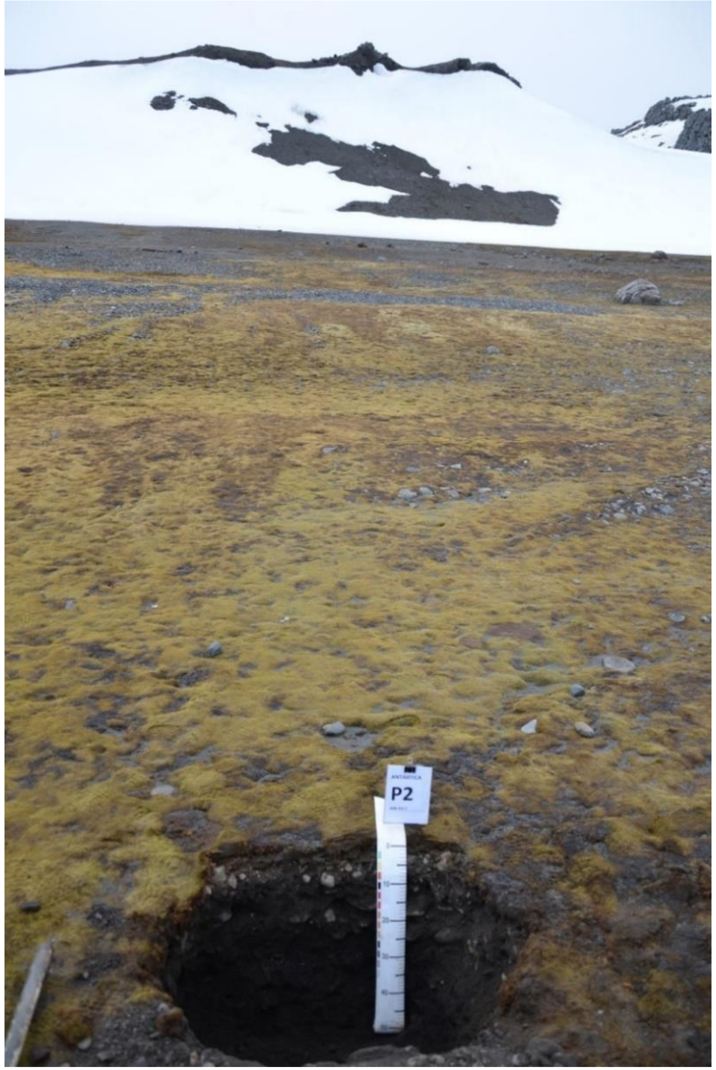


Fig. A.2. P2: Akroskeletic Protosalic Subaquatic Cryosols (Orthoeutric. Arenic. Akrofluvic. Protosodic); Moss carpet *Sanionia uncinata.*

Fig. A.3. P3: Hyperskeletic Protosalic Protic Reductaquic Turbic Cryosols (Hypereutric. Clayic. Protosodic); Moss carpet *Warnstorfia sarmentosa*- *Sanionia* spp.

Fig. A.4. P4: Hyperskeletic Protosalic Leptic Tidalic Cryosols (Hypereutric. Arenic. Protosodic); Moss carpet *Sanionia* spp.

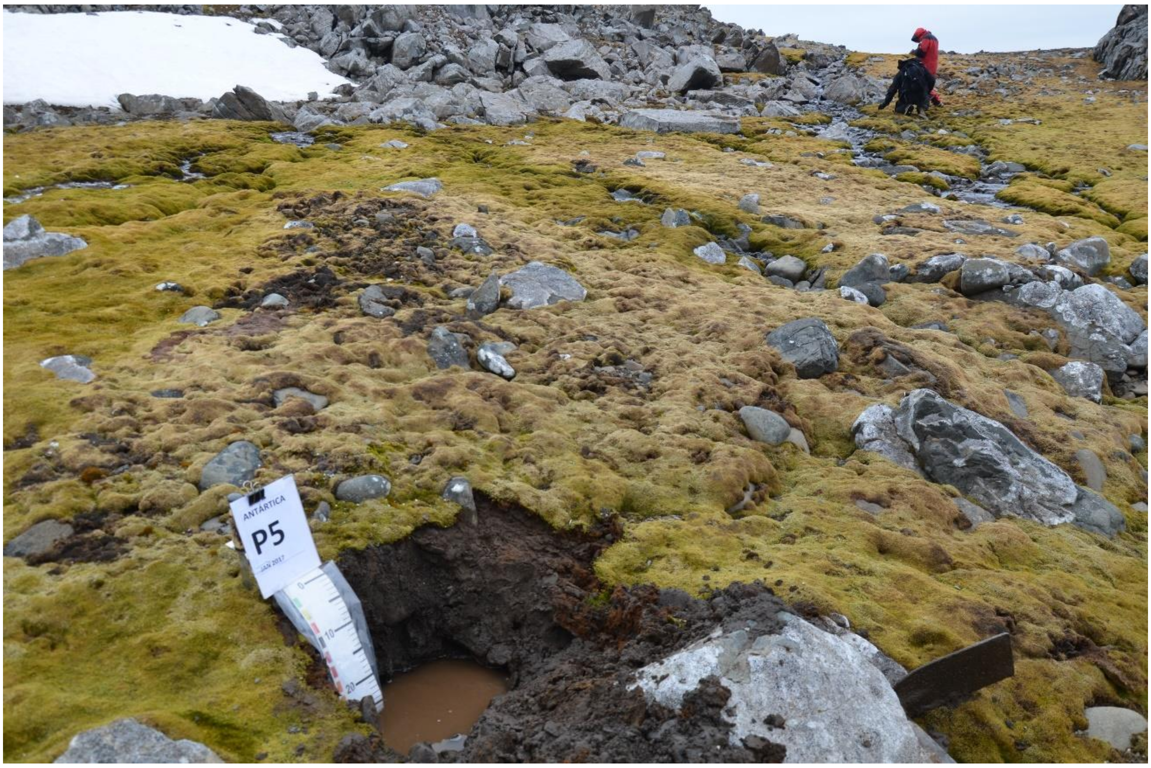


Fig. A.5. P5: Akroskeletic Subaquatic Turbic Cryosols (Hypereutric. Loamic. Sodic); Moss carpet *Sanionia* spp.

Fig. A.6. P6: Protic Relictiturbic Cryosols (Hypereutric. Loamic. Ornithic); Moss carpet *Sanionia georgicouncinata-Hennediela* association.

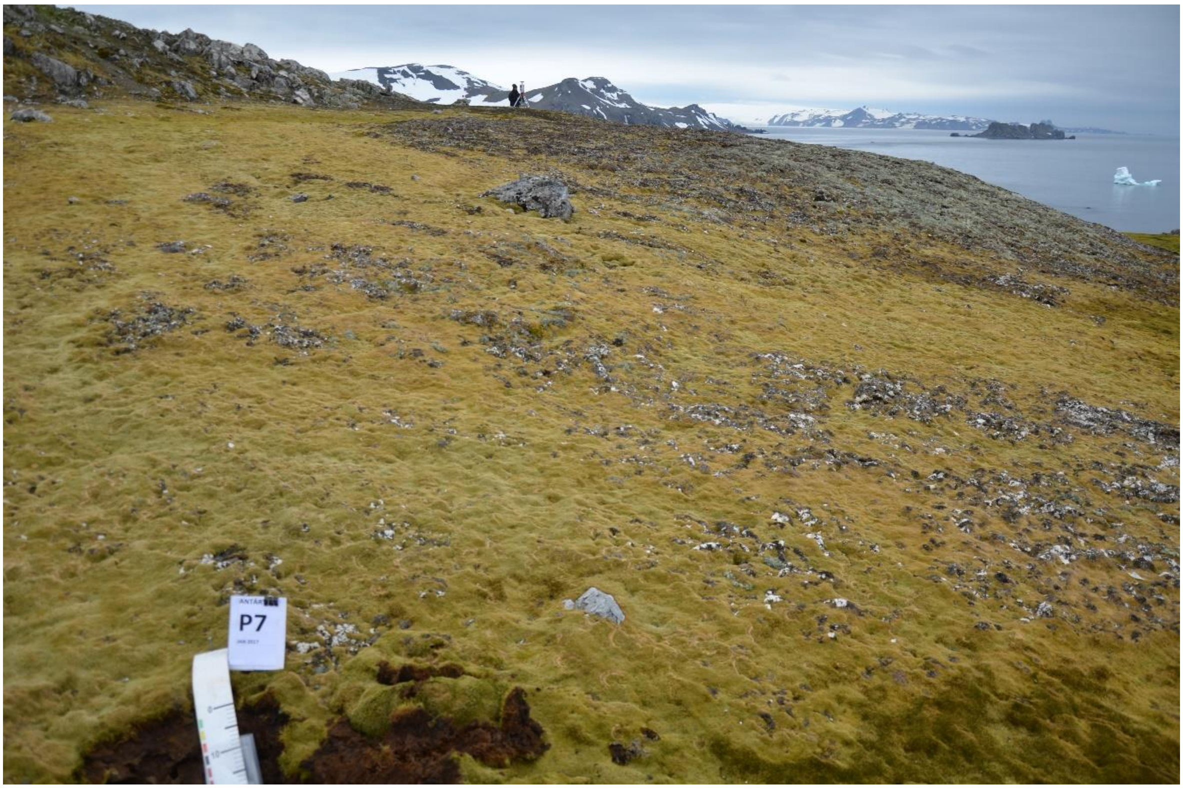


Fig. A.7. P7: Orthoskeletic Subaquatic Turbic Cryosols (Orthodystric. Loamic. Hyperhumic); Moss carpet *Warnstorfia-Sanionia georgicouncinata* association.

Fig. A.8. P8: Akroskeletic Subaquatic Turbic Cryosols (Orthoeutric. Loamic. Protosodic); Moss carpet *Sanionia uncinata.*

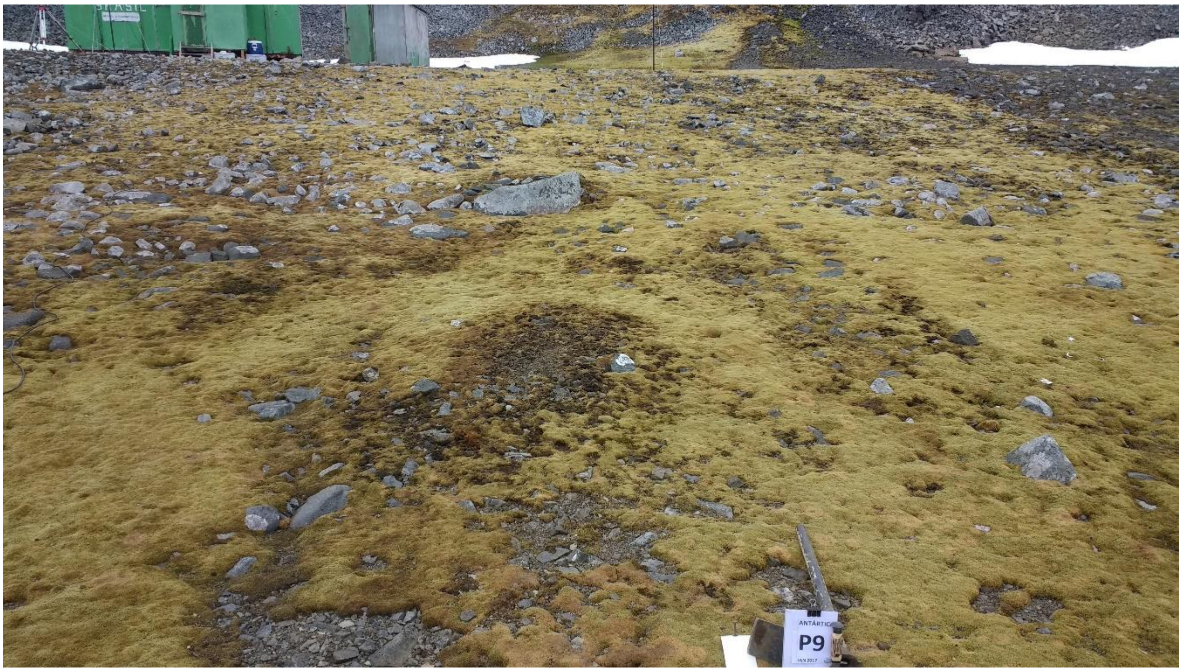


Fig. A.9. P9: Akroskeletic Turbic Cryosols (Hypereutric. Arenic); Moss carpet *Sanionia georgicouncinata-Syntrichia-Hennediela* association.

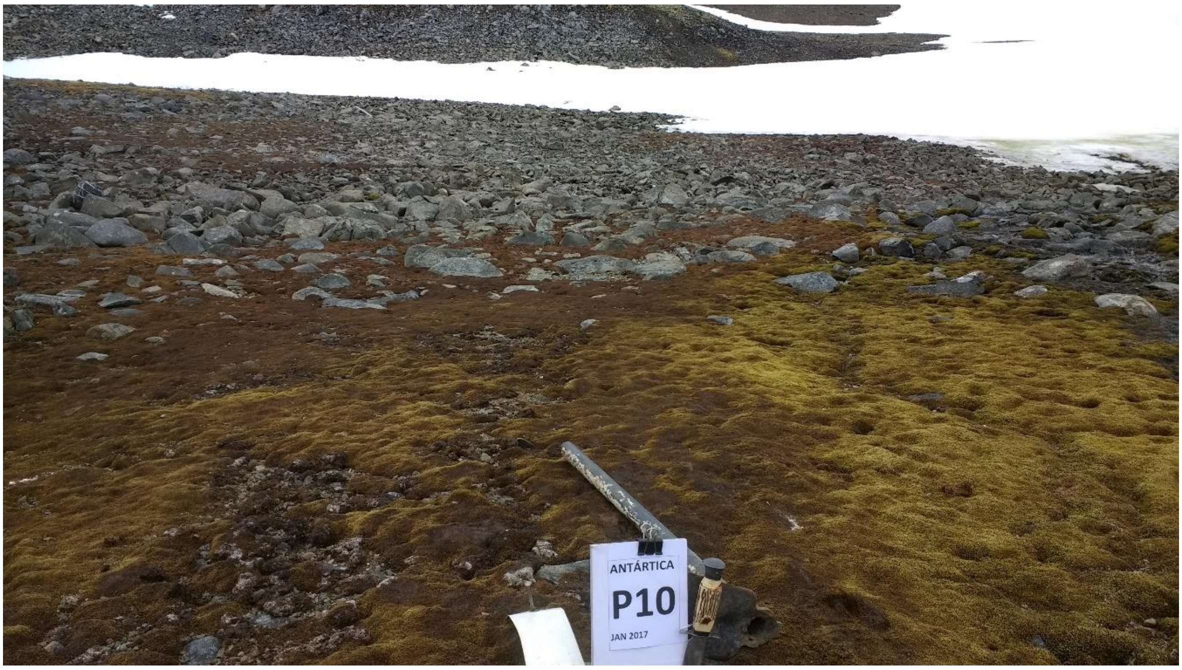


Fig. A.10. P10: Akroskeletic Turbic Cryosols (Orthoeutric. Loamic); Moss carpet *Sanionia georgicouncinata.*

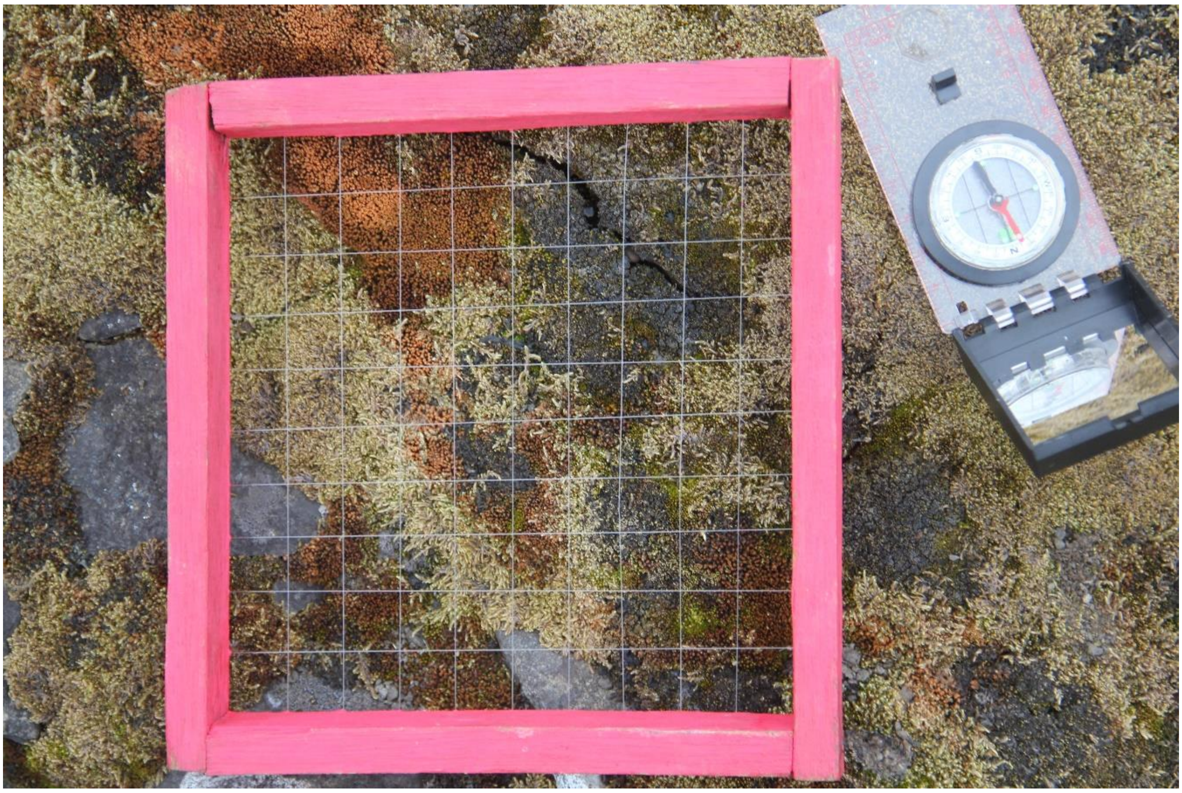


Fig. A.11. Phytosociology through the Braun-blanquet square methodology adapted to the Antarctic conditions (20x20cm).

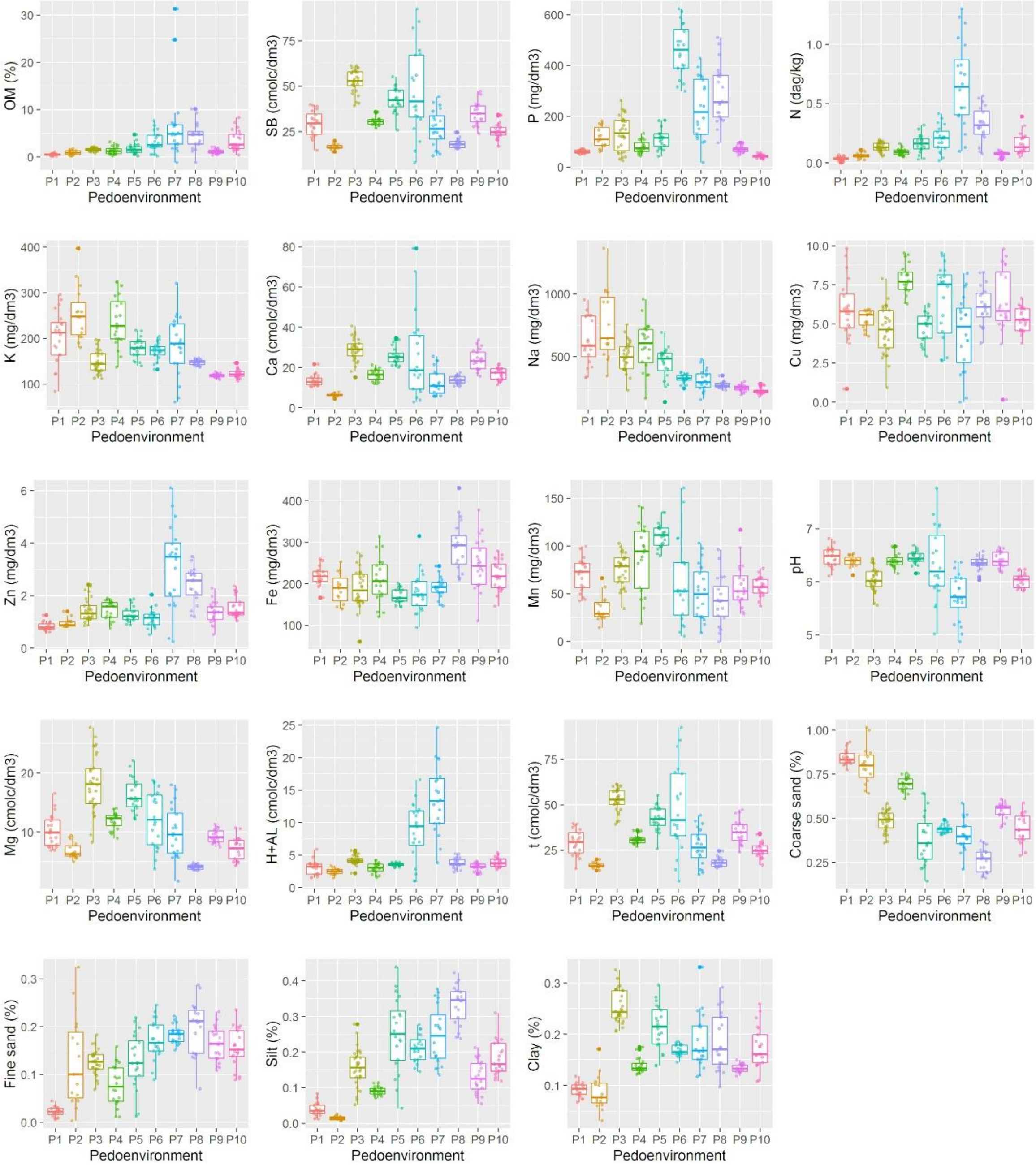


Fig. A.12. Box plots soil properties. For analysis, available: total N, available P, K, Ca, Na, Mg, Fe, Cu, Mn, Zn, exchangeable acidity (H + Al), pH (H_2O), organic matter (OM), sum of exchangeable bases (SB); effective cation exchange capacity (t), and the soil texture as coarse sand, fine sand, clay and silt contents were included.

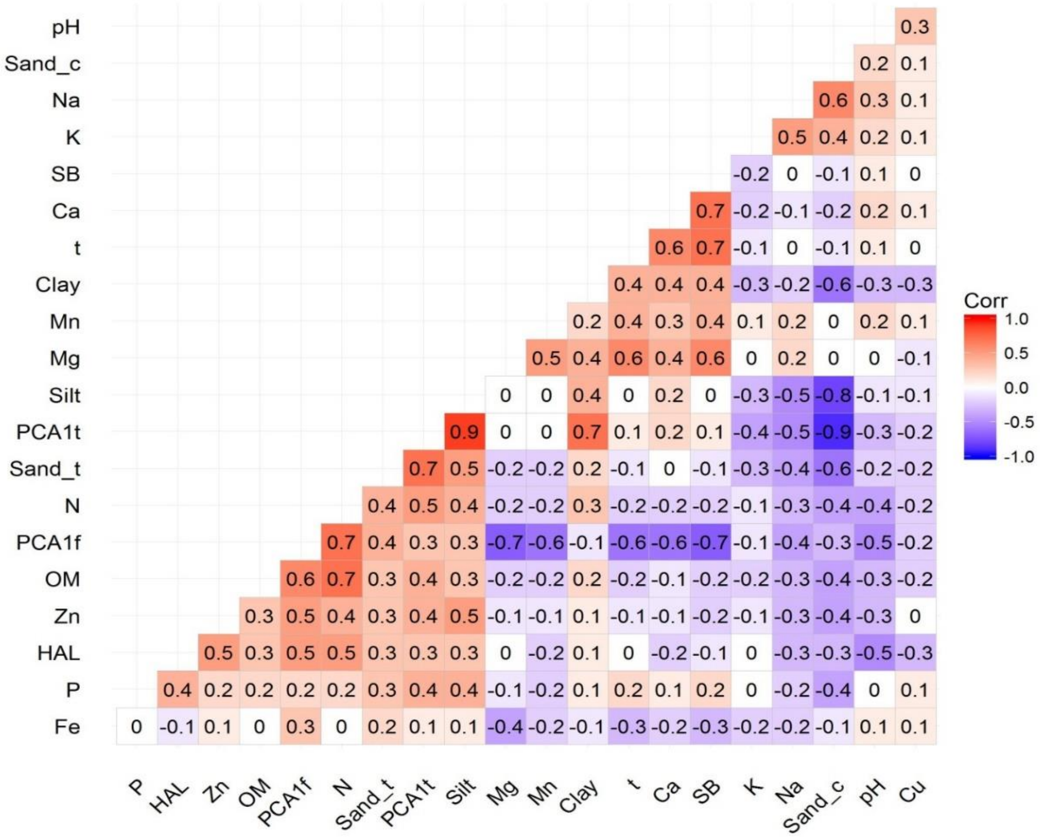


Fig. A.13. Pearson correlation among all individual variables measured in 206 plots along a pedoenvironmental gradient. For analysis: total N, available P, K, Ca, Na, Mg, Fe, Cu, Mn, Zn, exchangeable acidity (H + Al), pH (H_2O), organic matter (OM), sum of exchangeable bases (SB); effective cation exchange capacity (t), and the soil texture as coarse sand (Sand_c), fine sand (Sand_t), clay and silt contents were included.

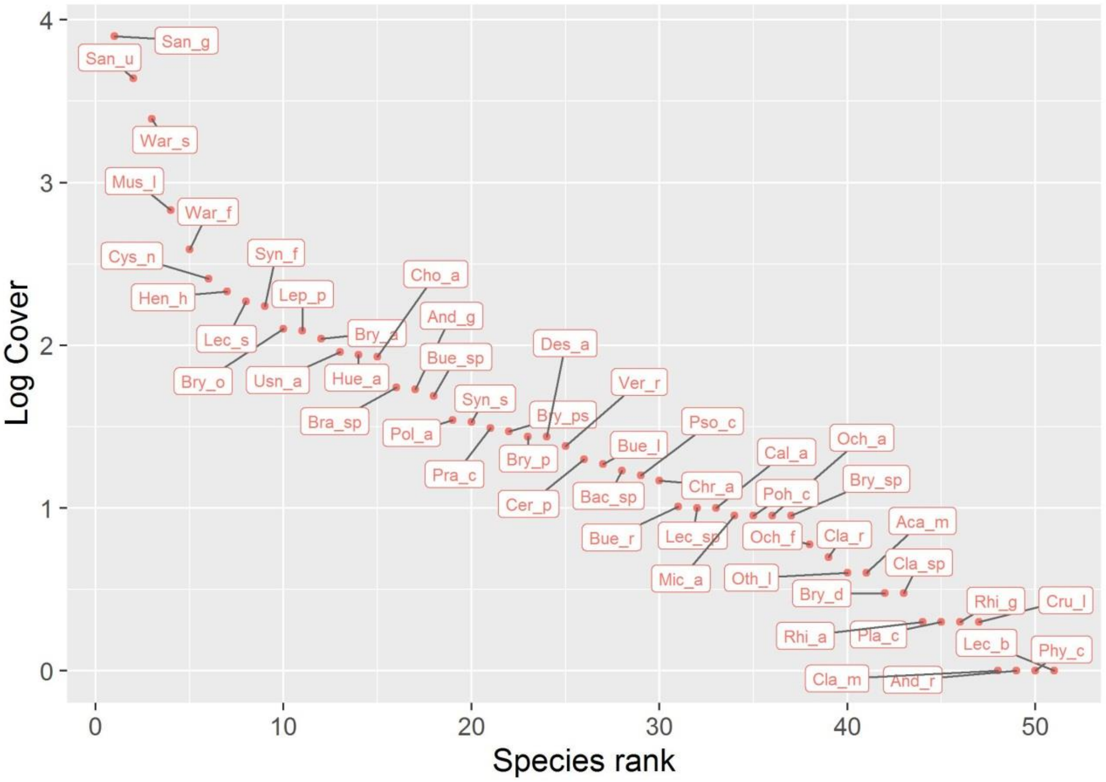
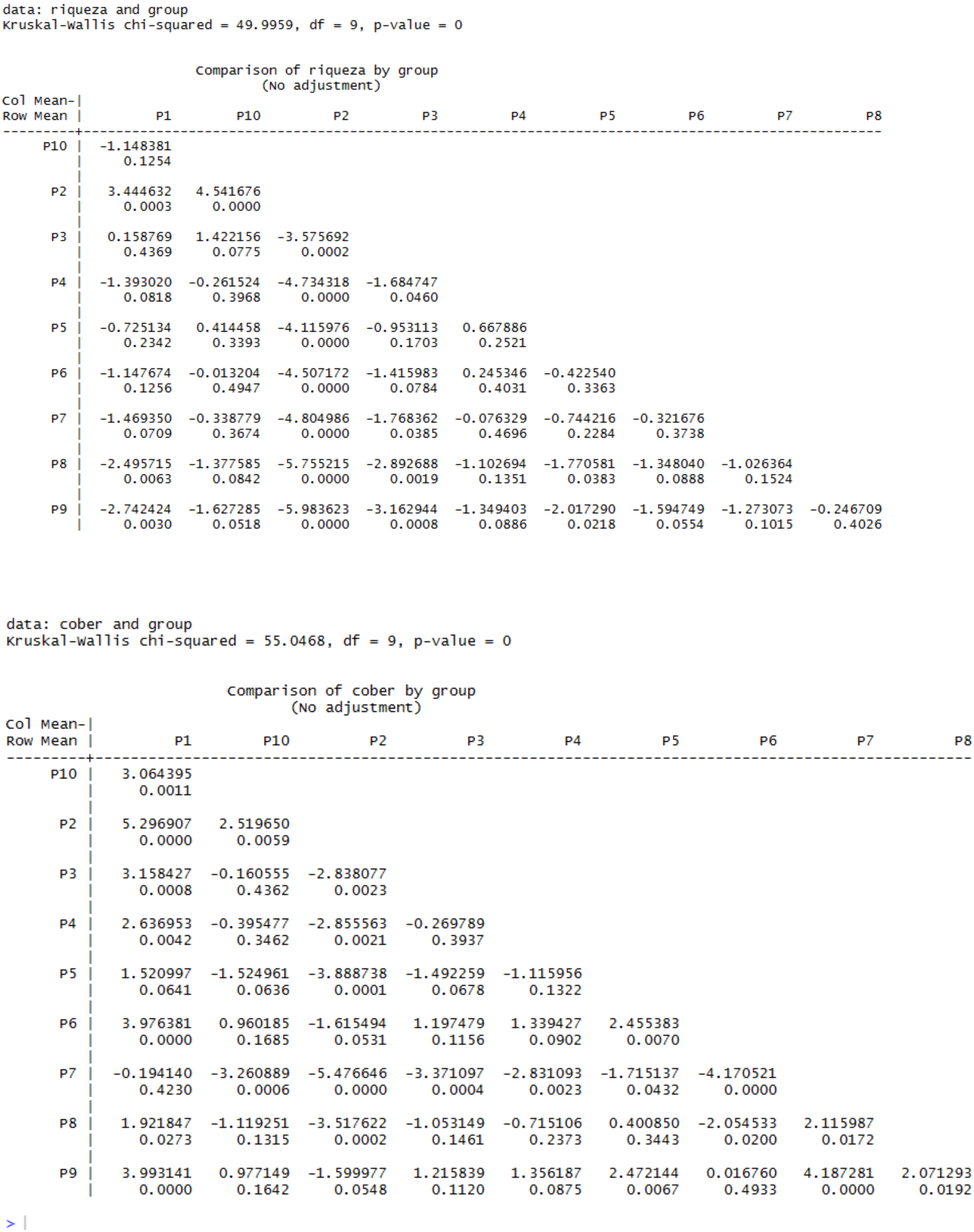


Fig. A.14. Specie coverage distribution at local scale. See full names of the species in Table A3 from ESM.



```
data: riqueza and group
Kruskal-Wallis chi-squared = 49.9959, df = 9, p-value = 0


                           Comparison of riqueza by group
                                  (No adjustment)
Col Mean-|
Row Mean |         P1        P10         P2         P3         P4         P5         P6         P7         P8
---------+---------------------------------------------------------------------------------------------------
     P10 |  -1.148381
         |     0.1254
         |
      P2 |   3.444632   4.541676
         |     0.0003     0.0000
         |
      P3 |   0.158769   1.422156  -3.575692
         |     0.4369     0.0775     0.0002
         |
      P4 |  -1.393020  -0.261524  -4.734318  -1.684747
         |     0.0818     0.3968     0.0000     0.0460
         |
      P5 |  -0.725134   0.414458  -4.115976  -0.953113   0.667886
         |     0.2342     0.3393     0.0000     0.1703     0.2521
         |
      P6 |  -1.147674  -0.013204  -4.507172  -1.415983   0.245346  -0.422540
         |     0.1256     0.4947     0.0000     0.0784     0.4031     0.3363
         |
      P7 |  -1.469350  -0.338779  -4.804986  -1.768362  -0.076329  -0.744216  -0.321676
         |     0.0709     0.3674     0.0000     0.0385     0.4696     0.2284     0.3738
         |
      P8 |  -2.495715  -1.377585  -5.755215  -2.892688  -1.102694  -1.770581  -1.348040  -1.026364
         |     0.0063     0.0842     0.0000     0.0019     0.1351     0.0383     0.0888     0.1524
         |
      P9 |  -2.742424  -1.627285  -5.983623  -3.162944  -1.349403  -2.017290  -1.594749  -1.273073  -0.246709
         |     0.0030     0.0518     0.0000     0.0008     0.0886     0.0218     0.0554     0.1015     0.4026
```

```
data: cober and group
Kruskal-Wallis chi-squared = 55.0468, df = 9, p-value = 0


                            Comparison of cober by group
                                  (No adjustment)
Col Mean-|
Row Mean |         P1        P10         P2         P3         P4         P5         P6         P7         P8
---------+---------------------------------------------------------------------------------------------------
     P10 |   3.064395
         |     0.0011
         |
      P2 |   5.296907   2.519650
         |     0.0000     0.0059
         |
      P3 |   3.158427  -0.160555  -2.838077
         |     0.0008     0.4362     0.0023
         |
      P4 |   2.636953  -0.395477  -2.855563  -0.269789
         |     0.0042     0.3462     0.0021     0.3937
         |
      P5 |   1.520997  -1.524961  -3.888738  -1.492259  -1.115956
         |     0.0641     0.0636     0.0001     0.0678     0.1322
         |
      P6 |   3.976381   0.960185  -1.615494   1.197479   1.339427   2.455383
         |     0.0000     0.1685     0.0531     0.1156     0.0902     0.0070
         |
      P7 |  -0.194140  -3.260889  -5.476646  -3.371097  -2.831093  -1.715137  -4.170521
         |     0.4230     0.0006     0.0000     0.0004     0.0023     0.0432     0.0000
         |
      P8 |   1.921847  -1.119251  -3.517622  -1.053149  -0.715106   0.400850  -2.054533   2.115987
         |     0.0273     0.1315     0.0002     0.1461     0.2373     0.3443     0.0200     0.0172
         |
      P9 |   3.993141   0.977149  -1.599977   1.215839   1.356187   2.472144   0.016760   4.187281   2.071293
         |     0.0000     0.1642     0.0548     0.1120     0.0875     0.0067     0.4933     0.0000     0.0192

>
```

Fig. A.15. Results of Dunn's test ($P < 0.05$) for species richness and coverage among the sampled pedoenvironments (P1-P10).

CAPÍTULO II:

Plant community diversity and coverage pattern along a pedoenvironmental gradient in Maritime Antarctica

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Abstract

SCHMITZ, Daniela, D.Sc., Universidade Federal de Viçosa, July, 2019. **Plant community diversity and coverage pattern along a pedoenvironmental gradient in Maritime Antarctica**. Adviser: Carlos Ernesto G.R. Schaefer. Co-adviser: Jair Putzke.

Maritime Antarctica is one of the major terrestrial ecosystems dominated by non-vascular plants (lichens and mosses), which represent important ecological indicators of climate change. Thus, we aimed to evaluate the changes in plant community diversity and plant coverage along a pedoenviromental gradient in Half Moon Island, Maritime Antarctica. We focused on how patterns in non-vascular species diversity (richness, species composition and beta diversity) and plant coverage are associated to soil properties using plant inventory data from 174 plots across fourteen contrasting pedoenvironments. This study reveals differences in environmental conditions (elevation, depth and chemical soil properties) between the fourteen contrasting pedoenvironments of Half Moon Island, a small island at Maritime Antarctica. The results clearly show marked differences in soil properties along the pedoenvironmental gradient, and this pedoenvironmental conditions determine differences in plant community diversity and plant coverage. Community composition of non-vascular species decreases in similarity with increasing of soil properties differences along the pedoenvironment gradient. Likewise, differences in soil properties along the pedoenvironment gradient promote high β-diversity. These variations are common in Maritime Antarctica, due to varying periglacial processes, weathering degree, parent material, and biological influence (especially by penguins and other birds). The species richness and plant coverage along the pedoenvironmental gradient were different; however, they shared common species that were present in the majority of the pedoenvironments, despite differences in plant coverage. We presumed that the most of the pedoenvironments recorded rare species that occurred only under specific soil conditions, which also contributes to the high species turnover between pedoenvironments and low floristic similarity, which promoted high β-diversity.

Key-words: beta diversity, community composition, non-vascular communities, plant community diversity, plant-soil relationships, soil filters

1. Introduction

Understanding how soil gradients shape plant community diversity and structure is one important question in ecology (Pekin et al., 2012; van der Ent and Lambers, 2016).

Plant -soil relationships have been an important approach in ecology studies to address diversity patterns at both large and fine spatial scales in different ecosystems worldwide (e.g., Carmo and Jacobi, 2016; Conti et al., 2017; Ali et al., 2019). Soil gradients may determine plant community assembly by selecting species from a regional species pool into a local habitat (e.g., Martins et al., 2015; Carmo and Jacobi, 2016). These patterns in plant community assembly have addressed changes in species diversity (i.e., species richness, community composition), and structure (e.g., abundance, plant coverage) along soil properties gradients (i.e., by soil fertility, texture, and depth filtering) based on multivariate analysis (e.g., Martins et al., 2015; Carmo and Jacobi, 2016; Wang et al., 2016; Villa et al., 2018). Thus, patterns of diversity are highly scale-dependent, and particularly high levels of diversity often match habitat patchiness and species turnover (e.g., beta diversity) along environmental gradients (e.g., van der Ent and Lambers, 2016; Hernández-Hernández et al., 2017; Villa et al., 2018).

The beta diversity (β-diversity) is a measure of the temporal and spatial variation in species composition (Tuomisto, 2010; Anderson et al., 2011). Taxonomic β-diversity corresponds to the percentage of dissimilarity in species composition between two distinct communities (Koleff et al., 2003). For instance, a high level of 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 emphasized vascular plant communities in different ecosystems of the world (e.g., Kraft et al., 2011; Ibanez et al., 2017). However, the relative importance of the spatial dissimilarities in non-vascular species composition (β-diversity) as ecological indicators along soil gradients, remains poorly understood as a fundamental basis for the monitoring of climatic changes and ensuing ecological adjustments and responses. In this context, changes in non-vascular plant communities along soil gradients can be important in face of ongoing climate change which may affect their response to increasing global temperatures (e.g., Robinson et al., 2018).

Antarctica has the main terrestrial ecosystems dominated by lichens and mosses (Poelking et al., 2015, Rodriguez et al., 2018), and is considered a key bioregion for the monitoring of global climate changes (Vieira et al., 2010; Michel et al., 2014). Antarctic vegetation is restricted to ice free areas, such as coastal zone, rocky slopes or in nunataks (Sharon et al., 2003; Bokhorst et al., 2007). Likewise, there are different types of Antarctic plant communities and associations that are modeled according to landforms and soil properties (Francelino et al., 2011; Poelking et al., 2015). However, differences in soil properties along the pedoenvironment gradient in relation to mosses and lichens diversity and community structure remain poorly understood in Antarctica (Leishman and Wild, 2001).

In this study, we aimed to evaluate the changes in plant community diversity and plant coverage along a pedoenviromental gradient in Half Moon Island, Maritime Antarctica. We focused on how patterns in non-vascular species diversity and plant coverage are associated to soil properties using plant inventory data from 174 plots across fourteen contrasting pedoenvironments. In order to evaluate the plant species diversity and plant coverage, we asked the following three research questions: 1) are soil properties different among the fourteen contrasting pedoenvironments? 2) How does species richness and plant coverage change along pedoenvironmental gradient? 3) Does the community composition and β-diversity change between pedoenvironments? Based on the premise that non-vascular communities have distributions shaped by soil filters (e.g. soil chemistry, depth) we sought to determine the following hypothesis: 1) Pedoenvironmental conditions of soil properties determine differences in plant community diversity and plant coverage; 2) Community composition of non-vascular species decreases in similarity with increasing of soil properties differences along the pedoenvironment gradient. These differences in community composition are driven by soil properties variables that are directly related to pedoenvironment gradient. 3) Differences in soil properties along the pedoenvironment gradient promote high β-diversity of species.

2. Materials and methods

Study area

This study was performed in Half Moon island (62°35'42.94"S 59°55'8.41"W), one of the smallest of the South Shetland Archipelago, Maritime Antarctica (Fig. 1). The total surface area is 171 hectares (Araya and Hervé, 1966), of which and 19.17% is covered by vegetation (Schmitz et al., 2018). There are three main hills on the island, among which Gabriel Hill (101 m.a.s.l) is the highest point (Schmitz et al., 2018). Penguin rockeries 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.

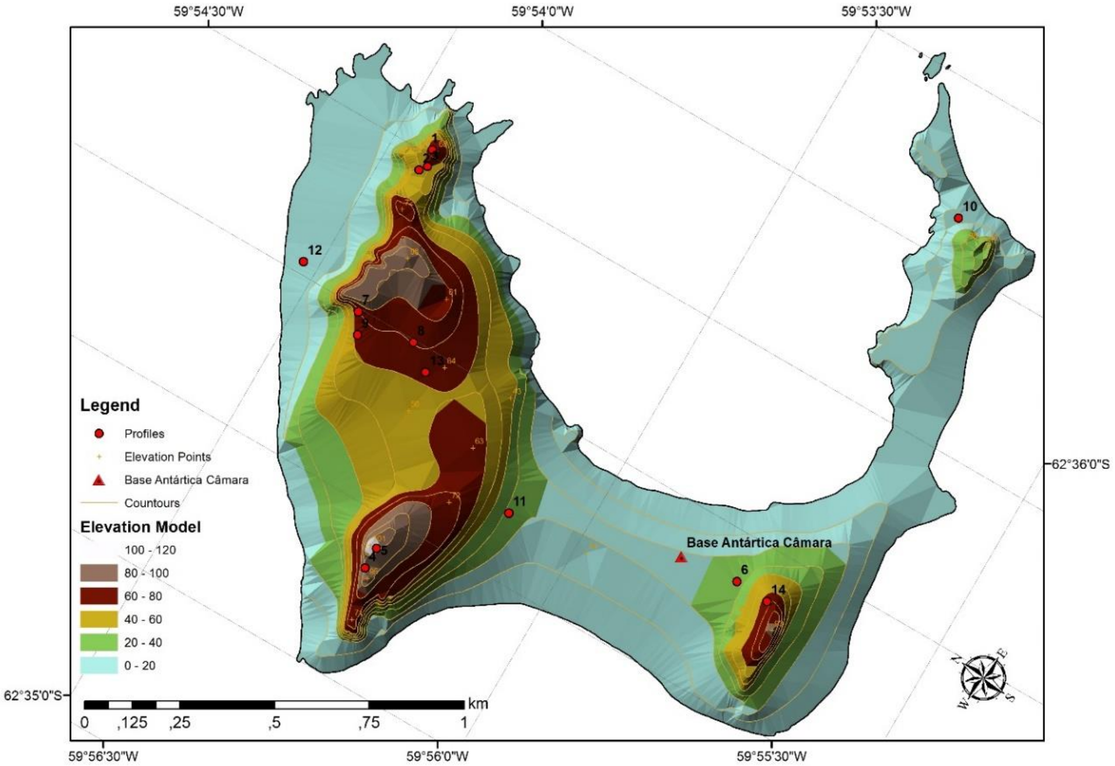

Fig. 1. Half Moon Island with the 14 pedoenvironments.

Selection of study pedoenvironments

We selected 14 pedoenvironments with contrasting soil, vegetation and landform characteristics (Table 1). We observed that soil chemical properties differed between the 14 environments, thus forming a pedoenvironmental gradient (Fig. 1, Table A.1). Since there are marked differences between environments that can be considered under the habitat filtering approach (Scherrer et al., 2018), the pedoenvironmental filters definition is appropriate for our present approach. Thus, the possibility of separating boundary between pedoenvironments provides an opportunity to study the effects of habitat filtering on species assemblages at a local scale in Maritime Antarctica (Poelking et al., 2015).

Table 1. 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)

Soil properties collection

In each a soil profile was dug and sampled according to Bockheim et al. (2006) recommendations, allowing its classification according to the World Reference Base for Soil Resources (IUSS Working Group WRB, 2015). In order 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 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). Dueto sample size limitation, physical analyzes could not be performed for all environments, so they were not included in the statistical analyzes.

Vegetation sampling

The pedoenvironments have different plant coverage areas so that the number of plots was enough to cover all the vegetation. The number of plots ranged from 5 to 21 plots of 20 x 20 cm (Table 1). A total of 174 plots across the 14 studied pedoenvironments were sampled, using the Braun-Blanquet (1932) square method, adapted to Antarctic vegetation conditions for measuring the coverage of species in each plot. Within each plot, the majority of mosses and lichens were identified to the species level. Mosses species were identified with the taxonomy keys presented by Putzke and Pereira (2001) and Ochyra et al. (1998, 2008), and the lichens species with the keys presented by Redon (1985), Ovstedal and Lewis-Smith (2001) and Olech (2004).

The types of plant communities were named according to Schmitz et al. (2018) and the landforms classification according to López-Martínez et al. (2012). Other characteristics such as elevation, depth and soil drainage levels, and face of exposure were measured in the field (Tab. 1).

Data analyses

All analyses were carried out in 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 homogeneity of variances by Bartlett´s test using the "*dplyr*" package (Crawley, 2013). In order to compare soil properties (non-normally distributed data), species richness and coverage between pedoenvironments sites, we used Kruskal-Wallis's test followed by a posterior Dunn's test performed with the 'dunn.test' package (Dinno, 2017).

Species richness in the fourteen contrasting pedoenvironments sampled 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 plots 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).

Soil variables were summarized by a principal components analysis (PCA) on the correlation matrix, using the 'FactoMineR' package (Husson et al., 2017). For that, all variables were centered and standardized.

We performed the Non-metric multidimensional scaling (NMDS) to analyze differences between pedoenvironments in terms of species composition by using

Euclidean distance. We carry through the NMDS using 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 used the Two Way Cluster Analyses using Sorensen measures dissimilarity, based on presence/absence data (Khan et al., 2016) to identify pattern dissimilarity in the species between pedoenvironments.

We used the analysis of multivariate homogeneity of group dispersions to assess β-diversity in each pedoenvironment (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 permutation test of homogeneity of multivariate dispersion (PERMDISP), which avoids problems of lack of independence among pairwise site comparisons (Anderson et al., 2006). After, we 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, 2001). 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).

3. Results

Soil classification

Soils at Half Moon Island are shallow skeletal (gravelly, cobbly and dominated by coarse grain) and poorly developed. Landforms changed according to the altitude, in which the most common landform between 0 and 20 m a.s.l. are raised beaches, cliffs, till, glacial deposits and debris slopes and cones; between 20 and 80 m a.s.l nivation niches, patterned ground, stone stripes, gelifluction sheets and lobes are dominant; at higher altitudes debris lobes and debris talus prevail, associated with resistant by andesite intrusions (saddleback Ridge, Serrano and López-Martínez, 1997). Soils structure ranged from moderate to weak, subangular to granular structure or single grain. Granular structures occur on Gabbro and Tonalite intrusions, while subangular structure and single grain are related to Andesite and Andesitic Lavas and Lapillistones, the first closely related to greater organic matter content and cryoturbation processes. The 14 pedons were classified as Cryosols and Leptosols due to presence of permafrost, continuous lithic contact within 25depth, or less than 20% fine earth (by volume). Soils are mostly arenic, cryoturbated; organic matter and buried ornithogenic horizons are common.

The results allowed classifying the Cryosols as Turbic, Leptic, Skeletic, most frequently, Reductaquic Umbric or Mollic (P1 through P9 and P11); Summer temperatures close to 0 °C were identified together with cryoturbation during sampling, and the landscape position and periglacial features suggest the presence of permafrost (IUSS Working Group WRB, 2015). These Cryosols are located at the top of the tombolo which links the two rock promontories and at the elevated parts of the landscape, La Morenita hill, Gabriel Hill, Xenia Hill and Baliza Point. They occur at sites dominated by periglacial and nival landforms and deposits. Leptosols (gelic) were all Skeletic, with arenic and ornithic characters frequent; they mainly occur at the present day and Holocene beaches at the coastal zone, always below 20 m a.s.l.; major landforms include tills, stone stripes and rock glaciers. Soils developed from Andesite intrusions and Andesitic lavas and lapillistones and Tonalite tend to be coarser while those developed from gabbro intrusions presented, which greater silt content.

Soil chemistry pattern

Soil chemical properties are highly variable at the 14 pedoenvironments (Figure 02). Many areas showed strong ornithogenic influence (including pedons located at higher altitude), presenting high acidity and very high available P values (242 to 2021 mg/dm^3), with exception of the pedoenvironments 11 (P= 61.08 mg/dm^3) and 12 (P=94.07 mg/dm^3), with very little ornithogenic influence. The P9 presented highest values for several attributes such as P, Ca, Mg, SB and t, and lowest for Zn (0.73mg/dm^3). P10 is an environment close to active penguin rookery and showed the lowest values of K, Ca, Mg, SB and t, probably due to intense leaching by acidification contrasting with the highest value of Zn (7.97 mg/dm^3). P6 is the most acid soil, with the lowest pH value (4.84) and the highest H + Al value (17.5). Organic matter content is high, mainly the range of P1-P6, with values greater than 7 (dag/kg) reaching 21.1 (dag/kg). Low values were recorded in P11 (0.51 dag/kg) and P12 (0.72 dag/kg) only BS and CEC are generally low, in comparison to other soils of the maritime Antarctica Simas et al., 2008), with values ranging from 1.83 to 12.05 ($cmol/dm^3$) and 2.17 to 11.08 ($cmol/dm^3$) respectively.

Fig. 2. Barplots soil properties. For analysis, 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), were included.

Species richness and plant coverage pattern

Were identified 21 bryophyte species (20 mosses and one liverwort), 42 lichen species and one macroscopic algae (*Prasiola crispa*) in the 14 pedoenvironments of Half Moon Island (Table A.2). We used the rarefaction curve to test the sample adequacy in the pedoenvironments and observe patterns of species richness (Fig. 3A). The number of plots made reached the asymptote in most of the pedoenvironments, i. e. the extrapolation did not differ significantly from the interpolation. Exception were P2, P5 and P6, suggesting that these environments could have shown more species with a greater sampling effort. Since plots were set along transects over the vegetation patches, in some cases sampling was limited. The pedoenvironments showed similar patterns of richness, but with different species. P12 had the lowest number of species (six); P1, P2, P3, P9, P10 and P11 had similar numbers (ranging from 10 to 20 species) (Table 1). The highest number was recorded for P4, P5, P6, P7, P8, P13 and P14 (22 to 30 species). The plant coverage also presented significant differences (chi-squared = 79.53, df = 13, p-value = 0.001) among pedoenvironments at plot scale (Fig. 3B).

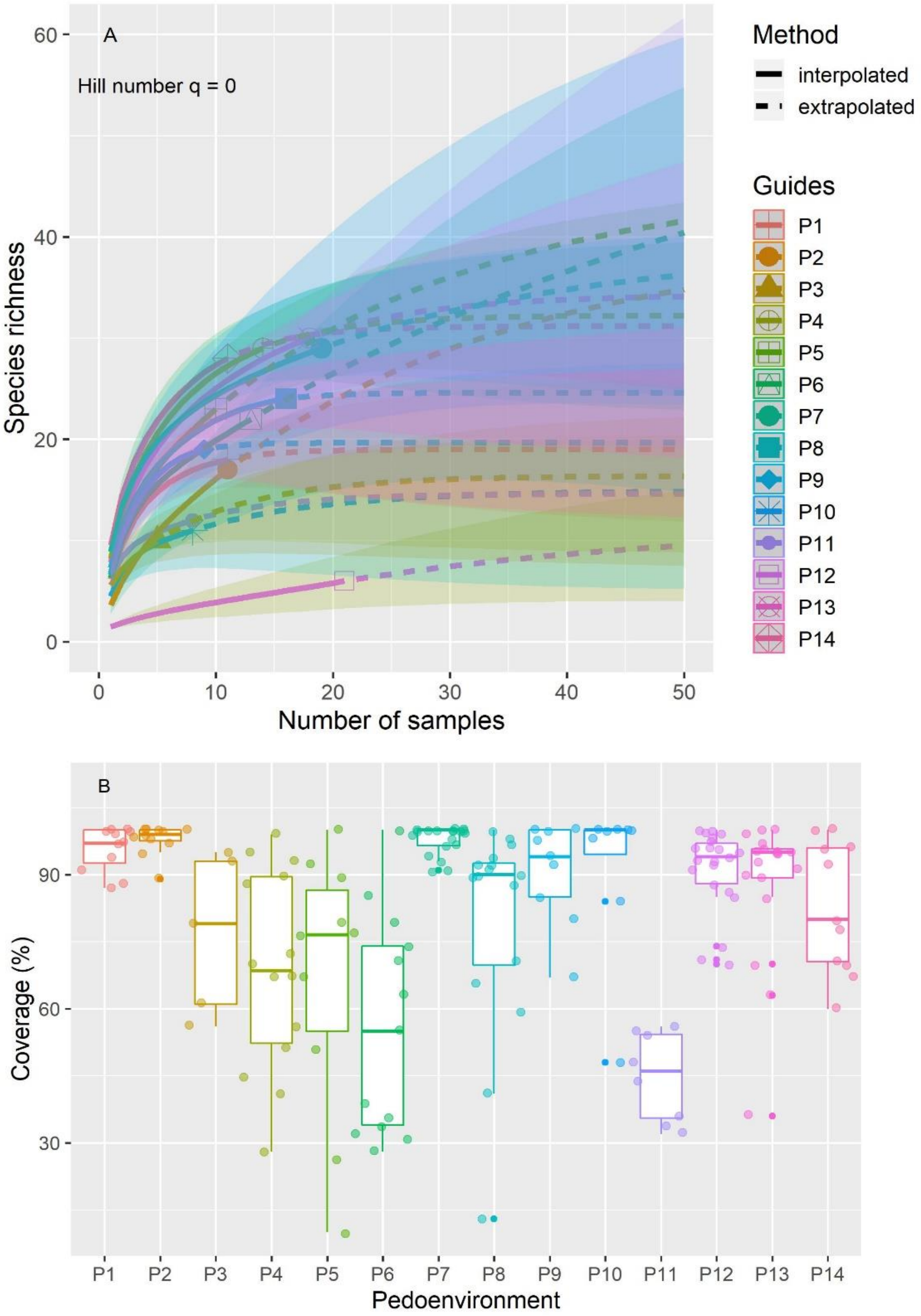

Fig. 3. Sampled-based rarefaction (solid lines) and extrapolation curves (dashed lines) of bryophyte species diversity based on the first Hill numbers (q = 0) for the sampled pedoenvironment (A), differences in species richness (B), and coverage (C) between sampled pedoenvironment. Rarefaction and extrapolation curves present the lines that represent the mean values and the bands the standard deviation with 95% confidence intervals.

Soil fertility descriptors

The first two axes of the soil fertility PCA explained 52.7 % of the data variance (Fig. 4). 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 (Fig. A.1) with pH ($R = 0.70$ $p < 0.05$), percentage of bases saturation ($R = 0.48$, $p < 0.05$), and nutrients such as Mn ($R = 0.60$, $p < 0.05$), and Mg ($R = 0.58$, $p < 0.05$), separating 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 ($R = -0.86$, $p < 0.05$). The second axis explained 18.4% of the variation and was negatively correlated with soil depth ($R = 0.88$, $p < 0.05$), elevation ($R = 0.70$, $p < 0.05$), phosphorus ($R = 0.67$, $p < 0.05$) along the pedoenvironmental gradient.

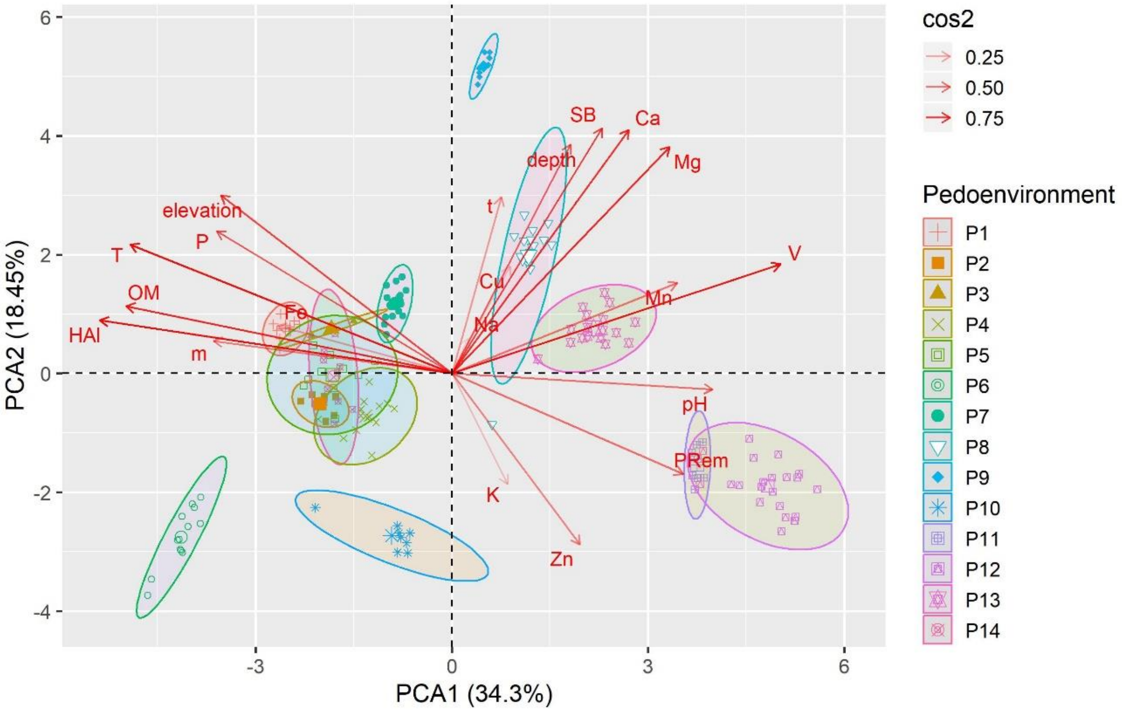

Fig. 4. Principal Component Analysis (PCA) for the soil parameters of different types of pedoenvironment sites. For analysis, available: P, K, Ca, Na, Mg, Fe, Cu, Mn, Zn, exchangeable acidity (H + Al), pH (H_2O), organic matter (OM), sum of exchangeable bases (SB); effective cation exchange capacity (t), potential cation exchange capacity (T), Al saturation (m), percentage of bases saturation (V), were included.

Species composition and beta diversity pattern

The pedoenvironments were significantly different in their species composition, forming 14 groups on the first and second axis (Fig. 5). Although some species are present in various pedoenvironments, their spatial distribution is concentrated in pedoenvironments such as P4, P6, P8, P9 and P13 (Fig.6). Others are restricted to specific environments with particular soil conditions, such as *Buellia racovitzae* and *B. russa* in P4; *Ceratodon purpureus* in P5; *Bartramia patens*, *Bryum* sp., *Bacidia* sp. in P6; *Physconia muscigena* and *Pohlia nutans* in P7; Candelaria murrayi, *Lecania brialmontii*, *Ramalina terebrata*, *Syntrichia magellanica* and *Xantoria elegans* in P10; *Bryum nivale* in P12; *Bryum dichotomum*, *Ceratodon grossiret*is and *Scapani*a sp in P13; *Sanionia* spp despite its absence in P10, was dominant in the other pedoenvironments.

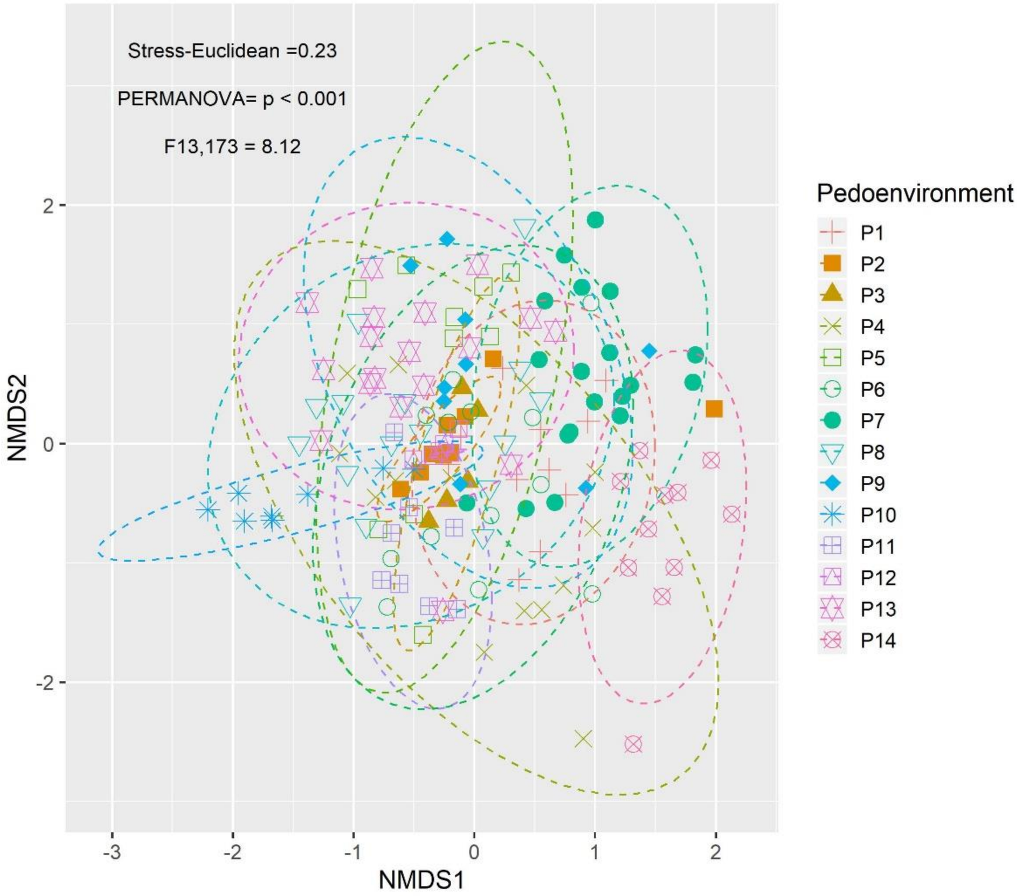

Fig. 5. Non metric multidimensional scaling (NMDS) based on species composition from different pedoenvironments.

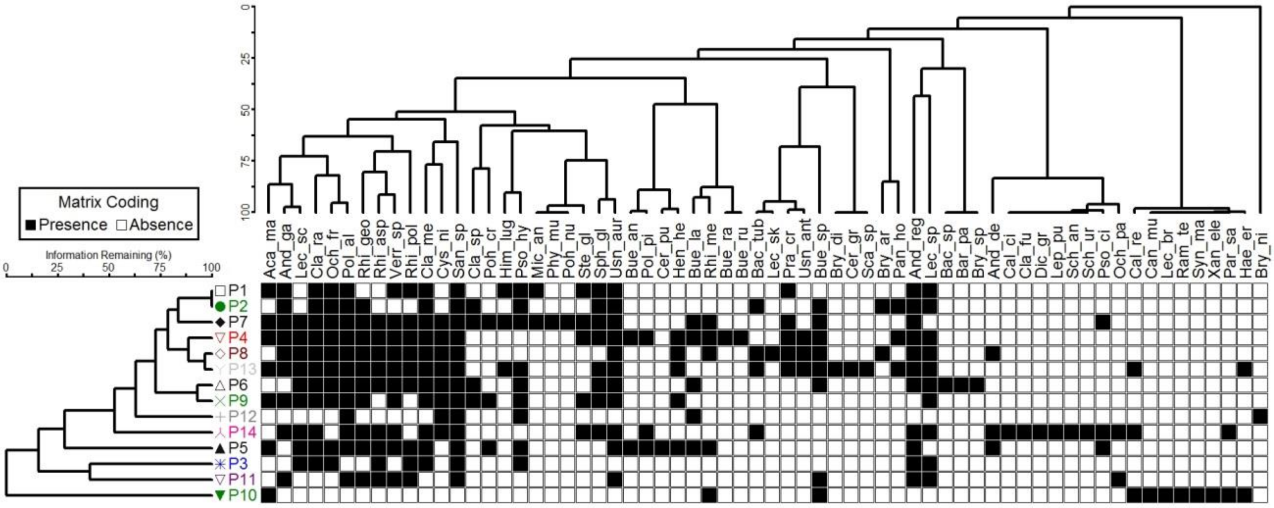

Fig. 6. Distribution of 64 species within 174 samples plots installed along a pedoenvironmental gradient by a two-way cluster dendrogram based on Euclidian distance. See full names of the species in Table A.2 from ESM.

Differences in β-diversity among pedoenvironments (PERMDISP: $F_{13,173} = 8.12$, $p < 0.001$) were noticed (Fig. 7). β-diversity, measured as the distance to group centroid, was higher in P13 and P14 pedoenvironments than in the P11 and P12 pedoenvironments.

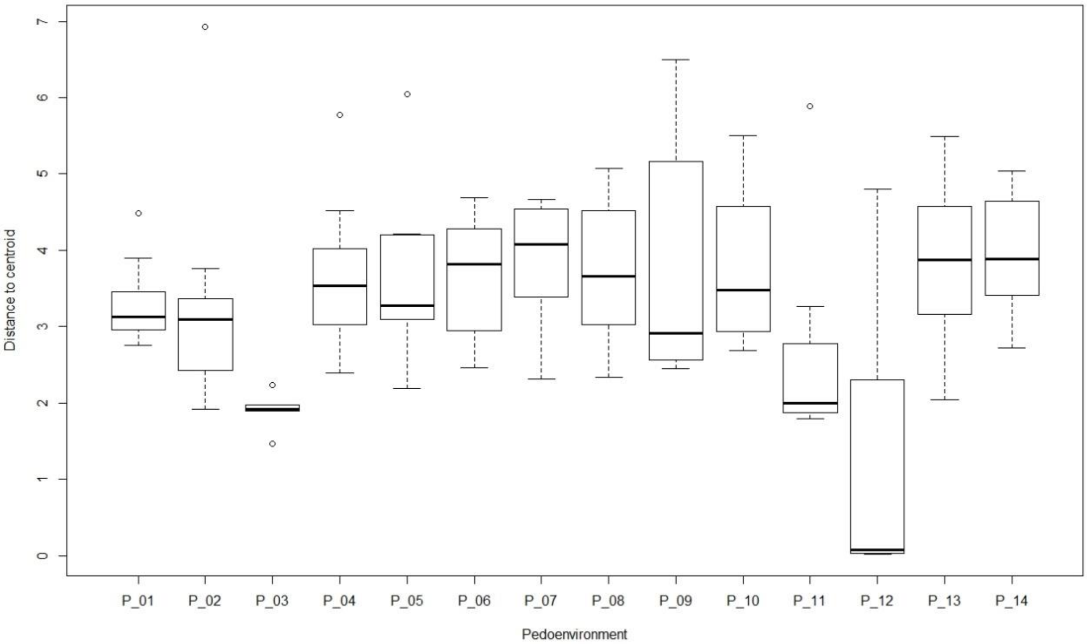

Fig. 7. Differences in β-diversity measured as distance to group centroid, along pedoenvironmental gradient. Average pairwise dissimilarity is presented. Beta diversity is significantly different among pedoenvironment.

4. Discussion

Our results clearly show 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, 2015; Schaefer et al., 2008). In Half Moon, the discontinuous permafrost affects sites located above the marine terraces, where landforms are mainly periglacial and include till. Many different landforms occur in 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 also showed marked differences in species richness and plant coverage, due to the differences in soil properties along the pedoenvironmental gradient, which corroborates our first hypothesis. Likewise, we observe that the community similarity decreases as the differences in soil properties between the pedoenvironments increases, which supports our second hypothesis. These changes in soil properties along the pedoenvironmental gradient promote a high species turnover between pedoenvironments (β-diversity) in spite of a fine spatial scale, which confirms our third hypothesis. Therefore, differences observed in the β-diversity can be related to differences in the soil properties evaluated through a direct gradient analysis.

Direct gradient analysis: plant community diversity and coverage pattern

The fourteen pedoenvironments are distributed throughout the entire length of Half Moon Island and showed a high soil variability. The different pedoenvironments studied in the work area have probably different levels of ornithogenic influence, where the formation and variability of soil chemical properties is shaped by penguins activity (Campbell and Claridge, 1987; Simas et al., 2007). Penguins incorporate organic matter in the soil through the excreta (known as guano), and depends on the long-term permanence of penguins at each specific pedoenvironment, changing nutrient cycling process in a fine scale (Zhu et al., 2014). In this way, we assume that most differences in soil properties between pedoenvironments are due to the temporal and spatial variation of penguin activity in the study area, resulting in contrasting values of available P and acidity (pH and H + Al) at the different pedoenvironments (Michel et al., 2006; Simas et al., 2007). According to Simas et al. (2007), guano is initially alkaline, but rapid progressive acidification occurs with the advance of microbial degradation of organic matter. Ornithogenic soils are well known in the Antarctic Maritime region, where phosphatization is the main soil formation process (Michel et al., 2006; Simas et al., 2007; Pereira et al., 2013; Dayer et al., 2019).

Some pedoenvironments, despite their proximity, showed differences in species composition, associated with large variation in soil properties at fine scale. For example, the adjacent P1 and P2 areas, located at the eastern of the Xenia hill in Half Moon, although covered by a similar mosses carpet in terms of species composition, showed large differences in soil chemical properties. In this example, P2 has soils with low acidity (pH 6.5), P, K and Ca values twice as much as P1, whereas P1 had the highest content of Na (1551.41 cmol/dm^3, table A2), due exposure to marine saline sprays and local aridity (Michel et al., 2006). This is corroborated by the presence of *Verrucaria* sp. which is associated with saline environments and wind exposure (Olech, 2004). Although in this study we focus mainly on the species distribution patterns and types of communities along a complex pedoenvironmental gradient system, presumably other environmental factors (e.g., sea spray, drainage, and biotic interations) may also influence plant community diversity and structure. On the other hand, P2 is located in a small depression is a poorly drained pedoenvironment, where the high water table and high organic matter content favor the growth of a thick mosses carpet. However, these two pedoenvironments along with P3, showed the highest organic matter content associated with high available P, suggesting that a former penguin colony inhabited the area (Michel et al. 2006) creating a phosphatized environment (Simas et al., 2007).

Soils P3 and P7 have a muscicolous lichens community, and both show similar soil patterns, only differing significantly in relation to OM and Mn. These soils are well-developed, with lichens growing on moribund or living mosses, confirming its advanced succession and favorable status for the coexistence of some species as suggested for similar soils from King George Island (Tatur and Mircha, 1993). However, P7 has greater species richness (29 spp), and P3 only 10, nine of them shared (Fig. 6).

The P4 (moss carpet community) and P5 (moss turf community) are located at Gabriel hill, at the more elevated sites. They follow similar soil fertility patterns, except for micronutrients (Fe and Zn), but have different plant composition. These pedoenvironments however, had different textural classes (Table A.1), where P4 is sandy-loam and P5 is sandy, i.e., P4 has higher percentages of clay, which, according to Schmitz et al. (*in press*) has a significant effect on species composition.

The high P, Ca, Mg contents combined with high effective cation exchange capacity levels and higher depth in P9, 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 abandoned penguin colony that, with glacio-isostatic uplift of the island, migrated to the lower parts of the island. There is ample evidence that deglaciation and the resulting of glacio-isostatic uplift during the Holocene (Fretwell et al., 2010), a large number of penguin rookeries moved from upland areas onto newly exposed marine terraces (Rodrigues et al., 2019), closer to the emerging coast, and into adjacent rock outcrops (Tatur et al. 1996; Michel et al. 2006). These highland areas, then, became inaccessible for penguins, while the newly emerged land become occupied by new populations (Dayer et al., 2019; Rodrigues et al., 2019) resulting in pedoenvironments with higher plant coverage, such as P9 (Fig. 3B).

This is consistent with known glacio-isostatic uplift rates, between (16 and 20 m, according Fretwell et al., 2010), and the highest beach ridge is located 16.8 m above the present day beach (P12). Present day periglacial processes in a warming scenario seem to be less intense corroborating the widespread presence of lichens over debris slopes and patterned ground, like P11 (López-Martínez et al., 2012). The environment P11 is a high marine terrace in Holocene, at an elevation of 20 m.a.s.l. (Table 1) located in the central tombolo formed by marine graves that connects the northern and southern part of the island. It presented the lowest P and OM amounts recorded in this study, with a very sparse vegetation of crustose lichens on cobbles and gravels at the soil surface, likewise similar areas from South Shetland islands (Kim et al., 2007; Simas et al., 2008; Albuquerque et al., 2012; Rodrigues et al., 2019). In spite of the intermediary species richness observed (Fig. 3A, Tab. 1), this pedoenvironment showed lowest plant coverage (Fig. 3B), due to its recent exposure and little bird activity, locally.

P10 is located in the extreme south of the island, called Baliza Point, near an active penguin colony, classified as a crustose lichens community (Schmitz et al., 2018). Some rare species such as *C. murrayi*, *R. terebrata* and *X. elegans*, which occur only in this pedoenvironment, are ornitocoprophilous (Redon, 1985; Olech, 2004), capable of surviving under high P and N levels present in penguin’s guano. Because it is a dry and stony pedoenvironment, it was the only one where *Sanionia* spp was not detected, although it is a genus of wide distribution in this island and elsewhere Maritime Antarctica. It is usually absent in dry habitats dominated by crustose lichens (Ochyra et al., 2008; Schmitz et al., 2018).

The P12 is located on current beaches on the northern side of the Half Moon island that receive melting water from the highest parts. Scattered bone and egg shell fragments, nest remains and bird droppings indicate the nesting activity by skuas, bestowing a weak ornithogenic influence (Simas et al., 2007). A discontinuous vegetation community composed of moss carpet *Sanionia* ssp is present (Tab. 1), and only six species were identified, being the lowest richness (Fig. 5B). The moss *Bryum nivale* is a rare species that only occurred in this pedoenvironment, often flooded or covered by snow, which recorded the highest values of V, P Rem and Mn. *B. nivale* record for South Shetland Islands is rare and recent, enabling to suggest that this species is currently colonizing areas after glacier retreat, as postulated by Wierzgoń et al., (2018).

The P6 and P14 are located at La Morenita Hill, at different elevations (40 and 85 m.a.s.l., respectively), and although some soil properties follow similar patterns (Fig. 2, table A.1). They showed plant coverage with distinct communities. While P6 has a moss carpet, P14 has a fruticose lichen community (Table 1). Both are closely related to drainage and landform, since P6 is a flat area in the lower part of La Morenita hill, classified as debris slope and cone (López-Martínez et al., 2012), whereas P14, at the top Hill, is classified as middle platforms. In P6 some rare species were found (*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, Cladonia furcata*, *Dicranoweisia grimmiacea*, *Leptogium puberulum*, *Schistidium antarctici* and *Schistidium urnulaceum* were only recorded in P14 (Fig. 6), where the highest levels of Cu were recorded (Fig. 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 areas with greater exposure less snow cover and high altitude locations (Kim et al., 2007). On the other hand, bryophytes which are positively associated with higher water content and waterlogging (Leishman and Wild, 2001), at moister, more sheltered habitats (Kim et al., 2007). This is the case of *Sanionia* spp., which often occurs in hydromorphic soils (Pereira and Putzke, 2013; Thomazini et al., 2018), regard less of chemical attributes (Ferrari, 2018).

P8 is located at a slightly higher landscape position than P13, and both have moss carpet communities. 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 highest richness of this study. The species that appear in P13 and are absent in P8 are mostly fruticose lichens (*Himantormia lugubris, Sphaerophorus globosus*) and crustose lichens (*Acarospora macrocyclos*, *Haematomma eryhtromma*) with a preference for growing on pebbles and boulders (Kim et al., 2007) in places of better soil drainage, such a stable Felsenmeer surfaces, platforms with high wind exposure and desiccation (Francelino et al., 2011). Despite having an ornithogenic influence in P13, it showed a neutral/alkaline pH (7.2), and lower values of Fe, and associated with the presence of *Scapania* sp., *Bryum dichotomum* and *Ceratodon grossiretis,* which indicate that these mosses are limited by soil acidity this consistent with reports that bryophytes diversity increases with higher soil pH (Robinson et al., 1989; Stephenson et al., 1995). Hence, this environment with higher soil fertility also presented higher β-diversity, probably because favorable soil conditions and high availability of resources allow a higher species coexistence (Tilman and Pacala, 1993; Laliberté et al., 2014), and environmental filtering has lesser importance compared to 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 about abiotic and biotic process 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 many other studies from elsewhere, 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 (Barbier et al. 2006; Rietkerk and 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 vegetation dynamics (Rietkerk and van de Koppel, 2008, Meloni et al., 2017). On the other hand, it is possible that the species coexistence in these patchy mosaics is crucial for increasing species richness by facilitation (Molina-Montenegro et al., 2012). Thus, we presumed that different non-vascular communities types and plant coverage levels between different soil conditions reported for Maritime Antarctica (i.e., Ferrari, 2018; Schmitz et al. 2018; Schmitz et al. *in press*), probably can also promote higher species turnover along pedoenviromental gradient. Previous studies showed that high vegetation density produces a niche differentiation, and promotes species coexistence and niche facilitation process between rare and common species (e.g., Sanaei et al., 2018).

5. Conclusions

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

2. The post glacial uplift of the island promoted a topographic gradient of ornithogenic influence, accounting for differences in soil chemical properties. These edaphic differences defined a heterogeneous pedoenvironmental gradient that drives non-vascular community diversity and coverage pattern.

3. Newly exposed pedoenvironments have lower species richness and plant coverage (P10, P11 and P12).

4. The species richness and plant coverage along the pedoenvironmental gradient were different; however, they shared common species that were present in the majority of the pedoenvironments, despite differences in plant coverage. However, most of the pedoenvironments recorded rare species that occurred only under specific soil conditions, which also contributes to the high species turnover between pedoenvironments and low floristic similarity, which promoted high β-diversity.

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Appendix A: Supplementary data

Table A.1. Mean of soil chemical atributes of the 14 sampled pedoenvironments of Half Moon Island, Maritime Antarctica.

	P1	P2	P3	P4	P5	P6	P7	P8	P9	P10	P11	P12	P13	P14
pH H_2O	4.97±0.01	6.47±0.01	5.38±0.25	5.07±0.22	5.23±0.49	4.84±0.11	5.32±0.18	5.46±0.26	5.58±0.08	5.47±0.05	7.02±0.32	6.45±0.78	7.20±0.04	5.09±0.26
P (mg/dm^3)	436.12±72.68	724.79±95.45	242.37±14.72	232.81±7.76	242.82±17.92	601.01±5.65	440.99±13.88	370.98±25.98	2021.08±141.16	1096.42±98.90	61.08±2.20	94.07±32.27	336.45±121.85	645.11±9.2
K (mg/dm^3)	107.36±4.83	211.40±5.24	116.85±9.72	135.18±14.95	112.70±39.47	137.27±24.68	101.79±3.55	110.10±38.09	90.20±4.99	71.37±3.36	118.43±1.99	164.68±30.92	139.46±32.16	135.12±6.54
Na (mg/dm^3)	1551.41±14.44	88.95±5.16	152.28±7.84	120.79±4.57	137.63±31.58	147.66±10.89	127.69±4.34	134.44±2.72	221.53±11.17	119.51±1.27	243.27±3.88	225.23±51.48	164.68±37.06	127.48±6.93
Ca^{2+} ($cmol_c/dm^3$)	1.38±0.06	3.61±0.04	2.29±0.14	1.60±0.34	1.80±0.06	0.63±0.24	2.04±0.52	6.11±1.41	7.82±0.17	0.85±0.03	2.31±0.60	2.36±0.61	3.75±0.66	1.43±0.31
Mg^{2+} ($cmol_c/dm^3$)	0.39±0.09	0.74±0.06	1.45±0.02	0.54±0.04	0.92±0.16	0.19±0.04	1.29±0.22	1.79±0.15	3.05±0.53	0.24±0.03	1.23±0.25	1.18±0.54	1.64±0.39	0.37±0.15
H + Al ($cmol_c/dm^3$)	13.71±1.04	16.62±1.20	15.19±0.91	11.06±0.28	11.21±1.49	17.57±0.20	10.05±0.05	3.96±0.27	6.71±0.41	7.03±0.37	1.26±0.04	0.92±0.37	4.24±0.88	17.73±3.36
SB ($cmol_c/dm^3$)	8.67±0.19	2.85±0.41	4.69±0.12	4.84±1.32	3.66±1.24	2.01±0.25	4.19±0.55	9.55±0.59	12.05±0.86	1.83±0.09	3.59±0.27	5.25±0.61	6.46±1.01	2.75±0.58
(t) ($cmol_c/dm^3$)	10.23±0.52	2.76±0.30	5.96±0.12	5.43±0.76	4.78±0.30	3.22±0.10	4.66±0.15	8.65±2.38	11.08±0.79	2.17±0.05	3.54±0.28	5.18±0.41	6.43±0.55	4.33±0.53
T ($cmol_c/dm^3$)	22.96±1.43	19.16±1.62	19.26±0.99	15.07±1.29	16.42±0.19	19.50±0.42	14.22±0.51	13.49±0.86	18.72±0.34	8.81±0.50	6.25±0.76	6.39±0.56	10.72±1.44	18.95±3.43
V (%)	34.57±2.56	14.04±2.18	23.97±1.48	24.15±3.46	24.38±2.57	9.50±0.91	27.70±1.16	69.96±0.06	64.15±3.12	20.32±0.67	78.99±2.54	82.14±3.27	59.30±2.94	13.62±0.88
m (%)	16.17±2.43	0	24.08±1.17	22.20±3.53	20.57±2.29	41.83±3.44	17.09±4.20	14.80±0.21	15.88±0.39	18.02±0.44	17.92±0.54	0	0	37.64±4.18
Prem (mg/L)	9.73±0.68	9.21±0.73	6.06±0.11	8.03±0.30	6.39±0.70	11.57±1.13	11.12±0.37	22.71±2.77	10.88±0.41	21.38±1.62	28.32±3.35	36.03±3.22	7.79±2.62	13.33±1.19
OM (dag/kg)	15.19±0.80	21.19±1.24	14.81±2.03	7.40±0.68	8.58±1.13	11.82±0.43	5.90±0.16	4.49±0.36	4.16±0.41	2.32±0.46	0.51±0.12	0.72±0.38	3.45±0.87	6.17±0.25
Cu (mg/dm^3)	3.39±0.01	3.36±0.06	4.0±0.44	3.52±0.47	4.61±0.53	3.72±0.40	5.27±0.85	9.15±0.73	8.06±0.17	9.15±1.01	4.98±0.25	4.84±1.90	10.72±3.01	21.62±0.79
Mn (mg/dm^3)	5.96±0.43	6.52±0.51	15.83±0.41	16.59±4.87	13.86±1.60	7.01±0.30	28.68±2.58	25.74±2.73	32.52±0.81	9.38±0.73	25.17±1.43	35.59±2.30	10.54±2.48	22.26±1.35
Fe (mg/dm^3)	749.92±20.10	513.67±24.70	623.63±24.23	339.76±20.46	631.69±28.75	823.38±44.42	707.50±55.88	614.65±68.74	711.92±46.08	598.66±47.40	348.47±1.51	465.90±95.47	274.72±71.44	364.05±5.14
Zn (mg/dm^3)	1.65±0.20	0.91±0.19	1.56±0.06	3.13±0.51	1.87±0.16	2.02±0.05	1.23±0.31	1.93±0.25	0.73±0.07	7.97±1.01	3.46±0.50	3.04±0.41	5.37±1.35	3.29±0.30
Course sand (%)	56	NA	64	49	63	54	69	63	NA	NA	55	NA	NA	NA
Fine sand (%)	40	NA	31	29	32	40	28	33	NA	NA	27	NA	NA	NA
Silt (%)	3	NA	3	11	2	3	2	2	NA	NA	14	NA	NA	NA
Clay (%)	2	NA	3	12	3	3	2	2	NA	NA	4	NA	NA	NA
texture	sand	NA	sand	sandy loam	sand	sand	sand	sand	NA	NA	Loam sandy	NA	NA	NA

pH: H_2O (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; T: potential cátion Exchange capacity; V: percentage of bases saturation; m: aluminium saturation; Prem: remaining phosphorus; OM: organic matter; Cu: copper; Mn: manganese; Fe: iron; Zn: zinc.

Table A. 2. List of species identified in the 14 study areas.

Family	Group	Species	Abbreviation	N. of plots
Amblystegiaceae	Moss	*Sanionia* spp	San_sp	141
Andreaeaceae	Moss	*Andreaea depressinervis* Card.	And_de	15
	Moss	*Andreaea gainii* Card.	And_ga	32
	Moss	*Andreaea regularis* Muell.	And_re	41
Bartramiaceae	Moss	*Bartramia patens* Brid.	Bar_pa	1
Bryaceae	Moss	*Bryum argenteum* Hedw.	Bry_ar	5
	Moss	*Bryum nivale* Müll. Hal.	Bry_ni	6
	Moss	*Bryum dichotomum* Hedw.	Bry_di	1
	Moss	*Bryum sp.*	Bry_sp	1
	Moss	*Pohlia cruda* (Hedw.) Lindb.	Poh_cr	8
	Moss	*Pohlia nutans* (Hedw.) Lindb.	Poh_nu	1
Ditrichaceae	Moss	*Ceratodon grossiretis* Cardot	Cer_gr	1
	Moss	*Ceratodon purpureus* (Hedw.) Brid.	Cer_pu	1
Grimmiaceae	Moss	*Schistidium antarctici* Card.) L.I. Savicz & Smirnova	Sch_an	5
	Moss	*Schistidium urnulaceum* (Müll. Hal.) BG Sino	Sch_ur	1
Polytrichaceae	Moss	*Polytrichastrum alpinum* G.L. Smith	Pol_al	77
	Moss	*Polytrichum piliferum* Hedw.	Pol_pi	6
Pottiaceae	Moss	*Hennediella heimii* (Hedw.)Zand.	Hen_he	19
	Moss	*Syntrichia magellanica* (Mont.) RH Zander	Syn_ma	2
Seligeraceae	Moss	*Dicranoweisia grimmiacea* (Müll. Hal.) Broth	Dic_gr	5
Scapaniaceae	Liverwort	*Scapania* sp Mig.	Sca_sp	1
Prasiolaceae	Chlorophyta	*Prasiola crispa* (Lightfoot) Kützing	Pra_cr	12
Acarosporaceae	Lichen	*Acarospora macrocyclos* Vain.	Aca_ma	20
Bacidiaceae	Lichen	*Bacidia* sp	Bac_sp	10
	Lichen	*Bacidia tubercullata* Darb.	Bac_tu	1
Physciaceae	Lichen	*Buellia latemarginata* Darb.	Bue_la	6
	Lichen	*Buellia racovitzae* CW rodeio	Bue_ra	1
	Lichen	*Buellia russa* (Hue) Darb.	Bue_ru	1
	Lichen	*Buellia anisomera* Vain.	Bue_an	3
	Lichen	*Buellia* sp	Bue_sp	37
	Lichen	*Physconia muscigena* (Ach.) Poelt	Phy_mu	1
Candelariaceae	Lichen	*Candelaria murrayi* Poelt	Can_mu	5
Cladoniaceae	Lichen	*Cladonia metacorallifera* Asahina	Cla_me	38

	Lichen	*Cladonia rangiferina* (L.) Weber ex F.H. Wigg.	Cla_ra	33
	Lichen	*Cladonia furcata* (Huds.) Schrad.	Cla_fu	2
	Lichen	*Cladonia* sp P. Browne	Cla_sp	15
Collemataceae	Lichen	*Leptogium puberulum* Hue	Lep_pu	1
Haematommataceae	Lichen	*Haematomma eryhtromma* (Nyl.) Zahlbr.	Hae_er	2
Lecanoraceae	Lichen	*Lecanora skottsbergii* Darb.	Lec_sk	1
	Lichen	*Rhizoplaca aspidophora* (Vain.) Redon	Rhi_ap	40
	Lichen	*Rhizoplaca melanophtalma* (Ram.)Leuckert & Poelt	Rhi_me	10
Lecideaceae	Lichen	*Lecidea sciatrapha* Hue	Lec_sc	62
	Lichen	*Lecidea* sp.	Lec_sp	26
Ochrolechiaceae	Lichen	*Ochrolechia frigida* (Sw.) Lynge	Och_fr	61
	Lichen	*Ochrolechia parella* (L.) A. Massal.	Och_pa	2
Pannariaceae	Lichen	*Pannaria hookeri* (Borrer) Nyl.	Pan_ho	3
	Lichen	*Psoroma cinnamomeum* Malme	Pso_ci	6
	Lichen	*Psoroma hypnorum* (Vahl) Gray	Pso_hy	36
Parmeliaceae	Lichen	*Himantormia lugubris* (Hue) Cordeiro IM	Him_lu	4
	Lichen	*Parmelia saxatilis* (L.) Ach.	Par_sa	6
	Lichen	*Usnea antarctica* Du Rietz	Usn_an	9
	Lichen	*Usnea aurantiacoatra* (Jacq.) Bory	Usn_au	67
Ramalinaceae	Lichen	*Ramalina terebrata* Hook. f. & Taylor	Ram_te	3
	Lichen	*Lecania brialmontii* (vã). Zahlbr.	Lec_br	5
Rhizocarpaceae	Lichen	*Rhizocarpon geographicum* (L.) DC.	Rhi_ge	30
	Lichen	*Rhizocarpon polycarpum* (Hepp) Th. Fr.	Rhi_po	37
Sphaerophoraceae	Lichen	*Sphaerophorus globosus* (Huds.) Vain.	Sph_gl	34
Stereocaulaceae	Lichen	*Stereocaulon glabrum* (Müll. Arg.) Vain.	Ste_gl	15
Teloschistaceae	Lichen	*Caloplaca regalis* (Vain.) Zahlbr	Cal_re	4
	Lichen	*Caloplaca cinericola* (Hue) Darb.	Cal_ci	1
	Lichen	*Xanthoria elegans* (Link) Th. Fr.	Xan_el	4
Thelenellaceae	Lichen	*Microglaena antarctica* IM Lamb	Mic_an	4
Verrucariaceae	Lichen	*Verrucaria* sp.	Ver_sp	67
-	Lichen	*Cystocoleus niger* (Huds.) Har.	Cys_ni	15

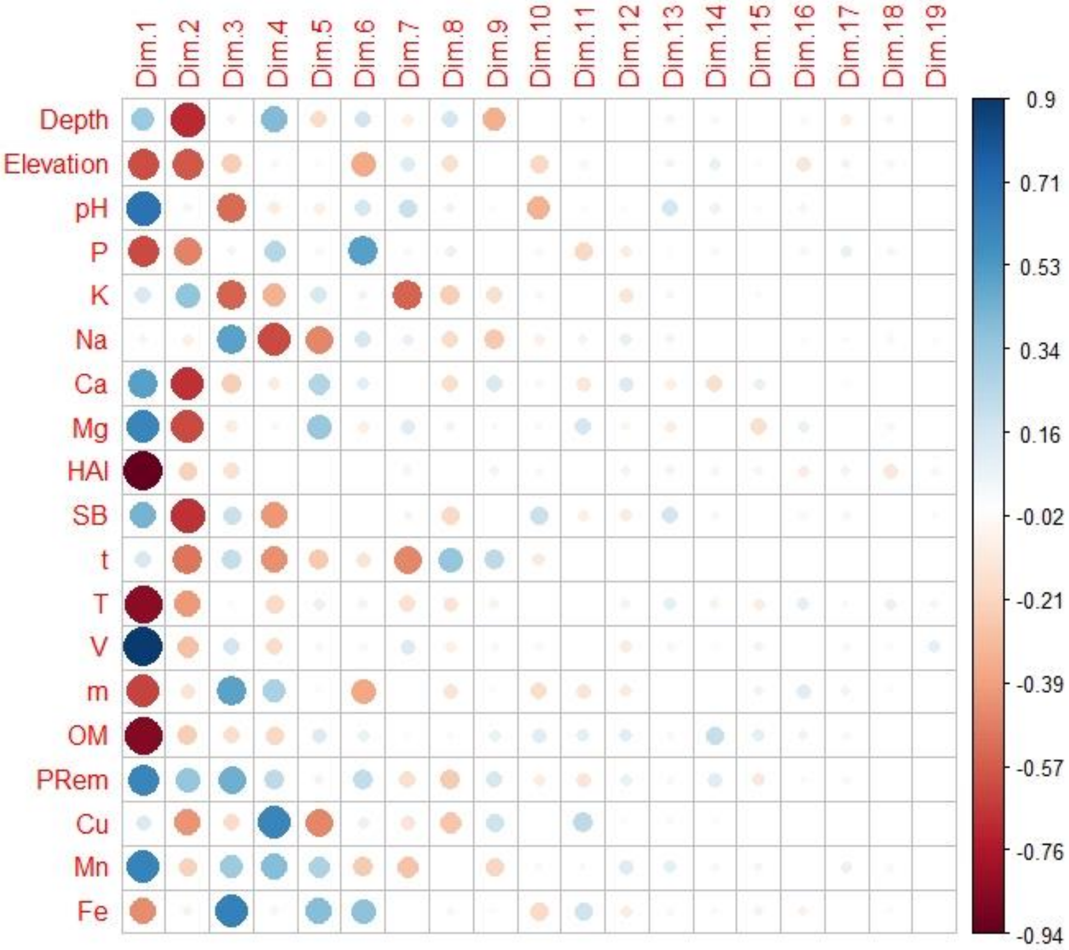

Figure A.1. Significance levels are based on Pearson's correlation coefficients between soil parameters and principal components of soil PCA from 174 different plots along the pedoenvironmental gradient.

CAPÍTULO III:

Fertilidade do solo determina variações na composição de espécies, mas não na riqueza de plantas não vasculares ao longo de um gradiente pedoambiental na Antártica Marítima

Proposto para submeter na revista ***Polar Biology***

Resumo

SCHMITZ, Daniela, D.Sc., Universidade Federal de Viçosa, julho de 2019. **Fertilidade do solo determina variações na composição de espécies, mas não na riqueza de plantas não vasculares ao longo de um gradiente pedoambiental na Antártica Marítima**. Orientador: Carlos Ernesto G.R. Schaefer. Coorientador: Jair Putzke.

A Antártica Marítima é o único ecossistema terrestre dominado por liquens e musgos, que representam importantes indicadores ecológicos de mudanças climáticas. No entanto, pouco se sabe sobre como a filtragem ambiental molda as comunidades criptogâmicas em fina escala nesta região. Neste estudo, analisamos as mudanças na riqueza de espécies, composição de espécies e cobertura de plantas não vasculares ao longo de um gradiente pedoambiental na Antártida Marítima. Nossa hipótese é de que os filtros ambientais (isto é, textura do solo e propriedades químicas) moldam variações na riqueza e composição de espécies. Selecionamos 15 diferentes pedoambientes e realizamos amostragem fitossociológica e coleta superficial de solo em 300 parcelas que foram usadas para avaliar o efeito principal da textura e fertilidade do solo na riqueza e composição de espécies não vasculares usando análise direta de gradiente e modelos lineares. Determinou-se o valor ecológico das espécies e caracterizou-se o tipo de comunidade vegetal e associações de espécies ao longo de cada pedoambiente. Diferenças na composição de espécies, riqueza, e cobertura vegetal foram detectadas ao longo do gradiente pedoambiental. No entanto, a análise de modelos mostrou que fertilidade do solo explica efeitos significativos sobre a composição de espécies, mas não na riqueza de espécies. No entanto, a análise de parâmetros em modelos univariados mostrou que a composição química do solo e a textura do solo não afetaram a riqueza de espécies. Com base na análise de gradiente, a variabilidade da fertilidade do solo e os teores de nutrientes foram importantes filtros pedoambientais para as comunidades vegetais na Antártica Marítima. A filtragem ambiental determina mudanças na composição de espécies, e provavelmente suportam um padrão determinístico. Este estudo revela que a heterogeneidade da escala fina contribui para associações específicas de espécies ao longo de um gradiente pedoambiental. Assim, a filtragem pedoambiental não só determina o padrão de composição florística de plantas não vasculares, mas também o tipo de comunidades.

Palavras-chave: cobertura vegetal, filtragem pedoambiental, líquens, musgos; plantas não vasculares.

1. Introdução

Existe um constante interesse em entender como múltiplos fatores controlam a distribuição, abundancia e diversidade de espécies ao longo de gradientes ambientais e diferentes escalas espaciais (Götzenberger et al., 2012). Se tratando particularmente da Antártica Marítima, esse interesse vem crescendo nas últimas décadas devido a sua importância para o monitoramento de mudanças climáticas (Thomazini et al., 2018) e seus impactos sobre a diversidade vegetal principalmente nos polos (Amesbury et al., 2017). Porém, poucos estudos relacionando fatores que moldam a montagem das comunidades vegetais ao longo de gradientes ambientais foram realizados nessa região (Leishman & Wild, 2001).

Na escala de paisagem, a disponibilidade de áreas livres de gelo determina a distribuição da vegetação terrestre na Antártica (Leishman & Wild, 2001). Essas áreas estão restritas a regiões costeiras, encostas rochosas ou nunataks e solos em diferentes estádios de desenvolvimento (Campbell & Claridge, 1987; Bokhorst et al., 2007). A vegetação é composta em sua maioria por briófitas e liquens, com apenas duas angiospermas nativas da região (Putzke & Pereira, 2001). As briófitas possuem maior biomassa e formam extensas comunidades e associações, bem como os liquens, que juntos formam um mosaico na paisagem (Victoria et al., 2013). Diferenças na composição de espécies pode ser encontrado dentro de uma pequena área (Victoria et al., 2009; Schmitz et al., 2018) devido à alta heterogeneidade ambiental, como por exemplo de microtopografia, formação geológica, propriedades físicas e químicas do solo (Victoria et al., 2013; Benavent-González et al., 2018).

Neste estudo, avaliamos a relação entre a riqueza e composição das comunidades vegetais com os atributos químicos e físicos do solo ao longo de gradiente pedoambiental, na Ilha Elefante, Antártica Marítima. Foram utilizados dados de inventário de plantas de

300 parcelas (20 × 20 cm) distribuídas em 15 pedoambientes, permitindo avaliar o efeito da textura do solo e fertilidade do solo na riqueza e composição de espécies de plantas não vasculares. Nesse sentido foram abordadas as seguintes questões: 1) como é a riqueza, a composição de espécies e a cobertura vegetal ao longo dos 15 pedoambientes? 2) São diferentes as propriedades do solo nos 15 ambientes? 3) Existe alguma variação das associações de espécies ao longo do gradiente pedoambiental? 4) quais são os efeitos das propriedades químicas e físicas do solo sobre a riqueza e composição de espécies?

Baseado na premissa de que as propriedades do solo tem uma alta variabilidade espacial na Antárctica marítima (Thomazini et al., 2018; Schmitz et al., *in press*) e esta é promovida pela posição na paisagem, diferença na cobertura vegetal, atividade biológica das aves e tempo de exposição, nossa hipótese é de que: 1) As propriedades químicas e físicas do solo variam ao longo dos 15 ambientes estudados; 2) Pedoambientes com maior fertilidade e maior quantidade de nutrientes disponíveis promovam maior riqueza de espécies, cobertura vegetal, e variação na composição de espécies.

2. Material e Métodos

Área de estudo

Esse estudo foi realizado em Stinker Point (61º21'S, 55º20'W), localizado na Ilha Elefante (Fig.1). A Ilha Elefante está situada ao norte do arquipélago das Shetland do Sul, entre o Estreito de Drake e o mar de Weddel (Pereira & Putzke, 1994) e tem um clima frio com maiores condições de nevoeiro e queda de neve.

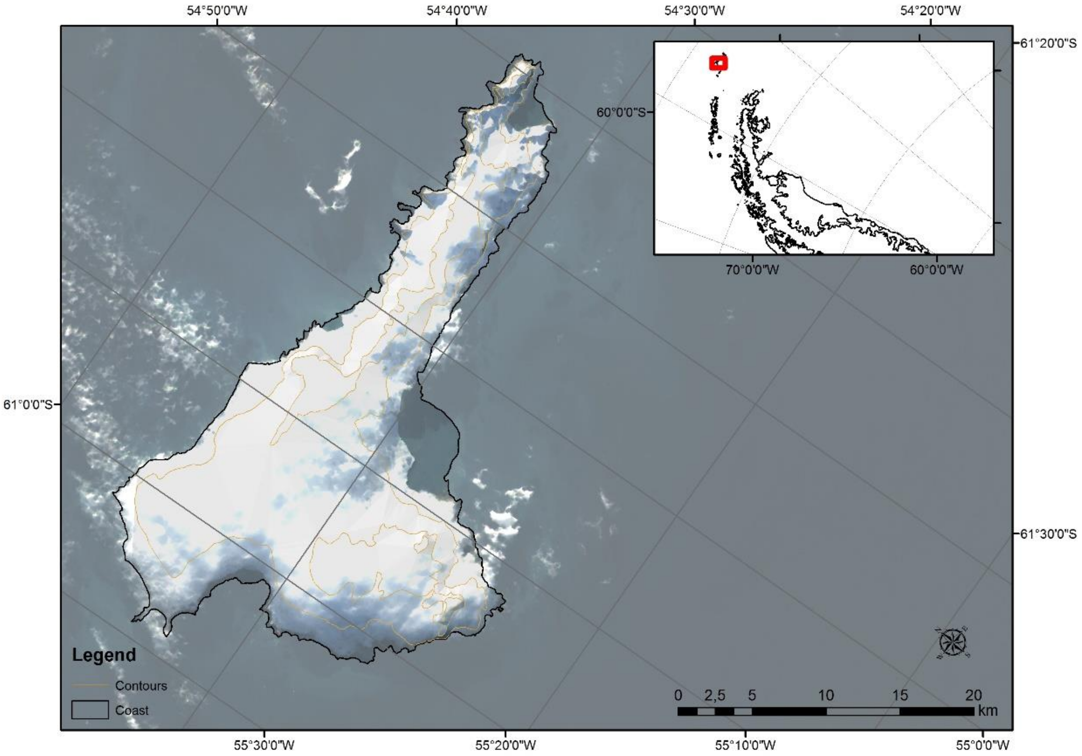

Figura 1. Ilha Elefante e sua localização na Antártica Marítima.

Geologicamente a ilha é composta principalmente de rochas metamórficas (O'Brien et al., 1979), as áreas livres de gelo são encontradas principalmente na região costeira em depósitos marinhos soerguidos pela deriva glacial, formando falésias alternadas com íngremes saídas de geleiras ou penhascos de gelo (Navas et al., 2018).

Stinker Point é uma das maiores áreas livres de gelo da Ilha Elefante (CGE-UAM-UFRJ, 2005; Navas et al., 2018) e possui grande riqueza de fauna e flora que de acordo com Pereira & Putzke (1994) é composta por duas angiospermas nativas registradas para a região da Antártica Marítima, *Colobanthus quitensis* (Kunth.) Bartl. e *Deschampsia antarctica* Desv., 38 espécies de musgos, sete hepáticas, 68 liquens, duas espécies de algas terrestres e quatro fungos macroscópicos.

Amostragem da vegetação

Foram selecionados 15 pedoambientes para o estudo. Em cada pedoambiente foram lançadas 20 parcelas de 20 × 20 cm. A amostragem foi conduzida utilizando a metodologia de quadrados de Braun-blanquet (1932), adaptada às condições da vegetação Antártica, para avaliar a cobertura de cada espécie na parcela. No total, foram realizadas 300 parcelas no verão austral de 2017/2018. Em cada parcela, as briófitas foram identificadas a nível de espécie, utilizando as chaves de identificação taxonômicas presentes e: Putzke & Pereira (2001), Ochyra et al. (2008), e Redon (1985), Øvstedal & Lewis-Smith (2001), Olech (2004) para liquens.

Índice de Significância Ecológica (IES)

Os locais foram avaliados quanto a frequência e o nível de cobertura de cada espécie dentro do quadrado (Lara & Mazimpaka, 1998), utilizados para a obtenção do Índice de Significância Ecológica (IES) que combina esses dois parâmetros (e.g., Marques et al. 2005; Schmitz et al. 2018), descritos na fórmula: $IES=f(1+C)$, onde f é a frequência relativa das espécies na área, obtido atrás da frequência absoluta (x) dividida pelo número total de amostras considerando (n): $F=100x/n$; e C é a cobertura média das espécies nas amostras, calculada como $C= \sum(ci)/x$, onde ci é a classe de cobertura e x é número de amostras em que a espécie ocorreu (e.g., Schmitz et al., 2018). Este índice determina a escala de importância das espécies na área, assim como as principais associações que ocorrem dentro das comunidades. Os valores variam de 0 a 600, onde valores acima de 50 indicam significância ecológica (Victoria e Pereira, 2007). As espécies com os maiores valores e sua forma de crescimento definem o nome das comunidades seguindo a classificação de Longton (1988). As associações são caracterizadas por espécies codominantes ou por ocorrência restrita em habitats mais específicos (Poelking et al., 2015) e nomeadas de acordo com a proposta de Longton (1988).

Coleta de solo

Para medir as propriedades do solo dentro de cada parcela, uma amostra simples de solo superficial (a 0-10 cm de profundidade) foi coletada seguindo as recomendações de Bockheim et al. (2006). As amostras foram secas ao ar e posteriormente peneiradas em malha de 2mm, sendo a porção de terra fina (TFSA) enviada para a análise de rotina do departamento de solos da Universidade Federal de Viçosa (UFV). As propriedades do solo foram medidas seguindo protocolos padronizados (Embrapa, 1997). As seguintes propriedades do solo foram avaliadas: pH (H_2O), P permutável, K, Ca, Na, Mg, Fe, Cu, Mn, Zn, Al^{3+}, acidez trocável (H + Al), matéria orgânica (MO), soma de bases trocáveis (SB); capacidade potencial de troca catiônica (T), porcentagem de saturação por bases (V), e a textura do solo, como areia grossa (C_sand), areia fina (F_sand), teores de argila e silte.

Análise de dados

Todas as análises foram realizadas no programa R (R Core Team, 2018). Avaliou-se a distribuição e homogeneidade dos dados usando os testes de Shapiro-Wilk e Bartlett (Crawley, 2013). Para comparar médias da cobertura vegetal e parâmetros do solo variáveis entre tratamentos, usou-se um teste de Kruskal-Wallis (para dados não distribuídos normalmente) seguido por um teste posterior de Dunn (Crawley, 2013).

Para comparar a riqueza de espécies entre pedoambientes foram estimadas curvas de rarefação e extrapolação baseado no número de parcelas e usando o primeiro número de Hill, q = 0 (Chao et al., 2014). As extrapolações foram feitas com base na presença /

ausência de espécies nas parcelas (Colwell et al., 2012). Estas estimativas foram obtidas usando o pacote "iNEXT" (Hsieh et al., 2016). O número de Hill foi estimado como a média de 100 repetições de *bootstrapping* para estimar intervalos de confiança de 95% (por exemplo, Rodrigues et al., 2019). Da mesma forma, consideramos sempre que os intervalos de confiança de 95% não se sobrepuseram, o número de espécies diferiu significativamente em P <0,05 (Colwell et al., 2012).

Realizamos o escalonamento multidimensional não-métrico (NMDS) para analisar as diferenças entre os pedoambientes em termos de composição de espécies usando a distância euclidiana. O NMDS foi realizado usando a função "metaMDS" do pacote "vegan" (Oksanen et al., 2018). Utilizou-se análise de variância multivariada permutacional (PERMANOVA, 9999 permutações) para determinar diferenças na composição de espécies utilizando a rotina de *adonis* disponível no pacote “vegan” (Oksanen et al., 2018).

As variáveis do solo foram resumidas por uma análise de componentes principais (PCA) na matriz de correlação para reduzir o número de propriedades do solo redundantes (por exemplo, Qian et al. 2014; Villa et al., 2018). Por tanto, todas as variáveis foram centralizadas e padronizadas; e finalmente calculamos as correlações de Pearson entre as propriedades do solo e os eixos de ordenação do PCA. O PCA foi realizado usando o pacote "FactoMineR" (Husson et al., 2017).

Avaliamos o efeito de potenciais preditores sobre a riqueza de espécies e composição de espécies (por exemplo, extraindo os valores eixo 1 do NMDS ponderado pela frequência; Oksanen et al., 2018; Villa et al., 2018) usando modelos lineais de efeito misto. Para reduzir quaisquer correlações fortes entre as condições ambientais locais, usamos os dois eixos do PCA para as variáveis de fertilidade do solo (PCA1f e PCA2f) e textura (PCA1t e PCA2t). Assim, estes eixos do PCA são considerados *proxy* para a fertilidade do solo e gradiente de textura do solo em todos os modelos testados (Ali et al., 2016; Villa et al., 2018). Utilizamos modelos de efeitos mistos lineares generalizados (GLMMs) com distribuição de erros de Poisson para investigar o efeito de propriedades individuais do solo, fertilidade do solo e textura do solo sobre a riqueza de espécies. A composição das espécies foi avaliada usando LMMs após verificação do teste de Shapiro-Wilk para gráficos de normalidade e Q-Q (Crawley, 2013). As variáveis preditoras (efeitos fixos) foram fertilidade do solo (eixos PCAf) e textura do solo (eixos PCAt), bem como parâmetros adicionais do solo como areia, silte, argila, SB, OM e T. A química e a textura do solo foram utilizadas, bem como os parâmetros isolados do solo como variáveis explicativas para a modelagem, porque os parâmetros individuais do solo também potencialmente mostram um efeito direto sobre a riqueza de espécies e composição de espécies (Villa et al., 2018; Schmitz et al. *In press*). Para a seleção do preditor, avaliamos a colinearidade entre as variáveis preditoras selecionadas usando a análise de correlação de Spearman; quando duas variáveis estavam fortemente correlacionadas ($r \geq 0,6$), os preditores mais relevantes ecologicamente foram selecionados, os quais foram incluídos em modelos separados (Fig. A.1. Material Suplementar). Em todos os modelos mistos, os pedoambientes foram incluídos como fator aleatório e os dois primeiros eixos da fertilidade e textura do solo foram utilizados como fator fixo (Villa et al., 2018; Schmitz et al. *In press*). Todos os modelos foram testados com o pacote "lme4" (Bates et al., 2014) da plataforma R (R-Core-Team, 2018); e para ilustração de gráficos, usamos o pacote "ggplot2" (Hadley, 2015).

Para avaliar os melhores modelos (GLMMs e LMMs), aplicou-se uma abordagem de inferência multi-modelo (Burnham & Anderson, 2002) com a função 'dredge' do pacote “MuMIn” (Barton, 2015), que retorna todas as combinações possíveis das variáveis explicativas incluídas no modelo global. Para determinar quais destas variáveis foram as mais decisivas para explicar as mudanças na riqueza de espécies e composição de espécies, usamos uma abordagem de teoria da informação baseada no critério de informação de Akaike (AIC) com uma correção para tamanhos de amostra finita (AICc) e pesos AIC (Burnham & Anderson, 2002). O modelo com o AICc mais baixo foi considerado o melhor, mas todos os modelos que diferiam menos de duas unidades do melhor modelo foram considerados modelos igualmente bons (Burnham et al., 2011).

3. Resultados

Padrões de composição e riqueza de espécies

Foram identificadas 39 espécies nos 15 ambientes estudados. Sendo 21 de briófitas (19 musgos e 2 hepáticas), 15 de liquens, duas angiospermas (*Deschampsia antarctica* e *Colobanthus quitensis*) uma alga macroscópica (*Prasiola crispa*, Tabela A.1. Material Suplementar). A família com maior riqueza de espécies foi Bryaceae para briófitas e Parmeliaceae para liquens, ambas com quatro espécies.

Utilizando a curva de rarefação de espécies foi possível observar que todos os pedoambientes foram suficientemente amostrados, pois a assíntota é atingida quando as curvas já estão estabilizadas (Fig. 2A). Foi observado um distinto padrão de riqueza entre os pedoambientes baseado nessa amostragem, onde o P1 foi o que apresentou o menor número de espécies, já os P2, P3, P4, P5, P7, P8, P12, P13 e P14 seguiram um padrão aproximado, variando entre seis e dez espécies, os P6, P9, P10 e P11 variaram entre 13 e 15 espécies e o P15, teve a maior riqueza, com 19 espécies (tabela 1).

A cobertura também variou significativamente entre os pedoambientes, onde alguns (P1, P2, P4, P5, P6, P9 e P14) chegam a atingir 100% de cobertura vegetal enquanto outros (P8, P12 e P13) quase não atingem 50% (Fig.2B).

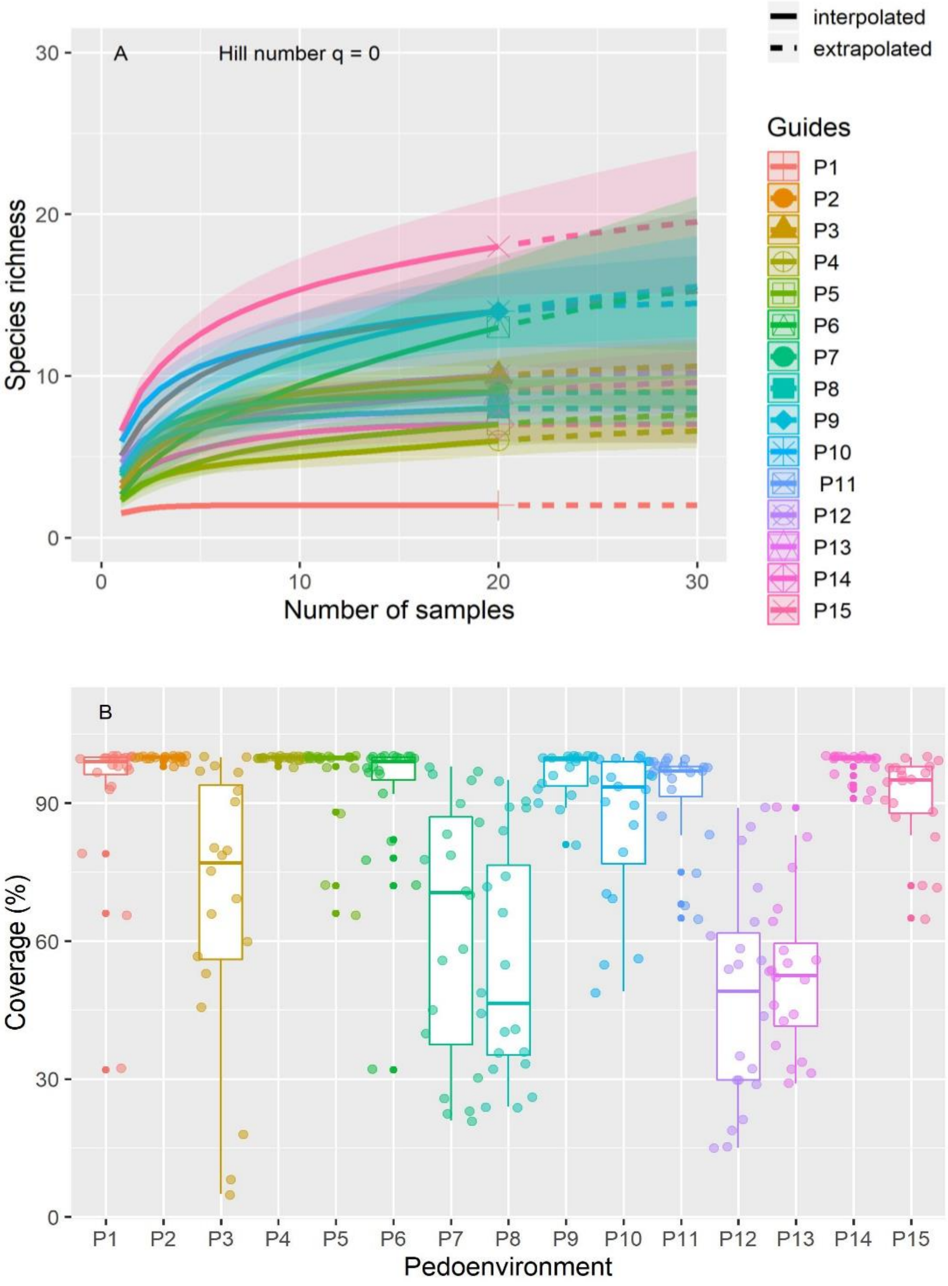

Figura 2. Rarefação baseada em amostragem (linhas sólidas) e curvas de extrapolação (linhas tracejadas) da diversidade de espécies vegetais com base nos primeiros números de Hill (q = 0) para o ambiente pediátrico amostrado (A), e cobertura (B) entre o ambiente de amostragem. As curvas de rarefação e extrapolação apresentam as linhas que representam os valores médios e as bandas o desvio padrão com intervalos de confiança de 95%.

O NMDS revelou que a composição de espécies variou entre os pedoambientes (PERMANOVA F 14, 299=33.70, P<0.001), porém com a sobreposição de algumas espécies na maioria dos ambientes (Fig. 3). Espécies como *Sanionia uncinata* se mostrou dominante e esteve presente em 139 das 300 parcelas amostradas, seguida de *S. georgicouncinata* (82), *Cystocoleus niger* (72) e *Usnea antarctica* (71), que também se mostraram dominantes e estiveram presentes em um elevado número de parcelas (tabela A1).

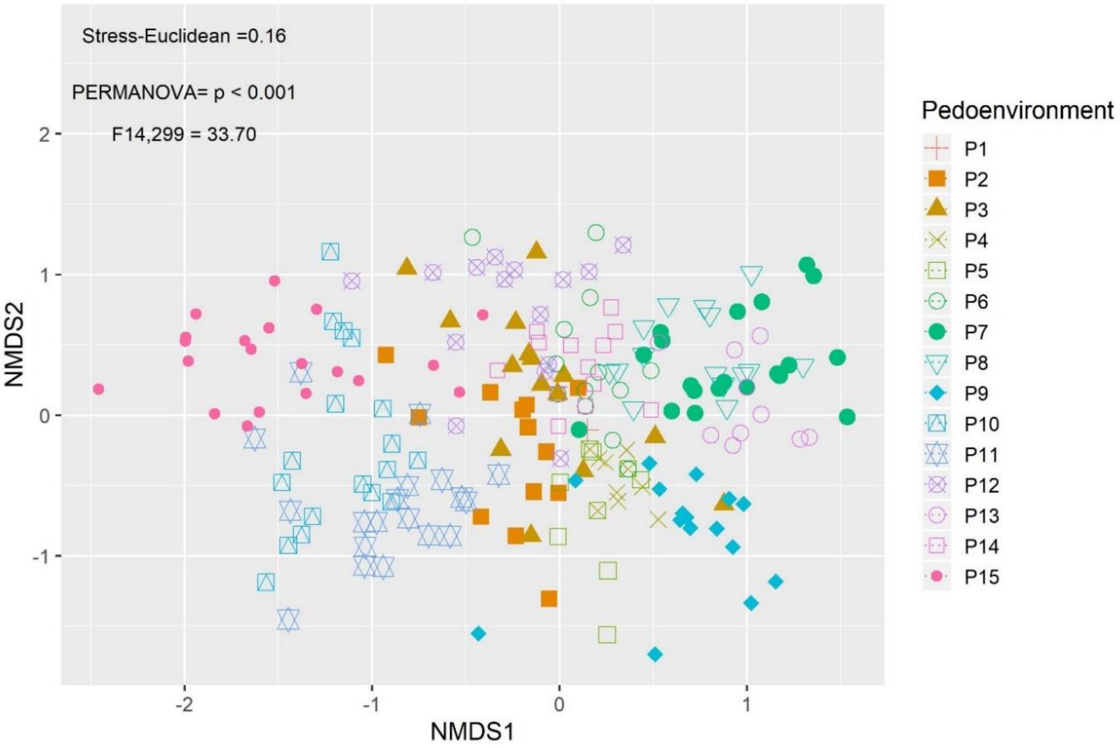

Figura 3. Análise multidimensional escalonado não métrico (NMDS) baseado na composição de espécies de diferentes pedoambientes.

Ainda assim, algumas espécies tiveram sua ocorrência restrita a alguns pedoambientes como pode ser observado na análise de cluster do dendrograma (Fig. 4). Como por exemplo, a espécie de musgo *Andreaea gainii* só ocorreu no P5; a angiosperma *Colobanthus quitensis* teve sua ocorrência registrada apenas nos ambientes P7 e P8, enquanto *Syntrichia magellanica* ocorreu somente em P7; *Hypnum revolutum* foi registrado somente em P6; Ceratodon grossiretis em P9; *Brachythecium* sp somente em

P14; *Leptogium puberulum, Physconia muscigena* e *Placopsis contortuplicata* somente em P15.

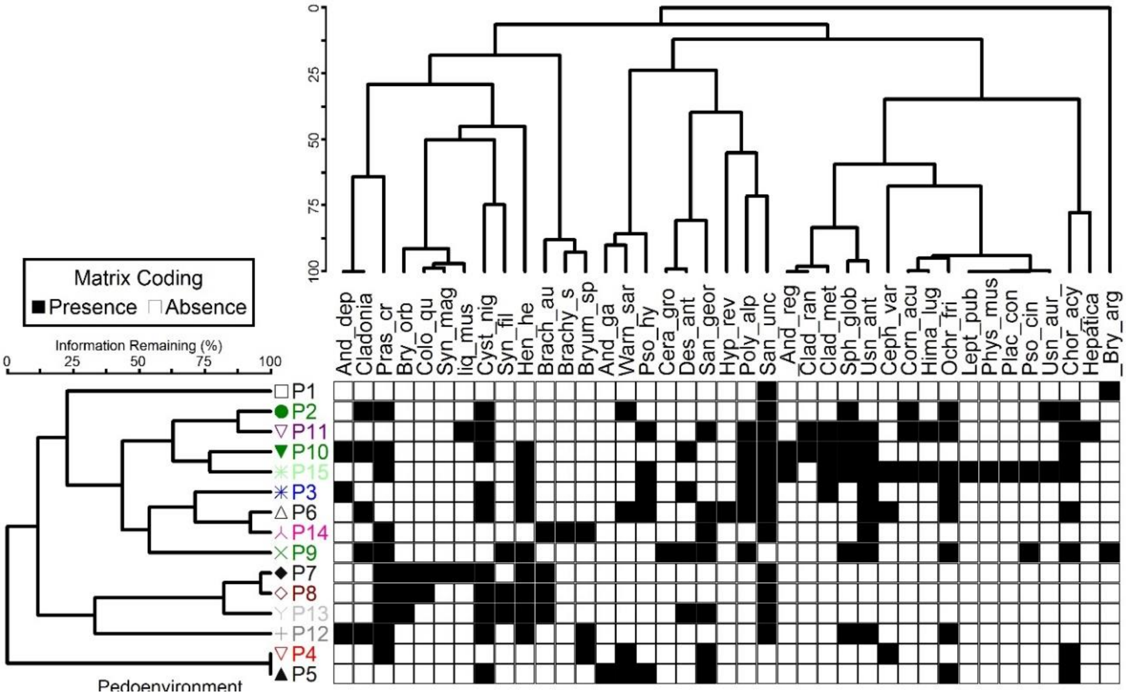

Figura 4. Distribuição de 39 espécies em 300 parcelas de amostras instaladas ao longo de um gradiente pedoambiental por meio de um dendrograma de dois caminhos baseado na distância euclidiana. Os nomes completos das espécies indicam-se na Tabela A.1 do material suplementar.

Índice de Significância Ecológica

Foram observadas diferenças na importância de espécies significativas (IES) entre os pedoambientes. Baseado na cobertura das espécies dominantes foram identificadas seis comunidades vegetais com onze associações distintas: Comunidade de musgos em coxim, com três associações: associação *Bryum-Sanionia* (P1), associação *Bryum-Brachythecium* (P7 e P8), associação *Bryum-Hennediella* (P13); Comunidade turfeira de musgos, com duas associações: associação *Chorisodonthium-Sanionia* (P2), e *Chorisodonthium*-liquens fruticosos (P11); Comunidade carpete de musgos com quatro associações: *Sanionia-Polytrichastrum* (P3), *Warnstorfia-Sanionia* (P4 e P5); *Sanionia* spp (P6), *Sanionia-Brachythecium* (P14); Comunidade fanerógama Antártica: associação

Sanionia-Deschampsia (P9); Comunidade de liquens fruticosos (P15) e associados a *Andreaea regularis* (P10); e comunidade de liquens muscícolas (P12).

Atributos gerais do solo

As propriedades do solo foram contrastantes em todos os pedoambientes, formando um marcado gradiente edáfico (Fig. 5). Os solos variaram de altamente ácidos a alcalinos (4.19-8.18). Os valores de P, variaram de 17.44 a 870.44(mg/dm^3), onde somente P2 e P4 não apresentaram influencia ornitogênica, com baixos níveis de P. As quantidades de matéria orgânica são baixas, exceto para P2 (16.94 dag/kg), P4 (35.39 dag/kg) e P5 (35.39 dag/kg) onde as quantidades representam valores elevados para a Antártica Marítima. O solo é dominado pela fração areia, e a classe textural predominante é franco arenosa, porém silte e argila são elevados em P5, P7, P10, P12 e P13 (tabela A.3). O P4 não pôde ser mensurado devido à alta quantidade de material orgânico presente nas amostras.

Descritores da fertilidade do solo

Um acentuado gradiente nas propriedades físicas e químicas do solo foi observado ao longo do gradiente pedoambiental (Fig. 5). Porém, alguns atributos formaram agrupamentos de pedoambientes (Fig. 6), como pode ser observado para pH, V, Mn, Fe e silte que separou P7, P8, P13 e P15 dos demais pedoambientes. No geral, a maioria dos pedoambientes apresentou altos valores de P Rem, areia grossa e areia fina (P1, P3, P4, P6, P9, P10 e P14). Os dois primeiros eixos da PCA explicaram 54.2% da variação nos dados do solo (Fig 5). O primeiro eixo explicou 29.7% da variação dos dados e esteve positivamente correlacionado com T ($R=0.95$, $p < 0.05$), acidez trocável (Hal, $R=0.89$, $p < 0.05$), Na ($R=0.82$, $p < 0.05$) e argila ($R=0.80$, $p < 0.05$). O segundo eixo da PCA explicou 24.5% da variação dos dados do solo, e esteve positivamente correlacionado com Mn ($R=0.89$, $p < 0.05$), V ($R=0.85$, $p < 0.05$), Fe ($R=0.83$, $p < 0.05$) e silte ($R=0.79$,

$p < 0.05$) e negativamente correlacionado com P Rem (R=-0.59, $p < 0.05$) (Fig. A.2. Material suplementar).

Relação propriedades do solo-vegetação

O primeiro eixo do CCA explicou 21.04% da composição de espécies com diferenças nas propriedades do solo, enquanto o segundo eixo explicou 18.2% (Fig. 6). De acordo com a CCA, a espécie de musgo *Andreae gainii* está relacionada com a matéria orgânica (MO), que condiz com os elevados valores encontrados em P5, único pedoambiente em que essa espécie foi registrada nesse estudo. O mesmo ocorre com *Warnstorfia sarmentosa*, que foi a espécie dominante em P4 e P5, que apresentaram os maiores valores de MO. *Hypnum revolutum* que ocorreu somente em P6, mostrou relação com areia grossa (C_sand), que teve os maiores teores nesse pedoambiente. A CCA também mostrou uma relação entre *Chorisodontium aciphyllum* e sódio (Na), apesar dessa espécie aparecer em vários pedoambientes que tem variados níveis de Na, sua cobertura foi dominante em P2 e P11 (tabela A.2), que apresentaram elevados valores desse atributo (tabela A.3). O liquen fruticoso *Cladonia rangiferina* mostrou relação com os altos níveis de P encontrados em P10 e P11. *Andreaea depressinervis* e *Cladonia* sp foram dominantes em P12 e podem estar relacionadas com os elevados níveis de K encontrados nesse pedoambiente.

Efeitos da fertilidade e textura do solo sobre diversidade

A partir da comparação de modelos entre pedoambientes, encontramos que em geral os preditores fertilidade do solo, textura do solo e propriedades individuais do solo (argila, areia, silte, T, MO, SB) não tiveram efeitos significativos na riqueza de espécies. Pelo contrário, de acordo com o nosso melhor modelo, observaram-se efeitos significativos da variabilidade da fertilidade do solo (LMM: $z = 3.01$, $p < 0.001$), sobre a composição de espécies (Tabela A4).

Figura. 5. Barplots das propriedades do solo. Para análise, foram avaliados: P disponível, K, Ca2+, Na, Mg2+, Fe, Cu, Mn, Zn, Al3+, acidez trocável (H + Al), pH (H2O), matéria orgânica (MO), soma das bases trocáveis (SB); capacidade de troca catiônica efetiva efetiva (t), capacidade de troca catiônica potencial (T), saturação de Al (m), porcentagem de saturação por bases (V), e textura do solo.

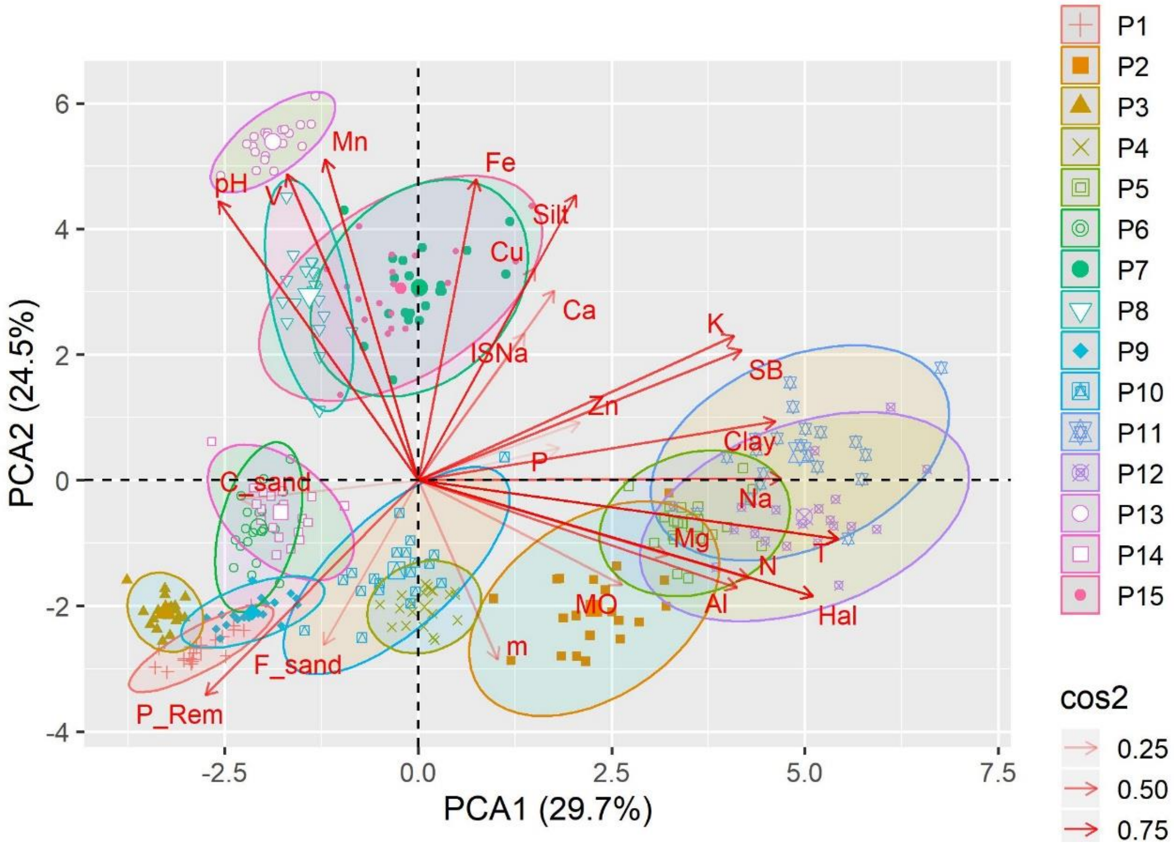

Figura 6. Análise de Componentes Principais (PCA) para os parâmetros de solo de diferentes tipos de sítios pedoambientais. Para análise, foram avaliados: P disponível, K, Ca^{2+}, Na, Mg^{2+}, Fe, Cu, Mn, Zn, Al^{3+}, acidez trocável (H + Al), pH (H2O), matéria orgânica (MO), soma das bases trocáveis (SB); capacidade de troca catiônica efetiva (t), capacidade de troca catiônica potencial (T), saturação de Al (m), porcentagem de saturação por bases (V), e textura do solo.

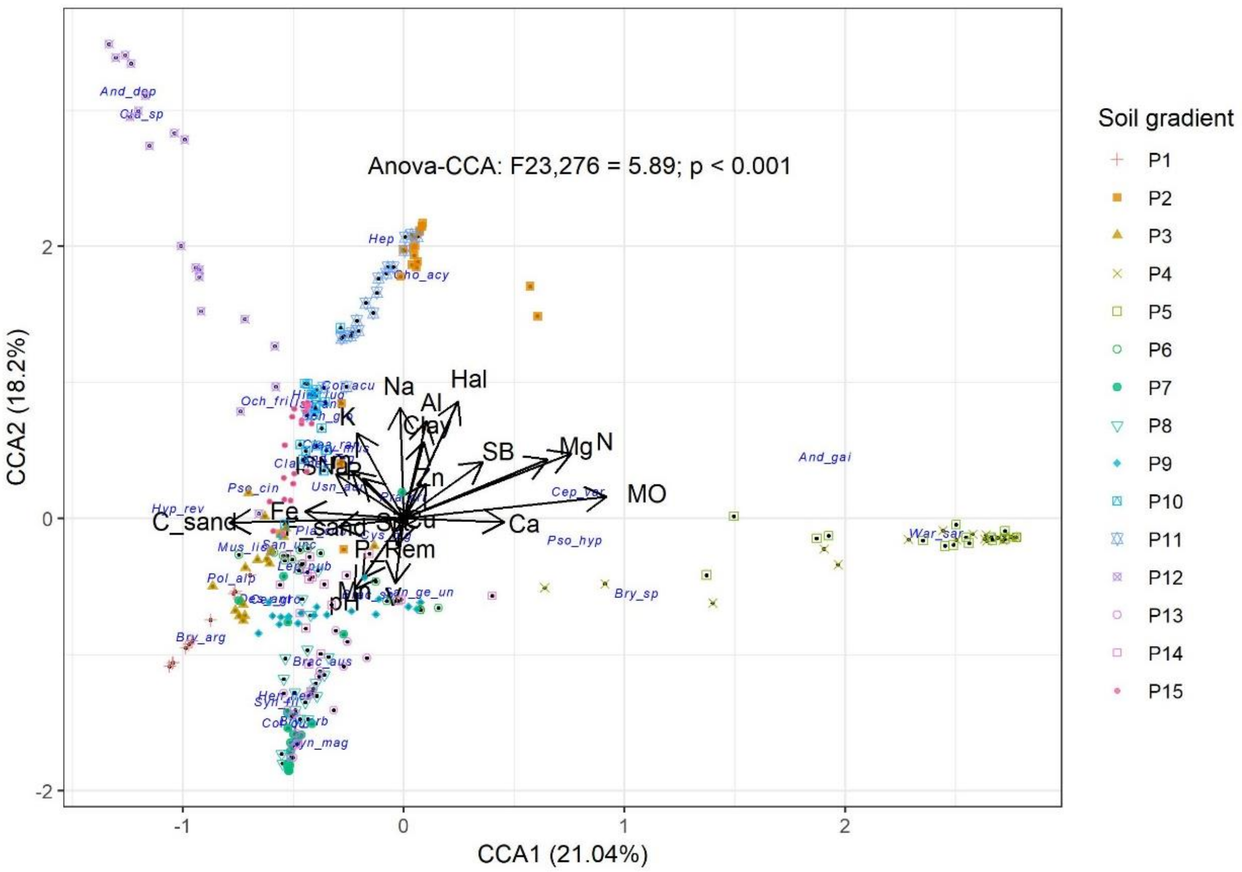

Figura 7. Análise de correspondência canônica (CCA) mostrando os escores de espécies e parcelas em função das propriedades do solo amostradas em diferentes tipos de pedoambientes. Para análise, Zn disponível, capacidade de troca catiônica efetiva (t), acidez permutável (H + Al), pH, matéria orgânica (MO), soma das bases trocáveis (SB); capacidade de troca catiônica efetiva (t), e a textura do solo como areia grossa (Sand_c), areia fina (Sand_t), argila e silte foram incluídos.

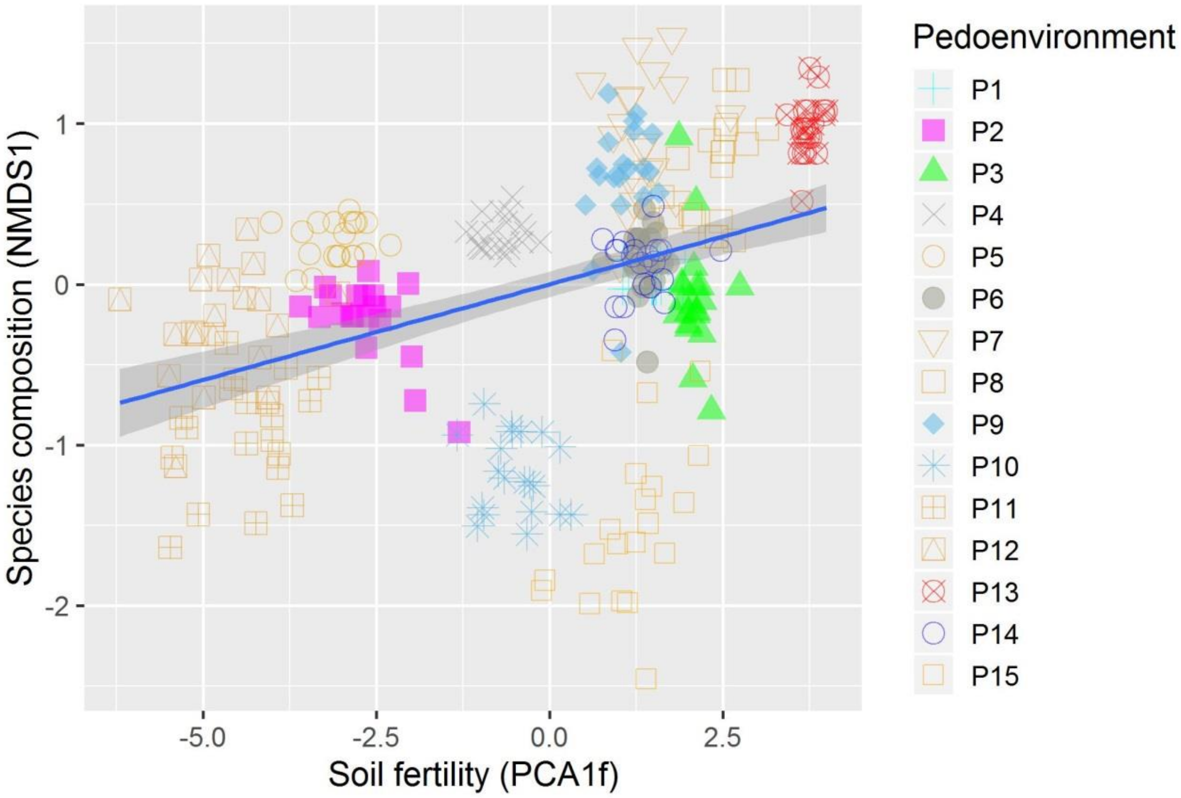

Figura 8. Species composition (NMDS1) and the main predictor's relationship according with GLM approach. The effect soil fertility using PCA1f on species composition. Color fill circles indicate data per treatments. Solid line represent the fitted value (prediction) of the model, and the shaded area the 95 % confidence interval of the predicted value of model.

4. Discussão

O resultado desta pesquisa demonstra que a análise direta do gradiente (CCA) pedoambiental molda variações na diversidade e cobertura das comunidades vegetais da Ilha Elefante. Além disso, nos modelos testados demonstramos os principais efeitos dos diferentes preditores ambientais (textura e fertilidade do solo), que nos permitem demonstrar como a fertilidade do solo tem uma forte influência na variação da composição de espécies ao longo do gradiente pedoambiental, mas não determina diferenças na riqueza. Neste sentido, para explicar os possíveis processos que determinam as variações na composição de espécies, nós descrevemos para cada um dos pedoambientes, a relação da vegetação com as propriedades do solo, principalmente a fertilidade. Simultaneamente, fizemos uma descrição detalhada dos diferentes tipos de associações de espécies que determinam diferentes comunidades vegetais em resposta ao gradiente pedoambiental.

A riqueza de espécies encontrada neste estudo foi inferior ao registrado por Alison & Smith (1973) para a ilha Elefante (80 espécies, destas, 24 foram musgos) e também ao de Pereira & Putzke (1994) em Stinker Point (115 espécies, 38 de musgos), porque foram selecionados pedoambientes representativos e contrastantes necessários para definir um gradiente, e assim testar nossas hipotesis. Porém, em nosso estudo foram identificadas espécies de musgos não relatadas (Putzke & Pereira, 2001; Pereira & Putzke, 2013) para o local, como: *Brachythecium* sp, *Bryum orbiculatifolium, Hypnum revolutum, Sanionia georgicouncinata e Syntrichia magellanica.* As recentes mudanças climáticas documentadas para a região da Península Antártica e Antártica Marítima (Turner et al., 2016) promoveram um aumento das áreas livres de gelo, e assim novas condições para que outras espécies possam colonizar e desenvolver-se (Amesbury et al., 2017). Por outro lado, nós presumimos que apesar da proximidade dos pedoambientes e da pequena variação altitudinal entre eles, este estudo mostrou diferenças na diversidade e na cobertura vegetal, provavelmente devido às diferenças contrastantes dos pedoambientes em fina escala.

Nossos resultados demostraram marcadas diferenças nas propriedades químicas e físicas do solo entre os pedoambientes estudados. O que provavelmente se deve ao fato de estarem sob distintos níveis de influência ornitogênica e também de estarem distribuídos em diferentes formas de relevo e processos de recuo de gelo (Michel et al., 2014; Turner et al., 2016). Os solos da Ilha Elefante estão se formando desde o último recuo glacial, em um clima mais úmido e quente, se comparado à Antártica continental, que favorece o desenvolvimento dos solos (Bockheim, 2015). Estudos recentes investigaram as características geomorfológicas e mapearam oito diferentes formas de relevo periglaciais em Stinker Point, de plataformas marinhas (vales de fundo plano, rochas com fraturas planas, campos de rochas verticais), depósitos de till (solos com padrões, lobos de gelifluxão, e campos de rochas verticais), e rampas (talus de colúvios e cones de detritos) (López-Martínez et al., 2006; 2012; Navas et al., 2018).

De acordo com o mapa proposto por Lopez-Martínez et al., (2012) e Navas et al., (2018) P1, P2, P3, P4, P5, P6, P9, P10, P11, P12 e P14 são plataformas, sendo P10, P11 e P12 encostas ou a borda da plataforma e P7, P8, P13, P15 áreas de acumulação de detritos glaciais recentemente expostas não consolidadas chamadas de morainas. O que pode explicar a grande variação no pH do solo encontrada nesses pedoambientes, que é alcalino nas morainas e apresenta elevada acidez nas plataformas (Navas et al. 2018). Essa diferença marcante corresponde ao tempo de exposição mais recente das morainas, que preservam a maioria das características do material de origem (Navas et al., 2018), que também coincidem com a disposição geográfica mais próxima a glaciares, enquanto que pedoambientes mais próximos a costa tendem a ter maior acidificação, devido ao aumento da atividade da fauna através da mineralização do guano (Tatur e Barczuk, 1985; Simas et al., 2007) e processos de formação do solo agindo por mais tempo (Beyer et al., 2000; Navas et al., 2017; 2018). Da mesma forma, maior conteúdo de matéria orgânica em solos de plataformas está relacionada com a proximidade da costa e consequente maior tempo de exposição, presença de aves marinhas, responsáveis pelo aporte de nutrientes (Beyer et al., 2000) no solo e presença de vegetação (Bockheim & Haus, 2014). Segundo Navas et al. (2018), os variados e elevados valores de P e K presentes não somente na costa mas também nas plataformas intermediárias da Ilha Elefante, estão relacionadas a atividade da fauna, tanto recente quanto a colônias de pinguins abandonadas (Michel et al., 2006; Simas et al., 2007).

O P1 se localiza numa área intermediária da plataforma próxima a uma pequena elevação para o lago, com baixos valores de fertilidade registrados (exceto P) foi o pedoambiente com a menor riqueza de espécies deste estudo (figura 2), formando uma comunidade densa de carpete de musgos com dominância de *Bryum argenteum* (IES=540) associada a *Sanionia uncinata* (IES=115) que só ocorre neste local de Stinker Point (tabela A.2). Os níveis de P podem ser explicados devido à presença de ninhos ativos de petrel gigante (*Macronectes giganteus*) nas partes mais altas, sendo lixiviadas quando ocorre o derretimento do depósito de neve, o que também pode explicar a acidez do solo (Simas et al., 2007). Ao contrário deste, o P2 apresentou maior fertilidade, elevada MO e maiores valores de Mg, porem baixos níveis de P. Localizada na área central da plataforma, em campos de rochas verticais, tem como fitofisionomia uma comunidade densa de turfeira de musgos com predominância de *Chorisodontium acyphillum* (IES=503.5) associada a *Sanionia uncinata* (IES=99) e com a presença do líquen muscícola *Cystocoleus niger* (IES=195.5) crescendo sobre ambos. Outras espécies também aparecem nessa comunidade, porém com baixa frequência e IES<50. O P3 é próximo a P1 e P2, e semelhante a P1, possui textura arenosa, baixa fertilidade (com exceção de P), com os menores valores registrados para Na, Ca e micronutrientes (Figura 4), porém com menor cobertura vegetal, maior riqueza (dez espécies) e formando uma comunidade de carpete de musgos com dominância de *S. uncinata* (IES=258.75) associada a *Polytrichastrum alpinum* (IES=115.5) e com a presença da gramínea *Deschampsia antarctica* (75.25).

O P4 e P5 são pedoambientes localizados em lados opostos da linha de drenagem que corta a área de Stinker Point, são frequentemente encharcados e possuem quantidades altas e semelhantes de MO (~35.5 dag/kg), porém os outros atributos químicos são muito discrepantes (tabela A.3). No entanto, a cobertura, riqueza (Figura 2) e composição de espécies (Figura 4) são muito semelhantes, ambos se tratam de uma comunidade carpete de musgos com predominância de *Warnstorfia sarmentosa* (tabela 1). Em P4, a mesma faz associação com a alga *Prasiola crispa* (tabela A.2) e em P5 com o musgo *Sanionia georgicouncinata*. Em nossa CCA (fig. 7), *W. sarmentosa* mostrou relação com matéria orgânica e Putzke & Pereira (2001) e Ochyra et al. (2008) afirmam que essa é uma espécie tipicamente hidrófila, crescendo em habitats constantemente molhados. No entanto, *P. crispa* é comumente associada a ambientes ornitogênicos (Kovacik & Pereira, 2001), o que não se aplica neste caso, pois os níveis de P nesse pedoambiente são os menores encontrados neste estudo (fig. 5).

O P6 é a única comunidade de carpete de musgos com dominância exclusiva de *Sanionia* spp. Apesar de outras dez espécies de musgos e liquens terem sido identificadas no local, somente *S. uncinata* (IES=303.75) e *S. georgicouncinata* (IES=231) obtiveram IES>50. Os níveis de P tiveram grande variação entre as parcelas até mesmo dentro do próprio pedoambiente, mas no geral foram elevados (498.13±313.52 mg/dm^3), essa elevação em alguns pontos pode ser devido a presença de ninhos abandonados (Francelino et al., 2011; Moura et al., 2012), mas que aparentemente não tenham modificado a vegetação, ou pela entrada de nutrientes trazidos pela água de degelo de locais próximos mais elevados (Sørensen et al., 2017). Apesar da baixa frequência, foi o único pedoambiente que registrou a presença do musgo *Hypnum revolutum,* que em nossa PCA se mostrou relacionada com areia grossa, que mostrou as maiores porcentagens para esse local. Assim estudos prévios encontraram comunidades dominadas por essa espécie próximas a linhas de drenagem ou áreas de acúmulo de neve (e.x., Bartak et al., 2005).

P7 e P8 são áreas muito próximas, localizadas em um terraço marinho elevado próximo a praia, acima de uma área de colônia de pinguins ativa. São os pedoambientes com as menores coberturas desse estudo, onde a vegetação é mais escassa (fig. 2B), e a riqueza e composição de espécies são muito semelhantes (fig 2A e fig 4). Ambos se tratam de comunidades de musgos em coxim, com dominância de *Bryum orbiculatifolium* associado a *Brachythecium austrosalebrosum*. Foram os únicos pedoambientes deste estudo que registraram, apesar de com baixa frequência, a presença da angiosperma *Colobanthus quitensis*, que em nossa CCA apresentou relação com o pH (5.8) e Mn (que variou entre 32 e 36mg/dm) porém segundo Parnikoza et al., (2007) pode habitar locais com uma grande amplitude ecológica. O P7 teve o registro do musgo *Syntrichia magellanica*, que só apareceu neste pedoambiente, podendo estar relacionado aos elevados níveis de Ca^{2+} e SB (Fig. 5), que foram os mais elevados deste estudo e os únicos que se diferenciaram notavelmente de P8. Segundo Ochyra et al. (2008), esse musgo cresce em uma gama de habitats, entre eles substratos ácido e ricos em bases, em rochas e solos arenosos e siltosos e sobre morainas, e ainda próximo a colônias de aves. Por outro lado, o P9 é uma comunidade fanerogâmica de *Deschampsia antarctica* (IES=369) associada ao musgo *S. uncinata* com a presença da alga *P. crispa.* Essa área se localiza em um declive suave, próximo ao lago, que é frequentemente visitada por skuas (*Stercorarius antarcticus*), e onde muitas delas acabam permanecendo, pois tem preferência de nidificação em locais secos junto a pequenos lagos (Quintana & Travaini, 2000), e acabam assim promovendo a entrada de nutrientes nesse ambiente.

Em relação ao P10, é uma área próxima a encosta da plataforma, com forte influência ornitogênica passada e atualmente se localiza próximo a ninhos de petréis gigantes, apresentou os maiores registros de P (870.44

Myrcha, 1993). Tem uma diversa composição de espécies e forma uma comunidade de liquens fruticosos com a dominância de *Sphaerophorus globosus* e *Usnea aurantiacoatra* associados ao musgo *Andreaea depressinervis*. Outras espécies como *Cladonia rangiferina*, a alga *P. crispa*, *S. uncinata e C. aciphyllum* apresentaram alto IES e são comumente associadas a *S. globosus* (Øvstedal & Lewis Smith, 2001; Olech, 2004). *C. rangiferina* foi identificado somente em P10 e P11, que tem características muito semelhantes no que se refere a fertilidade do solo e posição na paisagem. A composição das espécies é semelhante, porém se diferencia quanto à dominância, sendo P11 uma comunidade de turfeira de musgos *C. aciphyllum* associada a liquens fruticosos *como S. globosus*, *U. antarctica*, *Cornicularia aculeata* e *Himantormia lugubris.* Apesar das turfeiras de musgos estarem comumente associadas a *Polytrichum alpestre* (Longton, 1988; Putzke & Pereira, 2001) ou *P. strictum* (Ochyra et al., 2008) isso não ocorre nesse pedoambiente, somente *Polytrichastrum alpinum* está presente, porém com baixa frequência (IES<50). A CCA sugeriu uma relação entre *C. acyphillum* e Na, que teve os níveis elevados nesse pedoambiente, provavelmente devido à proximidade e exposição ao mar.

O P12 apresentou cobertura vegetal inferior a 60% (fig. 2B) devido à grande quantidade de rochas no local. É formada por uma comunidade liquens muscícolas *(Cladonia sp., Cystocoleus niger e Ochrolechia frigida*) que crescem sobre *Andreaea depressinervis* (IES=300) e *S. uncinata* (IES=165). Possui os solos mais ácidos, e com os maiores valores de K, Na, Al^{3+}, acidez trocável (H + Al) e capacidade de troca catiônica a pH 7 (T), está localizado em uma área adjacente a uma pinguineira atual e provavelmente se trata de uma pinguineira abandonada, próximo a encosta da plataforma. Seus elevados valores de Na, são influenciados pelos spray salino transportado pelos ventos de fonte marinha (Michel et al., 2006). Os nutrientes provenientes do guano são trazidos às áreas próximas através de mecanismos de redistribuição, como erosão eólica ou nival (Simas et al., 2004), o que propicia o desenvolvimento de espécies ornitocoprófilas (Longton, 1988), como a *P. crispa*, muito frequente nesse pedoambiente.

O P13 é uma área recentemente exposta, devido ao recuo glaciar, moderadamente drenada, próxima de vários lagos formados pela água de degelo. Esses lagos são frequentemente usados por skuas e muitas depositam o seu regurgito nas proximidades lagos (Quintana & Travaini, 2000), o que pode ser o passo inicial para a entrada de esporos e nutrientes nesses ambientes. O que corrobora com os consideráveis níveis de P, K e Ca^{2+} encontrados na área. Os solos são alcalinos (pH 8.18) e com os menores níveis de acidez trocável desse estudo, enquanto os de Fe (569.04mg/dm) foram os maiores. A vegetação tem cobertura abaixo de 60% (fig. 2B) pois ainda é esparsa, formada por uma comunidade de musgos em coxim, associação *Bryum orbiculatifolium-Hennediella heimmi*, ainda conta com a presença de mais setes espécies (tabela X), que se assemelham as encontradas em P7 e P8 (fig. 4).

O P14 é uma densa comunidade de carpete de musgos, associação *S. uncinata-Brachythecium austrosalebrosum,* localizada próxima ao córrego que corta a plataforma, é uma área parcialmente encharcada, o que promove a alta cobertura vegetal desse pedoambiente, uma vez que *B. austrosalebrosum* é um musgo hidrofílico e cresce em solo arenoso às margens de canais de água derretida (Ochyra et al., 2008). *Bryum* sp também foi registrado com significância ecológica (143.5), além de outras três espécies de musgos e a alga *P. crispa*, porem com baixa frequência (IES<50).

Finalmente, o P15 foi o pedoambiente que mostrou maior riqueza de espécies. Este pedoambiente localiza-se numa pequena elevação sobre uma moraina, e apesar de apresentar alta fertilidade, com elevados níveis de P, sugerindo influência ornitogênica, não foram observados ninhos atuais, e o pH ficou em torno de 6.4. Embora apresente a dominância de *S. uncinta* (IES=360), essa formação foi classificada como comunidade de liquens fruticosos, pois nesse caso, a mesma serve como substrato para o desenvolvimento de *S. globosus*, *U. antarctica*, *O. frigida*, *Psoroma cinnamomeum*, *C. aculeata* e *H. lugrubis*, além de outras espécies de musgos e liquens que estiveram presentes, porem com baixo IES (>50). *H. lugrubis* só foi encontrada em P11 e P15 e a CCA sugeriu uma relação com os altos níveis de K encontrados nesses pedoambientes. Choi et al. (2015) demonstraram que os principais fatores que influenciam na distribuição e desenvolvimento dessa espécie foram o tipo do substrato e a umidade da superfície do solo.

5. Conclusão

Houve diferenças na diversidade e na cobertura vegetal ao longo de um gradiente pedoambiental na Ilha Elefante. No entanto, os modelos avaliados mostraram que só a fertilidade do solo tem efeitos significativos sobre a composição de espécies, mas não houve efeitos sobre riqueza de espécies não vasculares. Portanto, a variabilidade da fertilidade do solo foi o principal preditor com efeito significativo nestas comunidades vegetais composição das espécies, mas não na riqueza de espécies ao nível da comunidade. Além disso, diferenças na composição de espécies não foram tão acentuadas quanto o esperado, mostrando altos graus de similaridade entre diferentes pedoambientes. Dessa forma, assumimos que a filtragem pedoambiental determinou diferenças na composição de espécies nesta ilha da Antártida marítima. Por outro lado, este estudo revelou que a heterogeneidade em escala fina contribuiu para associações típicas de espécies não vasculares ao longo do gradiente pedoambiental; assim, a filtragem do solo não apenas determinou os padrões de diversidade, mas também os tipos de comunidades.

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Material Suplementar

Tabela A.1. Lista de espécies identificadas na área de estudo

Family	Group	Species	Abrev	N. of plots*
Caryophyllaceae	angiosperm	*Colobanthus quitensis* (Kunth) Bartl.	Col_qui	7
Poaceae	angiosperm	*Deschampsia antarctica* Desv.	Des_ant	27
Amblystegiaceae	moss	*Sanionia georgicouncinata* (Müll. Hal.) Ochyra & Hedenäs	San_geo	82
	moss	*Sanionia uncinata* (Hedw.) Loeske	San_unc	139
	moss	*Warnstorfia sarmentosa* (Wahlenb.) Hedenäs	War_sar	44
Andreaeaceae	moss	*Andreaea depressinervis* Cardot	And_dep	23
	moss	*Andreaea gainii* Cardot	And_gai	1
	moss	*Andreaea regularis* Müll. Hal.	And_reg	20
Brachytheciaceae	moss	*Brachythecium austrosalebrosum* (Müll. Hal.) Kindb.	Bra_aus	53
	moss	*Brachythecium* sp. Schimp.	Bra_sp	2
Bryaceae	moss	*Bryum argenteum* Hedw.	Bry_arg	22
	moss	*Bryum orbiculatifolium* Card. Et Brothv	Bry_orb	59
	moss	*Bryum* sp Hedw.	Bry_sp	22
	moss	*Pohlia cruda* (Hedw.) Lindb.	Poh_cru	
Ditrichaceae	moss	*Ceratodon grossiretis Cardot*	Cer_gro	8
Dicranaceae	moss	*Chorisodontium aciphyllum* (Hook. f. & Wilson) Broth.	Cho_aci	61
Pottiaceae	moss	*Hennediella heimii* (Hedw.) R.H. Zander	Hen_hei	57
	moss	*Syntrichia filaris* (Müll. Hal.) R.H. Zander	Syn_fil	15
	moss	*Syntrichia magellanica* (Mont.) R.H. Zander	Syn_mag	12
Hypnaceae	moss	*Hypnum revolutum* (Mitt.) Lindb	Hyp_rev	1
Polytrichaceae	moss	*Polytrichastrum alpinum* (Hedw.) G.L. Sm.	Pol_alp	30
Cephaloziellaceae	liverwort	*Cephaloziella varians* (Gottsche) Steph.	Cep_var	3
Cladoniaceae	lichen	*Cladonia metacorallifera* Asahina	Cla_met	27
	lichen	*Cladonia rangiferina* (L.) Weber ex F.H. Wigg.	Cla_ran	14
	lichen	*Cladonia* (sp.) P. Browne	Cla_sp	25
Collemataceae	lichen	*Leptogium puberulum* Hue	Lep_pub	1
Not defined	lichen	*Cystocoleus niger (*Huds.) Har.	Cys_nig	72
Ochrolechiaceae	lichen	*Ochrolechia frigida* (Sw.) Lynge	Och_fri	37
Pannariaceae	lichen	*Psoroma cinnamomeum* Malme	Pso_cin	14
	lichen	*Psoroma hypnorum* (Vahl) Gray	Pso_hyp	18
Parmeliaceae	lichen	*Cornicularia aculeata* (Schreb.) Ach	Cor_acu	31

	lichen	*Himantormia lugubris* (Hue) I.M. Lamb	Him_lug	21
	lichen	*Usnea antarctica* Du Rietz	Usn_ant	71
	lichen	*Usnea aurantiacoatra* (Jacq.) Bory	Usn_aur	10
Physciaceae	lichen	*Physconia muscigena* (Ach.) Poelt	Phy_mus	1
Sphaerophoraceae	lichen	*Sphaerophorus globosus* (Huds.) Vain.	Sph_glo	63
Trapeliaceae	lichen	*Placopsis contortuplicata* I.M. Lamb	Pla_con	3
Prasiolaceae	algae	*Prasiola crispa* (Lightfoot) Kützing	Pra_cri	78

Table A.2. Where: F = relative frequency of the species; C = coverage*; ESI = Ecological Significance Index **.

Pedoenvironment	Species	F	C	ESI
P1	*Bryum argenteum*	100	4.4	540
P1	*Sanionia uncinata*	50	1.3	115
P2	*Chorisodontium aciphyllum*	95	4.3	503.5
P2	*Cystocoleus niger*	85	1.3	195.5
P2	*Sanionia uncinata*	45	1.2	99
P2	*Usnea aurantiacoatra*	30	0.3	39
P2	*Warnstorfia sarmentosa*	20	0.3	26
P2	*Ochrolechia frigida*	20	0.2	24
P2	*Cornicularia aculeata*	15	0.15	17.25
P2	*Prasiola crispa*	15	0.15	17.25
P2	*Sphaerophorus globosus*	15	0.15	17.25
P2	*Cladonia* sp	10	0.1	11
P3	*Sanionia uncinata*	75	2.45	258.75
P3	*Polytrichastrum alpinum*	55	1.1	115.5
P3	*Deschampsia antarctica*	35	1.15	75.25
P3	*Cladonia metacoraliphera*	30	0.3	39
P3	*Hennediella heimii*	30	0.3	39
P3	*Psoroma hypnorum*	25	0.35	33.75
P3	*Ochrolechia frigida*	20	0.35	33.75
P3	*Usnea antarctica*	20	0.2	24
P3	*Andreaea depressinervis*	5	0.1	5.5
P3	*Cystocoleus niger*	5	0.1	5.5
P4	*Warnstorfia sarmentosa*	95	4.25	498.75
P4	*Prasiola crispa*	70	0.75	122.5
P4	*Sanionia georgicouncinata*	35	1	70
P4	*Bryum sp*	35	0.65	57.75
P4	*Cephaloziella varians*	5	0.05	5.25
P4	*Chorisodontium aciphyllum*	5	0.05	5.25
P5	*Warnstorfia sarmentosa*	100	4.65	565
P5	*Sanionia georgicouncinata*	55	0.8	99
P5	*Cystocoleus niger*	25	0.25	31.25
P5	*Chorisodontium aciphyllum*	25	0.25	31.25
P5	*Psoroma hypnorum*	15	0.3	19.5
P5	*Andreaea gainii*	5	0.05	5.25
P5	*Ochrolechia frigida*	5	0.05	5.25
P6	*Sanionia uncinata*	75	3.05	303.75
P6	*Sanionia georgicouncinata*	70	2.3	231
P6	*Cystocoleus niger*	30	0.45	43.5
P6	*Hennediella hemii*	20	0.2	24
P6	*Psoroma hypnorum*	20	0.2	24
P6	*Polytrichastrum alpinum*	10	0.1	12

P6	*Cladonia* sp	10	0.1	11
P6	*Chorisodontium aciphyllum*	5	0.05	5.25
P6	*Hypnum revolutum*	5	0.05	5.25
P6	*Ochrolechia frigida*	5	0.05	5.25
P6	*Usnea antarctica*	5	0.05	5.25
P6	*Warnstorfia sarmentosa*	5	0.05	5.25
P7	*Bryum orbiculatifolium*	90	2.95	355.5
P7	*Brachythecium austrosalebrosum*	75	0.85	138.75
P7	*Syntrichia magellanica*	60	0.7	102
P7	*Hennediella heimii*	50	0.5	75
P7	*Sanionia uncinata*	35	0.65	57.75
P7	*Prasiola crispa*	30	0.5	45
P7	*Colobanthus quitensis*	30	0.35	0.5
P7	*Cystocoleus niger*	25	0.3	32.5
P7	Liquen muscicola	5	0.2	6
P8	*Bryum orbiculatifolium*	85	2.05	259.25
P8	*Cystocoleus niger*	75	1.15	161.25
P8	*Brachythecium austrosalebrosum*	65	1.15	139.75
P8	*Sanionia uncinata*	50	0.9	95
P8	*Syntrichia filaris*	50	0.65	82.5
P8	*Prasiola crispa*	25	0.3	32.5
P8	*Hennediella heimii*	25	0.25	31.25
P8	*Colobanthus quitensis*	5	0.05	5.25
P9	*Sanionia uncinata*	100	3.15	415
P9	*Deschampsia antarctica*	90	3.1	369
P9	*Prasiola crispa*	60	3.1	369
P9	*Ceratodon grossiretis*	40	0.4	56
P9	*Polytrichastrum alpinum*	40	0.4	56
P9	*Hennediella heimii*	15	0.45	21.75
P9	*Chorisodontium aciphyllum*	15	0.15	17.25
P9	*Syntrichia filaris*	15	0.15	17.25
P9	*Bryum argenteum*	10	0.1	11
P9	*Cladonia sp*	10	0.1	11
P9	*Sphaerophorus globosus*	5	0.1	5.5
P9	*Ochrolechia frigida*	5	0.05	5.25
P9	*Psoroma cinnamomeum*	5	0.05	5.25
P9	*Usnea antarctica*	5	0.05	5.25
P10	*Sphaerophorus globosus*	100	3	400
P10	*Andreaea depressinervis*	90	1.65	238.5
P10	*Usnea antarctica*	85	1.4	204
P10	*Cladonia rangiferina*	60	0.7	102
P10	*Prasiola crispa*	60	0.65	99
P10	*Sanionia uncinata*	50	0.8	90
P10	*Chorisodontium aciphyllum*	40	0.5	60

P10	*Cladonia metacoraliphera*	40	0.5	60
P10	*Cystocoleus niger*	30	0.35	40.5
P10	*Polytrichastrum alpinum*	10	0.15	11.5
P10	*Andreaea regularis*	10	0.1	11
P10	*Hennediella heimii*	10	0.1	11
P10	*Cladonia sp*	5	0.05	5.25
P10	*Deschampsia antarctica*	5	0.05	5.25
P11	*Chorisodontium aciphyllum*	95	3.4	418
P11	*Sphaerophorus globosus*	95	2.25	308.75
P11	*Usnea antarctica*	85	1.3	195.5
P11	*Cornicularia aculeata*	80	0.8	144
P11	*Himantormia lugubris*	45	0.45	65.25
P11	*Cystocoleus niger*	35	0.4	49
P11	*Ochrolechia frigida*	35	0.35	47.25
P11	*Cladonia metacoraliphera*	30	0.3	39
P11	Liquen não id	20	0.25	25
P11	*Sanionia uncinata*	20	0.25	25
P11	*Sanionia georgico uncinata*	20	0.25	25
P11	*Cladonia rangiferina*	10	0.1	11
P11	*Hepática*	5	0.05	5.25
P11	*Polytrichastrum alpinum*	5	0.05	5.25
P11	*Psoroma hypnorum*	5	0.05	5.25
P12	*Andreaea depressinervis*	100	2	300
P12	*Cladonia sp*	90	1.55	229.5
P12	*Sanionia uncinata*	75	1.2	165
P12	*Prasiola crispa*	85	0.85	157.25
P12	*Usnea antarctica*	40	0.45	58
P12	*Cystocoleus niger*	25	0.25	31.25
P12	*Ochrolechia frigida*	25	0.25	31.25
P12	*Hennediella heimii*	10	0.1	11
P12	*Sphaerophorus globosus*	10	0.1	11
P12	*Bryum sp*	5	0.05	5.25
P13	*Bryum orbiculatifolium*	100	1.91	291.66
P13	*Hennediella heimii*	95.83	1.75	263.54
P13	*Sanionia georgicouncinata*	91.83	1.25	206.25
P13	*Brachythecium austrosalebrosum*	45.83	0.91	87.84
P13	*Prasiola crispa*	25	0.41	35.41
P13	*Sanionia uncinata*	25	0.41	35.41
P13	*Cystocoleus niger*	20.83	0.20	25.71
P13	*Syntrichia filaris*	8.33	0.08	9.02
P13	*Deschampsia antarctica*	4.16	0.04	4.34
P14	*Sanionia uncinata*	90	3.45	400.5
P14	*Brachythecium austrosalebrosum*	70	1.9	203
P14	*Bryum* sp	70	1.05	143.5

P14	*Warnstorfia sarmentosa*	30	0.4	42
P14	*Sanionia georgicouncinata*	20	0.85	37
P14	*Brachythecium sp*	10	0.15	11.5
P14	*Prasiola crispa*	10	0.1	11
P15	*Sanionia uncinata*	360	2.6	360
P15	*Sphaerophorus globosus*	90	2.25	292.5
P15	*Usnea antarctica*	85	1.8	238
P15	*Ochrolechia frigida*	70	0.7	119
P15	*Psoroma cinnamomeum*	65	0.75	113.75
P15	*Cornicularia aculeata*	60	0.75	105
P15	*Himantormia lugrubis*	60	0.6	96
P15	*Cladonia metacoraliphera*	35	0.35	47.25
P15	*Polytrichastrum alpinum*	30	0.5	45
P15	*Chorisodontium aciphyllum*	25	0.25	31.25
P15	*Psoroma hypnorum*	25	0.25	31.25
P15	*Usnea aurantiacoatra*	20	0.4	28
P15	*Placopsis contortuplicata*	15	0.15	17.25
P15	*Andreaea regularis*	10	0.1	11
P15	*Hennediella heimii*	10	0.1	11
P15	*Cephaloziella varians*	5	0.05	5.25
P15	*Leptogium puberulum*	5	0.05	5.25
P15	*Physconia muscigena*	5	0.05	5.25
P15	*Prasiola crispa*	5	0.05	5.25

Table A.3. Mean of soil chemical atributes of the 15 sampled pedoenvironments of Stinker Point, Elephant Island, Maritime Antarctica.

	P1	P2	P3	P4	P5	P6	P7	P8	P9	P10	P11	P12	P13	P14	P15
pH H_2O	4.81±0.09	4.58±0.14	5.33±0.10	4.90±0.18	4.63±0.05	5.27±0.12	5.81±0.54	5.86±0.93	4.92±0.12	4.79±0.10	4.46±0.06	4.19±0.23	8.18±0.07	5.37±0.41	6.39±0.42
P (mg/dm^3)	403.02±238.3	52.38±25.1	265.61±63.3	17.44±6.02	520.08±426.35	498.13±311.52	252.49±59.55	290.04±53.62	283.34±225.12	870.44±635.89	858.08±265.69	612.06±114.48	290±25.77	235.07±16.14	583.40±84.57
K (mg/dm^3)	21.78±4.1	76.68±15.69	25.83±5.01	31.24±3.66	69.09±20.77	46.82±6.20	106.56±16.69	96.56±19.56	29.55±2.81	69.83±15.92	210.21±26.29	258.59±39.77	122.06±23.62	41.97±7.24	125.89±40.61
Na (mg/dm^3)	36.82±11.2	190.88±82.9	33.96±3.91	57.89±6.06	113.18±22.39	38.67±5.92	62.59±7.24	65.29±6.03	41.60±3.54	86.32±23.37	308.29±73.06	315.13±138.34	40.39±1.54	34.57±2.41	129.84±69.28
Ca^{2+} (cmol$_c$/dm^3)	0.65±0.19	2.47±0.96	0.63±0.14	2.71±0.46	3.10±0.46	0.68±0.08	4.39±0.63	2.23±0.16	1.37±0.52	1.51±0.27	1.98±0.79	1.18±0.84	2.86±0.33	0.78±0.18	2.34±0.77
Mg^{2+} (cmol$_c$/dm^3)	0.22±0.03	1.41±0.17	0.31±0,05	1.02±0.14	1.15±0.23	0.25±0.03	0.67±0.14	0.50±0.04	0.52±0.15	0.65±0.15	0.73±0.23	0.48±0.24	0.22±0.02	0.36±0.08	0.56±0.11
Al^{3+}	0.26±0.04	0.68±0.2	0.12±0.07	0.24±0.07	0.78±0.11	0.40±0.15	0	0	0.22±0.03	0.51±0.14	0.96±0.66	1.44±0.62	0	0.39±0.21	0.27±0.03
H + Al (cmol$_c$/dm)	3.53±0.7	11.08±0.9	2.01±0.5	5.93±1.31	9.94±0.72	2.74±0.24	2.63±0.83	1.45±0.76	4.02±0.84	6.35±0.87	15.19±2.74	16.28±3.16	0.04±0.03	3.12±0.59	3.02±1.25
SB (cmol$_c$/dm)	1.02±0.31	4.91±1.58	1.16±0.18	4.12±0.43	4.66±0.64	1.21±0.11	5.76±0.60	3.21±0.21	2.06±0.65	2.72±0.42	4.85±1.0	5.02±1.54	3.66±0.35	1.40±0.25	3.75±0.98
T (cmol$_c$/dm)	4.55±0.8	16.0±1.8	3.18±0.59	10.05±1.44	14.60±0.99	3.95±0.22	8.39±1.09	4.66±0.79	6.09±1.04	9.08±1.02	20.05±3.05	21.31±3.11	3.71±0.34	4.52±0.64	6.77±1.74
V (%)	24.54±2.2	30.95±4.96	36.20±4.32	44.19±3.66	32.81±3.32	31.00±3.40	68.69±6.77	71.84±12.80	32.10±3.91	30.28±2.18	23.63±4.13	22.36±8.86	98.96±1.43	30.60±6.14	62.43±9.01
m (%)	19.31±3.32	12.87±5.36	12.05±3.91	5.49±1.23	12.34±2.65	24.81±9.46	0	0	10.99±3.3	16.19±7.56	19.11±10.66	27.88±12.87	0	27.92±7.83	10.51±1.23
ISNa	3.55±0.53	4.54±2.12	4.60±0.78	2.79±0.42	3.55±0.61	4.21±0.74	3.12±0.92	6.32±1.55	3.74±0.90	3.56±0.89	6.09±0.75	6.51±1.96	4.98±0.60	3.57±0.67	8.18±2.74
OM (dag/kg)	1.87±0.4	16.94±5.43	1.25±0.14	35.39±5.95	35.67±13.81	0.82±0.10	4.81±1.67	1.47±0.95	2.75±0.64	4.34±1.36	9.15±4.07	6.94±3.76	0.44±0.11	1.49±0.82	1.17±0.52
P Rem (mg/L)	59.19±7.9	50.58±2.97	58.07±2.14	61.28±5.91	40.60±2.88	52.58±0.89	45.03±3.83	47.58±1.79	54.68±1.72	51.42±3.36	40.52±3.23	45.53±3.81	39.87±0.99	46.44±2.24	47.36±3.49
Cu (mg/dm)	2.77±1.5	2.25±1.08	1.41±0.73	3.91±0.47	15.42±5.93	12.72±4.73	10.03±2.56	10.66±1.31	3.76±2.29	8.50±4.37	11.96±2.29	10.81±4.55	13.91±0.91	12.51±2.39	17.89±9.47
Mn (mg/dm)	2.13±0.7	4.8±2.32	1.63±0.13	2.51±0.51	5.29±0.61	3.81±0.99	32.0±8.44	36.03±12.23	1.98±0.39	1.22±1.20	2.01±0.52	2.01±1.54	45.05±3.36	6.67±2.58	22.77±8.56
Fe (mg/dm)	148.26±30.9	161.33±58.8	94.31±15.43	40.67±11.41	135.02±68.74	350.57±111.39	434.44±49.52	465.44±45.31	97.17±22.40	235.51±121.35	406.32±41.17	405.23±81.85	569.04±45.61	268.64±31.64	489.77±70.93
Zn (mg/dm)	2.75±1.61	2.35±0.49	1.77±0.96	2.66±0.32	6.92±1.43	4.85±1.99	3.74±0.25	4.68±0.55	3.95±2.23	8.61±5.42	10.76±5.17	3.08±2.26	4.84±0.67	2.31±0.52	4.04±0.90
N (dag/kg)	0.07±0.02	0.68±0.07	0.04±0.0	0.82±0.09	0.97±0.28	0.03±0.00	0.24±0.10	0.07±0.04	0.11±0.02	0.17±0.04	0.56±0.12	0.66±0.34	0.01±0.0	0.05±0.02	0.06±0.03
Course sand (%)	0.59±0.04	0.52±0.02	0.61±0.05	NA	0.28±0.02	0.68±0.04	0.40±0.08	0.47±0.04	0.57±0.04	0.59±0.02	0.40±0.13	0.46±0.07	0.46±0.10	0.62±0.08	0.55±0.06
Fine sand (%)	0.37±0.04	0.28±0.02	0.33±0.05	NA	0.27±0.01	0.16±0.04	0.18±0.02	0.17±0.03	0.34±0.03	0.28±0.02	0.15±0.01	0.13±0.01	0.10±0.01	0.11±0.04	0.11±0.01

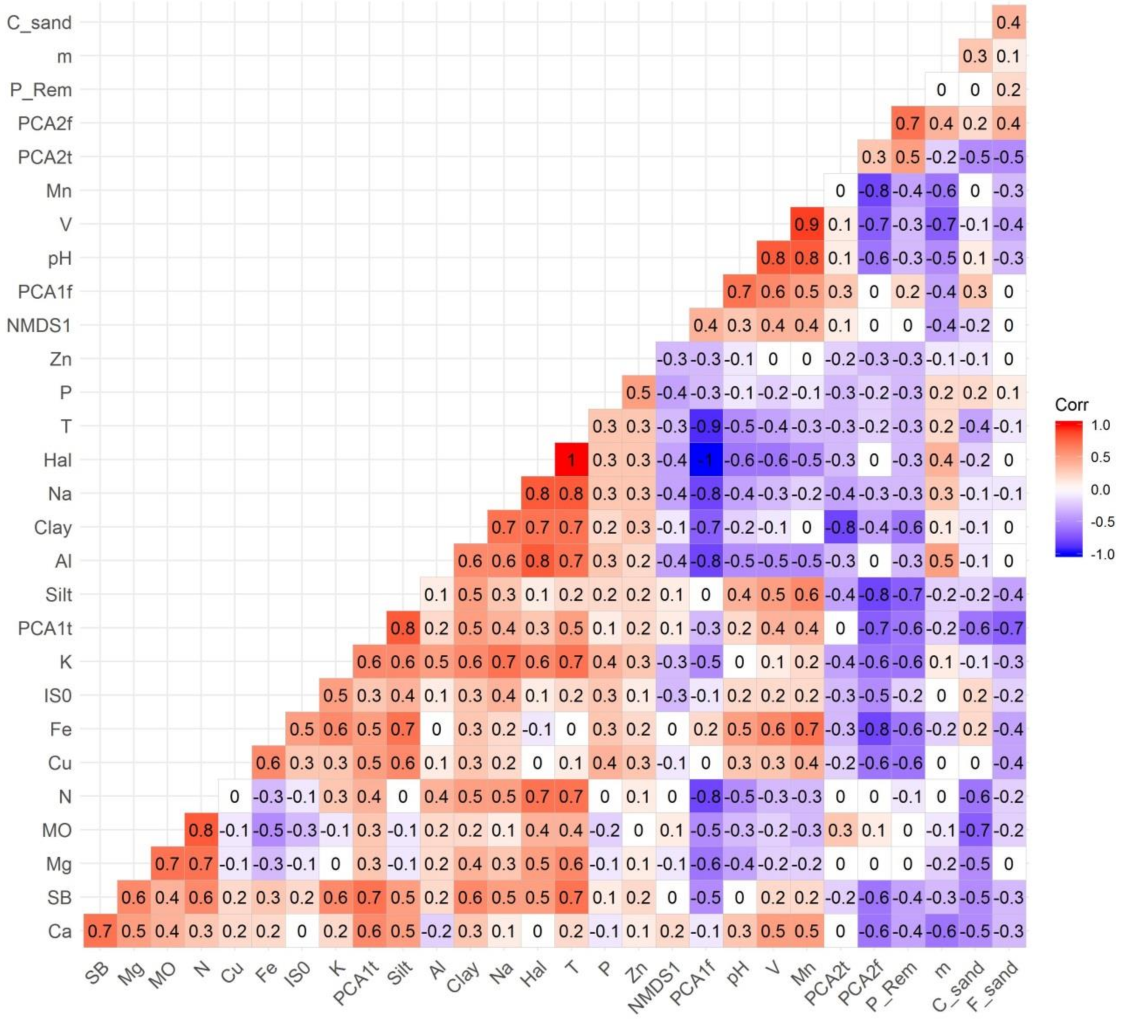
Silt (%)	0.01±0	0.03±0.01	0.01±0.0	NA	0.23±0.01	0.08±0.0	0.31±0.08	0.27±0.05	0.00±0.0	0.03±0.01	0.32±0.09	0.20±0.08	0.31±0.06	0.17±0.02	0.27±0.05
Clay (%)	0.05±0.01	0.17±0.0	0.04±0.0	NA	0.20±0.02	0.06±0.0	0.13±0.02	0.08±0.0	0.05±0.0	0.07±0.00	0.17±0.02	0.20±0.04	0.09±0.02	0.07±0.01	0.09±0.0
texture	Sand	Franco arenosa	areia	NA	Franco argilo arenosa	Areia franca	Franco arenosa	Franco arenosa	areia	areia	Franco argilo arenosa	Franca arenosa	Franco arenosa	Franco arenosa	Franco arenosa

pH: H_2O (relation 1:2:,;) P: phosphor; K: potassium; : sodium (Mehlich extractor 1); Ca: calcium; Mg: magnesium; H + Al: acidity potential (calcium acetate extractor , mol L^{-1} pH 7,); SB: sum of exchangeable bases; t: effective cation exchange capacity; T: potential cátion Exchange capacity; V: percentage of bases saturation; m: aluminium saturation; Prem: remaining phosphorus; OM: organic matter; Cu: copper; Mn: manganese; Fe: iron; Zn: zinc.

Table A.4. Modelos de efeito misto candidatos predizendo a riqueza de espécies com distribuição de erros de Poisson (modelo de efeitos mistos lineares generalizados - glmer), composição de espécies com distribuição de erro gaussiana (modelo de efeitos mistos lineares - lme) de diferentes pedestres da ilha de Elefante, Antártica Marítima. Os preditores são: textura do solo (PCA1t e PCA2t), fertilidade do solo (PCA1f e PCA2f), areia, argila, silte, matéria orgânica (OM), soma das bases trocáveis (SB), capacidade de troca catiônica potencial (T). O resultado da seleção do modelo baseado em informações teóricas é indicado (critério de Akaike corrigido para amostras pequenas). Consideramos como melhores modelos aqueles com valores de ΔAICc <2.

Response variable	Predictor	df	logLik	AICc	ΔAICc	AICw
Species composition	~ PCA1f*	4	-90.08	188.3	0	0.56
	~ Clay	4	-90.91	190.0	1.67	0.24
Gaussian lme	~ Silt	4	-91.84	191.8	3.53	0.097
	~ Sand	4	-92.52	193.2	4.89	0.05
	~ PCA2t	4	-93.91	196.0	7.66	0.01
	~ PCA1t	4	-94.13	194.4	8.10	0.01
	~SB	4	-94.31	196.8	8.47	<0.001
	~ PCA2f	4	-94.39	196.9	8.63	<0.001
	~T	4	-95.39	198.9	10.62	<0.001
	~OM	4	-96.72	201.6	13.28	<0.001
Response variable	**Predictor**	**df**	**logLik**	**AICc**	**ΔAICc**	**AICw**
Richness	~ OM	4	-548.78	1103.6	0	0.29
	~ PCA2f	4	-549.70	1105.5	1.85	0.11
Poisson glmer	~ Clay	4	-549.93	1105.9	2.30	0.09
	~ PCA2t	4	-549.96	1106.0	2.78	0.09
	~ PCA1f	4	-550.17	1106.4	2.94	0.07
	~ T	4	-550.24	1106.6	2.97	0.068
	~Sand	4	-550.26	1106.6	2.97	0.067
	~PCA1t	4	-550.293	1106.7	3.02	0.065
	~Silt	4	-550.298	1106.7	3.03	0.065
	~SB	4	-550.392	1106.9	3.22	0.059

Abreviaturas: O critério de informação de Akaike corrigido para amostras pequenas (AICc), diferença entre um AICc estimado e o AICc mais baixo, o melhor modelo (ΔAICc) e pesos do modelo (AICcwt).



	SB	Mg	MO	N	Cu	Fe	IS0	K	PCA1t	Silt	Al	Clay	Na	Hal	T	P	Zn	NMDS1	PCA1f	pH	V	Mn	PCA2t	PCA2f	P_Rem	m	C_sand	F_sand
C_sand																												0.4
m																											0.3	0.1
P_Rem																										0	0	0.2
PCA2f																									0.7	0.4	0.2	0.4
PCA2t																								0.3	0.5	-0.2	-0.5	-0.5
Mn																							0	-0.8	-0.4	-0.6	0	-0.3
V																						0.9	0.1	-0.7	-0.3	-0.7	-0.1	-0.4
pH																					0.8	0.8	0.1	-0.6	-0.3	-0.5	0.1	-0.3
PCA1f																				0.7	0.6	0.5	0.3	0	0.2	-0.4	0.3	0
NMDS1																			0.4	0.3	0.4	0.4	0.1	0	0	-0.4	-0.2	0
Zn																		-0.3	-0.3	-0.1	0	0	-0.2	-0.3	-0.3	-0.1	-0.1	0
P																	0.5	-0.4	-0.3	-0.1	-0.2	-0.1	-0.3	-0.2	-0.3	0.2	0.2	0.1
T																0.3	0.3	-0.3	-0.9	-0.5	-0.4	-0.3	-0.3	-0.2	-0.3	0.2	-0.4	-0.1
Hal															1	0.3	0.3	-0.4	-1	-0.6	-0.6	-0.5	-0.3	0	-0.3	0.4	-0.2	0
Na														0.8	0.8	0.3	0.3	-0.4	-0.8	-0.4	-0.3	-0.2	-0.4	-0.3	-0.3	0.3	-0.1	-0.1
Clay													0.7	0.7	0.7	0.2	0.3	-0.1	-0.7	-0.2	-0.1	0	-0.8	-0.4	-0.6	0.1	-0.1	0
Al												0.6	0.6	0.8	0.7	0.3	0.2	-0.4	-0.8	-0.5	-0.5	-0.5	-0.3	0	-0.3	0.5	-0.1	0
Silt											0.1	0.5	0.3	0.1	0.2	0.2	0.2	0.1	0	0.4	0.5	0.6	-0.4	-0.8	-0.7	-0.2	-0.2	-0.4
PCA1t										0.8	0.2	0.5	0.4	0.3	0.5	0.1	0.2	0.1	-0.3	0.2	0.4	0.4	0	-0.7	-0.6	-0.2	-0.6	-0.7
K									0.6	0.6	0.5	0.6	0.7	0.6	0.7	0.4	0.3	-0.3	-0.5	0	0.1	0.2	-0.4	-0.6	-0.6	0.1	-0.1	-0.3
IS0								0.5	0.3	0.4	0.1	0.3	0.4	0.1	0.2	0.3	0.1	-0.3	-0.1	0.2	0.2	0.2	-0.3	-0.5	-0.2	0	0.2	-0.2
Fe							0.5	0.6	0.5	0.7	0	0.3	0.2	-0.1	0	0.3	0.2	0	0.2	0.5	0.6	0.7	-0.3	-0.8	-0.6	-0.2	0.2	-0.4
Cu						0.6	0.3	0.3	0.5	0.6	0.1	0.3	0.2	0	0.1	0.4	0.3	-0.1	0	0.3	0.3	0.4	-0.2	-0.6	-0.6	0	0	-0.4
N					0	-0.3	-0.1	0.3	0.4	0	0.4	0.5	0.5	0.7	0.7	0	0.1	0	-0.8	-0.5	-0.3	-0.3	0	0	-0.1	0	-0.6	-0.2
MO				0.8	-0.1	-0.5	-0.3	-0.1	0.3	-0.1	0.2	0.2	0.1	0.4	0.4	-0.2	0	0.1	-0.5	-0.3	-0.2	-0.3	0.3	0.1	0	-0.1	-0.7	-0.2
Mg			0.7	0.7	-0.1	-0.3	-0.1	0	0.3	-0.1	0.2	0.4	0.3	0.5	0.6	-0.1	0.1	-0.1	-0.6	-0.4	-0.2	-0.2	0	0	0	-0.2	-0.5	0
SB		0.6	0.4	0.6	0.2	0.3	0.2	0.6	0.7	0.5	0.2	0.6	0.5	0.5	0.7	0.1	0.2	0	-0.5	0	0.2	0.2	-0.2	-0.6	-0.4	-0.3	-0.5	-0.3
Ca	0.7	0.5	0.4	0.3	0.2	0.2	0	0.2	0.6	0.5	-0.2	0.3	0.1	0	0.2	-0.1	0.1	0.2	-0.1	0.3	0.5	0.5	0	-0.6	-0.4	-0.6	-0.5	-0.3

Fig. A.1. Spearman correlation among all individual variables measured in plots along a pedoenvironmental gradient. For analysis: total N, 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), and the soil texture as coarse sand (Sand_c), fine sand (Sand_t), clay and silt contents were included.

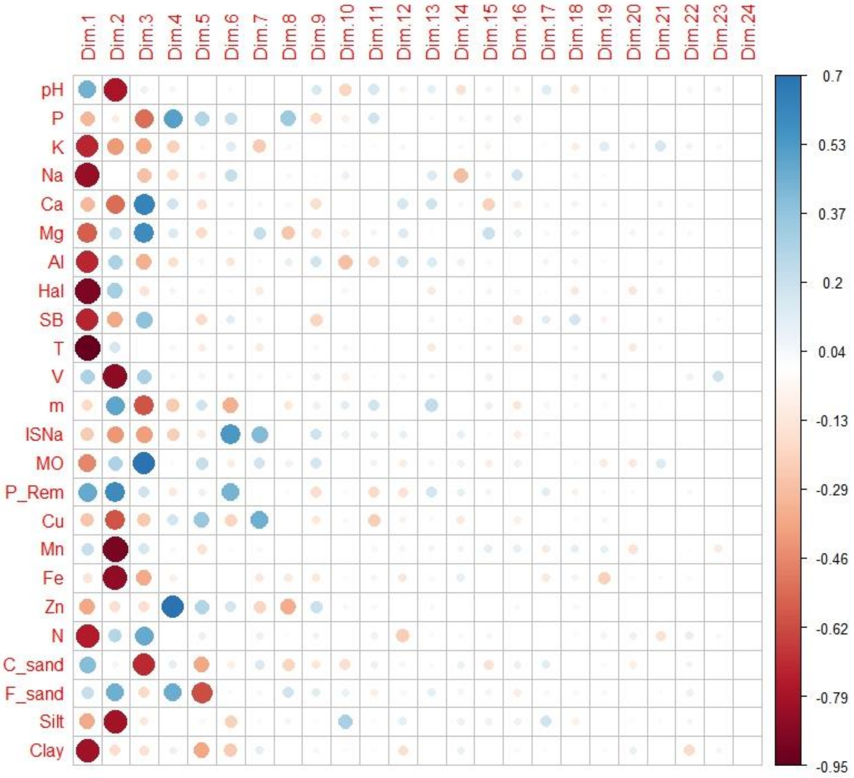


Figura A.2. Níveis de significância são baseados nos coeficientes de correlação de Pearson entre os parâmetros do solo e componentes principais do PCA do solo de 300 parcelas diferentes ao longo do gradiente pedoambiental.

PARTE 2- CAPÍTULO IV:

Fine scale active layer thermal and hygrometrical regime in three cryosols with different plant community coverage from Elephant Island, Antarctica

*Proposto para submeter na revista **Geomorphology***

Abstract

SCHMITZ, Daniela, D.Sc., Universidade Federal de Viçosa, July, 2019. **Fine scale active layer thermal and hygrometrical regime in three cryosols with different plant community coverage from Elephant Island, Antarctica**. Adviser: Carlos Ernesto G.R. Schaefer. Co-adviser: Jair Putzke.

Soil temperature and moisture are key determinants of abiotic and biotic processes in Antarctic region. These environmental variables are considered a central point for the monitoring of global climate changes. In this work we analysed changes in the thermal and hygrometric regimes of the fine scale soil between three Cryosols of Elephant Island, Maritime Antarctic. We established the following four questions: 1) How does soil properties and plant coverage change along the pedoenvironmental gradient? 2) How does active layer thermal and hygrometrical regimes change in three cryosols with different plant communities? 3) What are the main effects of soil fertility and soil texture on plant coverage? 4) What are the main effects of air temperature, hygrometrical regime and plant coverage on soil temperature in the active layer? We selected three sampling pedoenvironments, with contrasting soil properties and plant communities, moss carpet community (MCC), fruticose lichen community (FLC), and moss turf community (MTC). Ten plots (20 × 20 cm) were established in each pedoenvironment. In each plot the vegetation coverage, soil properties, air temperature, and soil temperature and humidity in the profile at three depths (10, 20, 30 cm) were measured. Plant coverage, soil properties, and active layer thermal and hygrometrical regime changes in the soil profile. We observed effects of soil fertility and soil texture on plant coverage, and effects of air temperature and plant coverage on soil temperature in the active layer. Our results allow us to infer that an increase in soil temperature promotes a higher organic matter decomposition that is reflected in higher soil fertility in MCC. Also plant coverage has allowed to conserve higher values of soil temperature with less variability, as well as to reduce evaporation despite the high soil moisture contents observed in MCC. The results indicate that plant coverage has an important role in mediating soil temperatures and moisture variation at fine spatial scale in the Antarctic ecosystem.

Key-words: freezing days, pedoenvironment, permafrost, plant coverage, soil moisture, soil temperature, thawing days.

1. Introduction

Understanding temperature and moisture distribution in the permafrost over the Antarctic cryosphere is considered a central point for the monitoring of global climate changes (Vieira et al., 2010; Michel et al., 2014). Antarctica is characterized by permanently frozen horizons, known as permafrost (Brown et al., 2000), where vertical variations in temperature and humidity can be analyzed through the active layer (e.g., Michel et al., 2014; Almeida et al., 2014; Schaefer et al., 2017a). The permafrost is a key component of the terrestrial cryosphere due to its high sensitivity to climate change (Smith and Brown, 2009), and it is evaluated through soil profiles that have seasonal thawing and freezing (Brown et al., 2000). Although warming air temperatures are contributing to permafrost degradation, understanding of permafrost and environmental feedbacks to climate change is limited (Jean and Payette, 2014). Thus, more research is still needed to understand the thermal and hygrometric variation in the active layer in different types of pedoenvironments with different plant coverage of bryophyte and lichens communities in Antarctica, as a fundamental basis for the monitoring of climatic changes.

The variations of the thermal active layer through the soil profile, as well as the permafrost distribution, depend on multiple factors, from a local-scale (i.e., air temperature), to a fine-scale, such as the dynamics of the snowpack, the soil moisture (i.e., volumetric water content), soil properties (i.e., fertility and texture), and the vegetation type and structure (Haeberli et al., 2010; Romanovsky et al., 2010, Almeida et al., 2014). However, in some cases it has been observed that vegetation does not always maintain the same permafrost distribution pattern, and tends to be closely related to air temperature (Streletskiy et al., 2008; Guglielmin et al., 2014). It has also been shown that vegetation can have effects on the active layer temperature in the soil profile; therefore variations in structural attributes of plant communities (i.e., coverage, density) can determine the soil temperature distribution (Guglielmin and Cannone, 2012; Almeida et al., 2014), reducing thermal extremes and evaporative moisture losses (e.g., Asbjornsen et al., 2011). Likewise, soil properties (soil fertility and texture) can also have effects on plant coverage (Ehrenfeld et al., 2005). For this reason, studies on effects of vegetation on active layer thermal and hygrometrical regime can provide important insights into the response of plants communities coverage and soil properties to changing climatic conditions.

Antarctica is the main terrestrial ecosystem dominated almost exclusively by non-vascular plants, mainly lichens and mosses (Ochyra et al., 2008; Poelking et al., 2015; Rodriguez et al., 2018). Antarctic vegetation is restricted to areas without ice, such as coastal areas, rocky slopes or in nunataks (Robinson et al., 2003, Bokhorst et al., 2007). Likewise, there are different types of plants communities and associations that are modeled according to the soil type and soil properties (Lewis-Smith, 2005; Francelino et al., 2011; Poelking et al., 2015). In this way, the plants communities can provide an isolation effect on the soil surface temperature, with air temperature, and this will depend mainly on community structural attributes, such as coverage and thickness (Cannone and Guglielmin, 2009). Some studies investigating and describing the active layer thermal regime have already been carried in Antarctica (Guglielmin, 2006; Cannone and Guglielmin, 2009; Guglielmin and Cannone, 2012; Guglielmin et al., 2014; Schaefer et al., 2017a; Almeida et al., 2017; Schaefer et al., 2017b) and still explaining and comparing patterns in relation to the vegetation cover in Maritime Antarctica (Cannone et al. 2006; Guglielmin et al., 2008; Michel et al., 2012; Almeida et al., 2014). However, this work is part of a South Shetland long term active layer program, and Elephant Island stands out because it is located to the north, near the Drake Strait, and also has a formation of metamorphic rocks (O'Brien et al., 1979) and that unlike the other islands of the archipelago.

In this context, the objective of this work was to analyze the changes in the fine scale thermal and hygrometric regimes of the soil between three Cryosols of Elephant Island, Maritime Antarctic. Hence, was asked the following research questions: 1) How does soil properties and plant coverage change along the pedoenvironmental gradient? 2)

How does active layer thermal and hygrometrical regimes change in three cryosols with different plant communities? 3) What are the main effects of soil fertility and soil texture on plant coverage? 4) What are the main effects of air temperature, hygrometrical regime and plant coverage on soil temperature in the active layer? Likewise, it is expected to describe the thermal regime of active layer in relation to three contrasting types plants communities with different plant coverage patterns.

2. Material and Methods

Study area

The three study sites are located at Stinker Point, in Elephant Island (61°10’48.32” S 55°16’13.39” W), Maritime Antarctica (Fig.1). All sites are located at the same altitude of ≈ 70 m a.s.l., with different plant cover (Tab. 1). The three areas are located at a middle of platform where patterned ground, gelifuction sheets and lobes occur, over Scotia metamorphic complex geology (Tanner et al., 1982; Dalziel, 1984; López-Martínez et al., 2012). The study sites are characterized by loose sediments (regolith) derived by in situ weathering of metamorphic rocks.

Vegetation sampling

We selected three sampling sites, with contrasting plant communities. In each environment ten plots of 20 × 20 cm were launched. The survey was conducted using the Braun-Blanquet (1932) square method, adapted to Antarctic vegetation conditions for to measure the coverage at the species level in each plot, as well as to calculate the total coverage of each plot. The mosses species were identified with the taxonomy keys present by Putzke and Pereira (2001), Ochyra et al. (1998, 2008), and the lichens species with the key presented by Redon (1985), Ovstedal and Lewis-Smith (2001), Olech (2004).

The sites were evaluated for the frequency and degree of coverage of each species in the square (Lara and Mazimpaka, 1998), accomplishing the Ecological Significance

Index (ESI), which combines the parameters of abundance (Marques et al., 2005), described as $ESI=F(1+C)$, 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): $F=100x/n$; and C is the average coverage of the species in the samples, calculated as $C= \sum(ci)/x$, where ci is the class of coverage and x is the number of sampling dots in which the species occur. This index determines the scale of importance of the species in the area; which ranges from 0 to 600, and values above 50 indicate ecological significance (Victoria and Pereira, 2007). The species with the highest values along with their form of growth will define the name of the community, following the classification by Longton (1988).

Soil collection

Three profiles were opened for insertion of the sensors and samples at each horizon were collected for description and classification, following the recommendations of Bockheim et al. (2006). These soils were classified according to the world reference base for soil resources 2014 (WRB/FAO. 2014). In order to measure the soil properties within each pedoenvironment, a superficial soil sample (0-10 cm depth) was performed for each plot. The following parameters were assessed: available P, N, K^+, Ca^{++}, Mg^{++}, Fe, Cu, Mn, Zn, remaining phosphorus (P-rem), exchangeable acidity (H + Al), pH (H_2O), organic matter (OM), sum of exchangeable bases (SB); effective cation exchange capacity (t), percentage of bases saturation (V), potential effective cation exchange capacity (T), and the soil texture as coarse sand (Sand_c), fine sand (Sand_f), clay and silt contents.

Microclimatic sampling

The monitoring systems consist of soil temperature probes (Campbell L107E thermocouple, accuracy of ±0.2 °C) arranged in a vertical array at different depths at both sites (10, 20 and 30 cm); an air temperature thermistor with a ventilated radiation shield (accuracy of ±0.1ºC) was installed at 100 cm above the soil surface to measure temperature; and eight soil moisture probes (CS616 water content reflectometer, accuracy of ±2.5 %), two in the moss carpet site (10 and 20 cm) and three in the other two sites (10, 20 e 30 cm) to determine the volumetric water content. All probes were connected to a Campbell Scientific CR 3000 data logger that recorded data at hourly intervals from February 2016 to January 2011. The main characteristics of the monitored sites are presented in Table 1.

We calculated the following thermal regime parameters using the criteria and approach proposed by Guglielmin et al., (2008): (1) thawing days (TD- days with all hourly measurement positive with at least one reading warmer than +0.5 °C); (2) freezing days (FD- days with all hourly measurements negative with at least one reading colder than -0.5 °C); (3) the number of isothermal days (ID- days with all hourly measurements range only between ±0.5 °C); (4) the number of freeze-thaw days (FTD- days with both negative and positive temperatures with at least on value greater than ±0.5 °C).

Data analysis

All analyses were carried out in R Environment (R Core Team 2018). Plant coverage and soil properties data were checked for homogeneity of variances and normal distribution. Thus, we tested homogeneity of variances by Bartlett´s test, QQ-plots, and histograms of residuals to assess normality using the "*dplyr*" package (Crawley 2013; Hadley et al., 2015). To compare means of the plant coverage among three pedoenvironments, we used a one-way Anova (for normally distributed data) followed by a posterior Tukey test. To compare means of soil properties we used a Kruskal-Wallis's test (for non-normally distributed data) followed by a posterior Dunn's test (Dinno 2017). All these analyses were performed with the "*stats*" and "*dunn.test*" packages (Dinno 2017).

The principal components analysis (PCA) for summarized soil variables was used on the correlation matrix to reduce the number of dimension of less important soil properties (Qian et al., 2014; Villa et al., 2018). In addition, we analyzed soil texture and fertility data in separate PCA (PCA texture and PCA fertility) with the purpose of extracting the axes ($PCA1_f$ and $PCA2_f$ with fertility data; and $PCA1_t$ and $PCA2_t$ with texture data) as possible predictors that explain variation in plant coverage (Fig. A.3. from ESM). Likewise, a PCA with microclimate data (moisture and temperature in the soil profile) was used. Thus, all variables were centered and standardized; and finally was calculated the Spearman correlations among soil properties with the PCA1 and PCA2 ordination axes (Fig. A.4, A.5. from ESM). We performed the PCA using the 'FactoMineR' package (Husson et al., 2017). We represented the spatial distribution of soil properties from each pedoenvironment using Kriging maps with the "Field" package (Nychka et al., 2017).

To test main effect of soil fertility and soil texture (predictors) on plant coverage (response variable) a covariance analysis (ANCOVA) was used, after tested normal distribution and homogeneity of variances. Predictor variables were soil fertility ($PCA1_f$ and $PCA2_f$) and soil texture ($PCA1_t$ and $PCA2_t$), defined as the first two principal components from PCA, considering all analyzed parameters (see above). For predictors selection, we assessed collinearity between selected predictor variables using Spearman correlation analysis; when two variables were strongly correlated ($r \geq 0.50$), was selected the most compelling predictors which were included in separate models (Fig. A.6., from ESM). To reduce any strong correlations among soil properties we used the first two axes of PCA for soil fertility (PCA1f and $PCA2_f$) and texture (PCA1t and $PCA2_t$) variables. Thus, the first two axis was considered as a proxy for soil fertility and soil texture across all tested models (Ali and En-Rong., 2018; Villa et al., 2018; Schmitz et al., in press).

Finally, we tested the main effects of air temperature and plant coverage on temperature in the soil profile and soil moisture (variable response) using an ANCOVA.

Predictor variables were grouped into three categories, i.e., plant coverage and air temperature as continuous explanatory variable and soil depths (categorical explanatory variable). The soil profiles at different depths included and soil moisture three levels (i.e., 10, 20 and 30 cm). We detected that there is no positive relationship in the interaction of plant coverage and air temperature on soil temperature, which is why we use these predictors in separate models.

3. Results

Plant community and coverage pattern

Were identified seven bryophytes species (five mosses and two liverwort), nine lichen species in the three pedoenvironments selected on Elephant Island (Table A.1). Through the ESI, it was possible to classify each site in distinct plant communities, according to the dominant species (Table A.2). The first, with dominance of the moss *Sanionia georgicouncinata* (ESI = 600) was classified as Moss carpet community (MCC); in the second site, the lichen specie *Sphaerophorus globosus* (ESI = 520) was the highest coverage, classifying the area as Fruticose lichens community (FLC); in the last site, *Chorisodontium aciphyllum* (ESI = 405) was the moss with the highest coverage and characterized as Moss turf community (MTC) this environment. We observed significant differences in plant coverage (chi-squared = 20.99, df = 2, p-value = 0.01) among pedoenvironments (Fig. 2), where MCC presented the highest coverage, followed by FLC and MTC (with ≈ 40%).

Soil classification and general properties

The three profiles were classified as Cryosols Turbic Leptic (table 1), which is the presence of permafrost, characteristics of cryoturbation and presence of continuous rock starting ≤100cm. However, they differ in terms of drainage, amount of coarse material (table A3) and fertility, such as base saturation (V) (table A4). The pH increased with depth in MCC and FLC, but remained around 5.4 in MTC. The P values were elevated in all three profiles, being that in MCC and FLC the quantity was higher in B horizon, while in MCC it was in A horizon and decreasing with depth.

Significant differences in soil properties among pedoenvironments were observed (Figure 3). We observed as a general pattern in the study area, that the MCC and FLC had the highest values of soil properties associated with fertility, such as sum of exchangeable bases (SB), effective cation exchange capacity (t), and nutrients. However, the MTC environment presents a high proportion of coarse sand (Fig. 3).

Soil fertility and microclimate gradient

A marked soil fertility and texture gradient was observed along the pedoenvironments and plant communities (Fig. 4A). Overall, the three pedoenvironments presented high soil fertility, with high nutrient availability and organic matter, mainly in FLC community. The first two axes of the overall PCA explained 75.2% of the variation in the soil data (Fig. 4A). The first axis of PCA explained 46.1% of variance, and was positively correlated with pH ($R = 0.70$, $p < 0.05$), phosphorous ($R = 0.74$, $p < 0.05$), sum of exchangeable bases ($R = 0.93$, $p < 0.05$), and some micronutrients, such as Ca, Mg, Mn, Cu, Zn, Fe (Fig. A.5. from ESM). Coarse sand had a high correlation negatively with both PCA1 and PCA2 ($R \sim 0.65$, $p < 0.05$). The second axis explained 29.1% of the variation in soil data and was negatively correlated with pH and phosphorous, but was positively correlated with N ($R = 0.93$, $p < 0.05$), potassium ($R = 0.863$, $p < 0.05$), and magnesium ($R = 0.55$, $p < 0.05$); and with soil texture properties as fine sand ($R = 0.62$, $p < 0.05$) and clay content ($R = 0.7$, $p < 0.05$) (Fig. A.5. from ESM). Finally, a marked microclimate gradient was observed along the pedoenvironments (Fig. 4B). The PCA microclimate showed that the first two axes explained 74% of the variation in the soil data, where soil temperature had a high correlation positively with both PCA1, and soil moisture had a high correlation negatively with PCA1 (Fig. 4B).

Local scale climate pattern

The climate conditions at the study site were similar for both years and analogous to other Shetland Islands, mean annual air temperature (MAAT) recorded at 1 m above ground ranged between − 1.2 °C (2016) and − 1.6 °C (2017) (data from January 2016 was not collected), -1.3 °C for the whole study period. The maximum hourly air temperature was 10.4 °C recorded in March 20th 2017, and the highest mean daily air temperature was 6.1 °C in February 20th 2016 (Fig. A7). The minimum hourly air temperature record (− 22.0 °C) and daily average (− 21.0 °C) occurred in August 20th 2016. Standard deviation considering the study period was 4.2 °C and the variance was 17.7 °C. Mean daily air temperature (MDAT) reaches consecutive negative values in the beginning of April (14th in 2016 and 19th in 2017) although positive MDAT occur even in June and July (Table 2).

Soil temperature and soil water content pattern in active layer thermal

Despite great proximity of the study sites and the similarity of the soil profiles soil thermal regime contrasted. The Moss Carpet (MCC) recorded mean annual soil temperature (MAST) of -0.4°C (10 cm), -0.6°C (20 cm) and -0.7°C (30 cm) in 2016 and -0.8°C (10 cm), -1.0°C (20 cm) and -1.1°C (30 cm); superior to the MAST verified at the Fruticose Lichen (FLC) and Moss turf community (MTC) sites, -1.3°C (10 cm), -1.4°C (20 cm) and -1.4°C (30 cm); -1.2°C (10 cm), -1.3°C (20 cm) and -1.3°C (30 cm) in 2016; -1.2°C (10 cm), -1.4°C (20 cm) and -1.4°C (30 cm); -1.2°C (10 cm), -1.4°C (20 cm) and -1.3°C (30 cm) in 2017 (Table 2). Maximum soil temperature was similar in all depths at all sites while distinct minimum soil temperature was found at MCC, -12.5°C, -11.2°C and -9.8°C at the consecutive study depths, higher than values found at FLC; -17.6°C, -16.6°C and -15.6°C and MTC; -16.6°C, -16.3°C and -15.7°C at the consecutive study depths.

Standard deviations (SDV) and variance (VAR) show less temperature fluctuation at MCC at all depths (Table 2, Fig. A.8) when compared to FLC and MTC 2.6°C, 2.2°C and 1.9°C (SDV at MCC) compared to 3.3°C, 2.8°C and 2.6°C (SDV at FLC) and 3.1°C, 2.9°C and 2.6°C (SDV at MTC); 7.1°C, 4.9°C and 3.8°C (VAR at MCC) compared to 11.1°C, 8.3°C and 7.2°C (VAR at FLC) and 9.7°C, 8.6°C and 6.9°C (VAR at MTC).

Soil water content readings were similar at all sites mean annual values (MASW) were equal for both years ranging from 3% at 5 cm under FLC and MTC to 6% at 5 com under MCC, values are stable for MCC profile and increase in depth at FLC and MTC. Contrast in found in the maximum values, 27% (5 cm) and 30% (10 cm) under MCC compared to 9% (5 cm) and 17% (10 cm) under FLC; 9% (5 cm) and 15% (10 cm) under MTC (Table 2; Fig. A.8.).

Thawing, freezing, isothermal and freeze-thaw days pattern

The analysis of the number of days predominantly influenced by freezing thawing freeze-thaw or isothermal conditions allow a better understanding of the insulation provided by the vegetation and the conditions it faces during the year. The number of thaw days was greater for all vegetation when compared to the air probe (Table 3), MCC recorded 48, FLC recorded 28 and MTC 23 more days of thawing conditions in surface (Thaw days, TD) when compared to the atmosphere. In subsurface all sites verified less TD and conditions were always milder at MCC. All vegetation types recorded more freeze days (FD) at all depths varying from 97 to 185 more FD in surface at MCC and FLC (Table 3). The number of isothermal days (ID) was also very discrepant when comparing soil and air temperatures, and MCC being the site with greater contrast, for example 172 more ID compared to air, 122 at FLC and 134 at MTC (Table 4). These resemblances are also verified when analyzing the number of freeze-thaw days (FTD), the atmosphere recorded greater number of days with great temperature once more MCC recorded only 3 FTD (317 less than air), FLC recorded 37 and MTC recorded 32 FTD in surface.

Effects of soil properties on plant coverage, and plant coverage and air temperature on soil temperature

The main model explained the significant effects of soil fertility and soil texture on plant coverage (Table 5). We observed that the temperature in the soil profile varies significantly by positive effect of air temperature (Fig. 5; Fig. A.9., from ESM), as well as the significant differences by the effect of plant coverage (Table 5). There was no significant effect of these predictors on soil moisture and the deeper soil profile (figure A.10. from ESM).

4. Discussion

Climate pattern

The average annual temperature in 2017 was lower than in 2016, however if we observe the monthly averages it is possible to notice that the summers have increased temperature, and that in 2017, monthly averages were negative until November, i.e., had a longer and cold winter in this year. The mean air temperature for the entire study period (-1.2 ° C) was higher than that found by Almeida et al. (2014, 2017) in Lions Rump between 2009-2011 (-3.0°C) and Low Head in 2011 (-4.3 ° C) and 2013 (-2.5 ° C), both on King George Island.

Soil properties, plant coverage and microclimate

Despite the proximity of the soil profiles, and similarity in terms of altitude, local climate and position in the landscape, the pedoenvironments showed different vegetation cover, soil properties and thermal regimes of the active layer. The contrasting behavior regarding the water content and soil temperature is attributed to the vegetation cover, soil structure and the microenvironment at each site. This pattern occurs especially in function of the heterogeneity imposed by the biological inputs of nesting birds (Thomazini et al.

2018).

The stoniness on the surface of FLC and MTC was higher than in MCC. Thus, a favorable site for the dominance of fruticose lichens and the *Chorisodontium aciphyllum* in these pedoenvironments, as they develop preferably on mineral soil between rocks and stones, on stony soil (Ochyra et al., 2008; Ovstedal and Lewis-Smith, 2001). The presence of other species growing in these communities formed a discontinuous vegetation, with lower vegetation cover, unlike MCC, which with its continuous *S. uncinata* carpet of, had greater vegetation cover. The surface organic matter was higher in MCC, but the B horizon of FLC also presented considerable levels.

The means for the whole period of the study were higher in the soil in relation to air, except for the depths 20 and 30cm of FLC. The mean annual soil temperature were same or lower in 2017 that 2016, in all plant communities and depths (table A.5), as well in the air temperature (table 2). Overall, MCC showed the highest mean annual temperature in the two years of study, and most of the maximum monthly averages (10 and 30cm), while FLC had the lowest monthly averages recorded (10 and 30cm). In the 2016 winter, FLC and MTC had monthly means well below MCC (tab. 2; fig. A8).

Although the higher moisture means were recorded for the deeper horizons of MTC (20 and 30cm) and 20cm of FLC, was MCC that showed the highest moisture records (26.9%) and kept constant levels throughout the year, which confirms the preference of mosses for more humid environments (Leishmann and Wild, 2001; Schaefer et al., 2004; Kim et al., 2007). The averages were low for FLC, except in the B horizon, probably by A being very gravelly (96.8%) and allow a rapid flow of water to B, with higher soil presence, and higher levels of silt + clay. coarser texture soils and therefore with higher macroporosity have a lower water holding capacity, while soils to finer texture, retains more water (Michel et al., 2012). Almeida et al. (2014) found similar results, where the lichen cover profile had lower moisture rates than mosses. A fruticose lichens cover generally indicates stony soils and a better drainage (Schaefer et al., 2004; Kim et al., 2007).

In general, the moisture contents were low for the three communities when compared to other areas of South Shetland. Although deeper (90cm), Michel et al., (2012) obtained the annual average of 10.5% for Potter Peninsula with lichens cover, and 43.2% for mixed lichen and moss cover in Fildes Peninsula, both on King George Island. Almeida et al. (2014) also obtained higher levels, mainly in moss cover, where the average for two years was 27%, in Lions Rump.

Thawing, freezing, isothermal and freeze-thaw days pattern

The thawing days of soil surface (10 cm) were higher than the air in all communities, mainly in MCC with *Sanionia uncinata* cover, which recorded the highest number of days. This is probably due to the higher vegetation cover (fig.2), and this, along with the moisture present on the surface contributed to the heating and buffer effect (Almeida et al., 2014) leading to a higher resistance to temperature change. However, other factors not measured in this study may be related to the buffering effect of the different types of vegetation with influence of vegetation on snow distribution, thickness and longevity (Liston and Sturm, 1998; Liston et al., 2002), and on the radiative balance of the surface (Chapin et al., 2000).

The freezing days were superior in the intermediate layer (20cm) of MCC and in the deepest of MCC and FLC. In April, freezing days were more frequent in the superficial layer, in May and June the direction of freezing varied between the communities, and from July to September, the entire active layer remained frozen. When the air temperature started to become positive (November and December) the deeper layers remained frozen for more days.

The number of isothermal days (ID) was very discrepant when comparing soil and air temperatures, and MCC being the site with greater contrast. The opposite occurs for the freeze-thaw days (FTD), the atmosphere recorded a greater number of days with great temperature variations which were buffered by the vegetation and did influence soil temperature; MCC expressed greater shielding capacity with the lowest number of freeze-thaw days. In the soil the freezing days defrost for MCC and FLC were always higher in the intermediate layer, while in MTC in the deeper layer.

Frequent freeze-thaw cycles destroy the original structure of soils and rock (Lai et al., 2008). The demolition of freeze–thaw action on soil bodies originates from water migration in the soil, while the temperature gradient from the positive and negative variations of surface temperature drives this phenomenon (Wang et al. 2005; Xie et al., 2015). Xie et al. (2015) argue that an increase in the freeze-thaw cycles increases the volume strain of the soil and variation pattern of porosity, reducing soil cohesion.

Effects of soil properties on plant coverage

Our results showed that soil fertility and soil texture affect plant coverage. Our results corroborate this relationship that has been observed in different types of plant communities and ecosystems (e.g., Sanaei et al. 2018a, 2018b). However, despite not having quantified the direct effects of temperature on soil properties, our results allow us to infer that an increase in soil temperature promotes a higher decomposition of organic matter that is reflected in higher soil fertility in MCC where present the highest values of P, SB, t, and micronutrients (Fig. 3). For example, the mineral content of thermal layer fluid is absorbed by the organic matter and clay minerals in the soil, which are responsible for elevated concentrations of micronutrients (Nicholson, 2012). Previous studies have reported that P transformation rate (organic P mineralization) is determined by soil temperature (Song et al. 2012), and soils with low temperature have low availability of phosphorus because the release of phosphorus from organic material is hindered by low temperature (Gahoonia et al., 2003). Furthermore, probably there is a closed cycle of nutrients in MCC pedoenvironment where higher fertility allows a higher plant biomass production, and consequently higher plant coverage (Fig. 2). Thus, the organic matter turnover to the soil allows maintaining high levels of nutrients and fertility. Thus, variations in plant coverage or changes in vegetation growth and renewal could modify feedbacks between the surface and the atmosphere and, therefore, the local climate.

Effects of plant coverage and air temperature on soil temperature

In our study, the temperature in the soil profile varies significantly by positive effect of air temperature, as well as the significant differences by the effect of plant coverage. There is sufficient evidence that there is a close relationship between air temperature and soil temperature, and as a general pattern it has been observed that an increase in air temperature induces an increase in soil temperature in Maritime Antarctica (Michel et al., 2012; Almeida et al., 2014). Our results corroborate this positive relationship; however, it was also possible to observe that the higher coverage, the higher the soil temperature and the lower soil temperature variability, mainly in the first profile where the most important biogeochemical processes usually occur (Beer et al., 2018). Warmer soil temperature is a prime mover in most soil processes, rapid decomposition or organic matter and quicker nutrients release (Karmakar, 2016).

Likewise, the plant cover cushions the colder air temperature as has been reported in previous studies (e.g., Almeida et al., 2014), and this allows us to infer that MCC with greater coverage allows to maintain a lower temperature oscillation in the soil and maintain release nutrients. For example, a bare soil quickly absorbs heat, becomes hot during the hot season and becomes cold during the cold season (Michel et al., 2012). Thus, plant coverage acts as a thermal insulator and significantly affects the soil temperature (Vieira et al., 2014).

On the other hand, these higher levels of fertility, plant coverage and temperature in MCC, could be having a marked influence on relative humidity, where the highest values are presented in comparison to FLC and MTC. It is likely that this cushioning effect of the plant coverage in MCC not only allows maintaining a higher soil temperature compared to FLC and MTC, but it is also important for the freezing and thawing process (Beer et al., 2018), since soil structure is responsible for the movement of nutrients and water (Ehrenfeld et al., 2005). The soil structure quality is strongly influenced by the amount and quality of organic matter present with high clay contents, and freeze-thaw behavior (Ehrenfeld et al., 2005). A decline in soil organic matter levels induces a decrease in soil aggregate stability and soil moisture (Ehrenfeld et al., 2005). Thus, some studies concluded that soil temperature and moisture are mainly controlled by local soil properties, such as texture and fertility (Wundram et al., 2010; Scherrer and Körner, 2011).

We no observed significant effect of plant coverage and air temperature on soil moisture. Soil moisture is mainly related to soil texture and porosity (Legates et al., 2010) and therefore highest soil moisture contents are found in soils with high organic content (Aalto, 2013). We presume that the high values of clay and silt in MCC and FLC in comparison with MTC allow a greater accumulation of organic matter and consequently increase the soil moisture contents. Thus, Aalto et al. (2013) argue that the soil temperature (and soil moisture) is even more strongly driven by soil properties than local topographical variables. These researchers found that soil moisture correlates negatively with soil temperatures as the increase in soil temperatures increases evaporation and in turn lowers the moisture content of the soils. On the contrary, increased moisture intensifies evapotranspiration, which in turn lowers soil temperature (Legates et al., 2010). In this sense, we infer that the plant coverage has allowed to conserve higher values of soil temperature with less variability, as well as to reduce evaporation despite the high soil moisture contents com observed in MCC. Moisture influences soil heat dissipation down the profile, and the rate of heat dissipation increases with moisture content (Aalto, 2013), which probably explains part of the higher ground temperature in MCC in our study.

5. Final remarks

Despite having defined specific objectives of our study, such as soil properties and plant coverage pattern along the pedoenvironmental gradient, active layer thermal and hygrometrical regime changes in the soil, effects of soil fertility and soil texture on plant coverage, and effects of air temperature, hygrometrical regime and plant coverage on soil temperature in the active layer thermal; we assume that other factors have close relationships for different processes in permafrost that should be better studied. For example, it has been reported that soil thermal gradients have dominating effect on vegetation establishment and growth (van Manen and Reeves, 2012; Nishar et al., 2017), and vegetation mediates soil temperature and moisture (Aalto, 2013), having simultaneously effects on the abiotic and biotic processes determining the distribution and density of vegetation (Saito et al., 2009; Aalto et al., 2013; Olefeldt et al., 2013). On the other hand, soil temperature and moisture can have multiple effects on the abiotic and biotic processes, such as microbial activity, nutrient availability and cycling (Legates et al., 2010; Olefeldt et al., 2012). While soil properties can strongly affect plant community patterns, plants may also have strong feedback effects on soil thermal and hydrological properties (Ehrenfeld et al., 2005). In this sense, we recommend evaluating these processes on plant-soil-atmosphere relationship, in order to have a better understanding of active layer dynamics in the permafrost is crucial for future climate change impact studies.

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Table 1. General characteristics of monitored sites.

Plant community	**Geographic position**	**Altitude** m.a.s.l.	**Vegetation**	**N° of species**	**Soil class WRB/soil taxonomy**	**Depth** (cm)
Moss carpet community	S 61°13'78.9" W 55°21'73.7"	68	*Sanionia georgico uncinata*	3	Cryosols Turbic Leptic Reductaquic	30
Fruticose lichen community	S 61°13'38.5" W 55°21'60.0"	70	*Sphaerophorus globosus*	12	Cryosols Turbic Leptic Skeletic	30
Moss turf community	S 61°13'38.5" W 55°21'59.1"	70	*Chorisodontium aciphyllum*	12	Cryosols Turbic Leptic Eutric Skeletic	40

Table 2. Monthly mean air temperature (°C) and water content (%) at each horizont (10, 20, 30 cm) by sites in the period 1st February 2016–29th January 2018, and at the bottom anual synthesis with mean, maximum, minimum and standard deviation calculated from hourly readings.

		MCC			FLC			MTC		
Month	Air (°C)	10cm	20cm	30cm	10cm	20cm	30cm	10cm	20cm	30cm
feb/16	1.47	1.78	1.24	0.96	1.53	1.03	0,81	1,56	1,30	1,07
mar/16	1.91	1.21	0.82	0.64	1.32	0.9	0,75	1,24	1,03	0,85
apr/16	-2.86	-1.53	-1.05	-0.57	-1.71	-1.15	-0,94	-0,85	-0,55	-0,15
may/16	-2.58	-2.27	-2.07	-1.79	-2.64	-2.4	-2,27	-1,87	-1,72	-1,41
jun/16	-1.46	-0.51	-0.59	-0.59	-1.65	-1.52	-1,43	-1,73	-1,76	-1,65
jul/16	-3.78	-1.87	-1.87	-1.8	-4.34	-4.18	-4,01	-4,31	-4,28	-3,95
aug/16	-6.78	-3.39	-3.37	-3.26	-6.93	-6.66	-6,44	-6,84	-6,77	-6,35
Sep/16	0.12	-1.04	-1.25	-1.33	-1.51	-1.75	-1,85	-1,50	-1,70	-1,90
oct/16	0.52	-0.12	-0.36	-0.43	-0.37	-0.55	-0,59	-0,33	-0,51	-0,57
nov/16	0.06	0.17	-0.26	-0.34	0.07	-0.3	-0,36	-0,02	-0,29	-0,34
dec/16	0.38	2.49	1.38	0.76	1.88	0.77	0,41	1,11	0,53	0,08
jan/17	1.5	2.69	1.93	1.52	2.23	1.41	1,12	2,08	1,69	1,41
feb/17	2.23	2.94	2.26	1.88	2.55	1.83	1,56	2,44	2,15	1,89
mar/17	1.03	0.83	0.53	0.41	0.81	0.51	0,42	0,59	0,47	0,43
apr/17	-2.12	-0.82	-0.47	-0.17	-0.85	-0.46	-0,33	-0,54	-0,28	0,02
may/17	-2.33	-1.79	-1.57	-1.34	-1.81	-1.59	-1,41	-1,36	-1,30	-0,91
jun/17	-5.76	-4.81	-4.48	-4.15	-5.25	-5.02	-4,80	-5,11	-5,10	-4,65
jul/17	-3.85	-2.77	-2.7	-2.58	-4.35	-4.19	-4,04	-4,36	-4,36	-4,04
aug/17	-4.91	-4.14	-4.05	-3.9	-5.27	-5.17	-5,05	-5,22	-5,24	-5,02
sep/17	-3.21	-2.66	-2.77	-2.78	-3.2	-3.25	-3,24	-3,23	-3,32	-3,29
oct/17	-1.91	-1.18	-1.39	-1.43	-1.27	-1.46	-1,51	-1,24	-1,43	-1,50
nov/17	-0.74	-0.33	-0.67	-0.74	-0.47	-0.74	-0,80	-0,35	-0,61	-0,67
dec/17	1.05	2.03	0.84	0.27	1.92	0.78	0,44	1,30	0,62	0,05
jan/18	1.9	3.15	2.24	1.73	2.81	1.94	1,63	2,58	2,09	1,68
Mean	-1.27	-0.51	-0.75	-0.80	-1.12	-1.32	-1.34	-1.10	-1.24	-1.22
Min	-22.0	-12.55	-11.21	-9.83	-17.63	-16.66	-15.62	-16.61	-16.34	-15.76
Max	10.39	7.27	5.60	4.16	7.81	4.81	3.94	6.26	5.48	4.75
St dev	4.2	2.6	2.2	1.9	3.4	2.9	2.7	3.1	2.9	2.6

	MCC		FLC			MTC		
Month	10cm	20cm	10cm	20cm	30cm	10cm	20cm	30cm
feb/16	5.7	5.9	2.7	12.8	3.5	1.6	13.5	9.6
mar/16	6.1	6.0	3.0	12.0	4.1	1.8	13.6	9.9
apr/16	4.2	4.2	1.8	7.4	3.0	1.3	9.6	8.2
may/16	4.5	4.1	1.5	4.7	2.2	0.9	4.3	5.0
jun/16	7.3	7.6	3.2	6.6	4.2	2.5	5.2	5.8
jul/16	5.1	5.5	4.2	5.9	3.5	4.1	4.9	5.1
aug/16	4.9	5.3	4.1	5.8	3.4	4.1	4.8	5.0
Sep/16	5.3	5.6	4.4	6.4	3.7	4.4	5.2	5.5
oct/16	6.3	6.3	4.7	7.1	4.1	4.7	5.8	6.2
nov/16	7.5	8.3	4.0	9.7	4.9	4.0	7.1	7.0
dec/16	5.9	7.5	2.5	10.1	4.8	1.9	13.1	10.2
jan/17	6.0	6.3	2.5	9.9	4.6	1.7	13.1	11.4
feb/17	5.7	5.9	2.6	9.7	4.4	1.7	12.9	11.6
mar/17	4.9	5.3	2.4	8.5	4.1	1.6	11.6	10.9
apr/17	4.2	4.8	2.0	7.7	3.9	1.4	10.1	10.5
may/17	6.7	7.7	3.3	7.0	4.9	1.7	6.5	5.0
jun/17	5.0	5.5	3.7	6.2	3.7	2.9	5.7	3.7
jul/17	5.1	5.5	4.3	6.2	3.8	4.1	5.6	3.6
aug/17	4.9	5.4	4.2	6.1	3.7	4.1	5.5	3.6
sep/17	5.0	5.5	4.3	6.2	3.8	4.2	5.6	3.7
oct/17	5.2	5.6	4.4	6.6	3.9	4.3	5.9	4.0
nov/17	7.5	6.1	4.4	7.4	4.2	4.1	6.8	5.4
dec/17	7.2	8.8	2.7	9.7	5.5	2.3	13.0	9.3
jan/18	6.3	6.6	2.7	9.3	5.3	1.9	13.7	13.2
Mean	5.6	6.0	3.3	7.8	4.0	2.8	8.4	7.2
Min	2.2	2.3	1.0	3.6	1.7	0.8	4.0	3.2
Max	26.9	30.4	8.6	17.2	12.9	9.1	15.4	15.3
St dev	2.1	2.6	1.1	2.4	1.1	1.4	3.7	3.2

Table 3. Thawing and freezing days (ºC) of the studied sites in Stinker Point during a period of 24 months.

Month	Thawing days										Freezing days									
	Air	MCC			FLC			MTC			Air	MCC			FLC			MTC		
		10	20	30	10	20	30	10	20	30		10	20	30	10	20	30	10	20	30
Jan/16	2	2	2	2	2	2	2	2	2	2	0	0	0	0	0	0	0	0	0	0
Feb/16	17	24	19	22	25	17	17	26	20	16	0	0	0	0	0	0	0	0	0	0
Mar/16	19	26	21	20	25	21	20	28	21	19	0	0	0	0	0	0	0	0	0	0
Apr/16	3	1	1	1	1	1	1	2	2	2	11	16	14	12	19	15	14	17	15	6
May/16	1	0	0	0	0	0	0	0	0	0	11	29	28	29	28	29	29	28	28	29
Jun/16	3	0	0	0	0	0	0	0	0	0	12	12	17	22	25	24	24	26	28	27
Jul/16	3	0	0	0	0	0	0	0	0	0	21	27	31	30	30	31	31	31	31	31
Aug/16	2	0	0	0	0	0	0	0	0	0	24	31	31	31	31	31	31	31	31	31
Sep/16	7	0	0	0	0	0	0	0	0	0	4	18	30	30	21	30	30	19	30	30
Oct/16	9	0	0	0	0	0	0	0	0	0	4	0	19	24	9	26	27	7	25	23
Nov/16	7	8	0	0	2	0	0	2	0	0	5	1	5	9	4	8	12	3	8	5
Dec/16	5	30	16	12	28	12	10	22	7	3	3	0	0	0	0	0	0	2	0	0
Jan/17	14	29	25	26	28	21	20	27	24	19	2	0	0	0	0	0	0	0	0	0
Feb/17	19	28	26	26	26	25	25	25	26	24	1	0	0	0	0	0	0	0	0	0
Mar/17	22	19	14	13	17	15	14	16	12	11	6	5	2	0	7	3	2	7	4	0
Apr/17	8	4	4	4	5	4	4	4	4	4	12	11	9	6	14	9	9	14	12	3
May/17	5	0	0	0	0	0	0	0	0	0	10	16	18	18	21	19	21	20	18	19
Jun/17	1	0	0	0	0	0	0	0	0	0	24	28	29	29	28	28	29	28	28	28
Jul/17	2	0	0	0	0	0	0	0	0	0	12	31	31	31	29	31	31	31	31	31
Aug/17	0	0	0	0	0	0	0	0	0	0	20	31	31	31	31	31	31	31	31	31
Sep/17	1	0	0	0	0	0	0	0	0	0	16	30	30	30	30	30	30	30	30	30
Oct/17	2	0	0	0	0	0	0	0	0	0	21	31	31	31	25	31	31	26	31	30
Nov/17	4	2	0	0	2	0	0	2	0	0	8	8	18	25	9	18	26	9	16	12
Dec/17	10	28	10	5	20	11	7	20	5	1	1	0	3	7	0	2	5	0	0	2
Jan/18	16	29	29	29	29	28	28	29	27	24	0	0	0	0	0	0	0	0	0	0
total	182	230	167	160	210	157	148	205	150	125	228	325	377	395	361	396	413	360	397	368

Table 4. Isothermal and freeze-thaw days (ºC) of the studied sites in Stinker Point during a period of 24 months.

Month	Isothermal days										Freeze-thaw days									
	Air	MCC			FLC			MTC			Air	MCC			FLC			MTC		
		10	20	30	10	20	30	10	20	30		10	20	30	10	20	30	10	20	30
Jan/16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Feb/16	0	5	3	3	3	1	1	3	1	0	12	0	7	4	1	11	11	0	8	13
Mar/16	0	5	3	4	4	3	5	3	2	3	12	0	7	7	2	7	6	0	8	9
Apr/16	0	13	11	13	8	10	10	11	8	17	16	0	4	4	2	4	5	0	5	5
May/16	0	2	3	2	3	2	2	3	3	2	19	0	0	0	0	0	0	0	0	0
Jun/16	0	18	13	8	5	6	6	4	1	2	15	0	0	0	0	0	0	0	1	1
Jul/16	0	4	0	1	1	0	0	0	0	0	7	0	0	0	0	0	0	0	0	0
Aug/16	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0
Sep/16	0	12	0	0	9	0	0	11	0	0	19	0	0	0	0	0	0	0	0	0
Oct/16	0	31	2	1	22	2	2	24	3	0	18	0	10	6	0	3	2	0	3	8
Nov/16	0	20	7	7	11	6	6	20	6	4	18	1	18	14	13	16	12	5	16	21
Dec/16	1	1	1	2	1	1	2	1	2	5	22	0	14	17	2	18	19	6	22	23
Jan/17	0	1	0	0	2	0	0	0	0	0	15	1	6	5	1	10	11	4	7	12
Feb/17	0	0	0	0	1	0	0	1	0	0	8	0	2	2	1	3	3	2	2	4
Mar/17	0	6	4	10	2	3	7	2	7	10	3	1	11	8	5	10	8	6	8	10
Apr/17	0	15	11	17	10	12	13	11	13	16	10	0	6	3	1	5	4	1	1	7
May/17	0	15	11	17	10	9	10	11	10	11	16	0	2	1	0	3	0	0	3	1
Jun/17	0	2	1	12	2	2	1	2	2	1	5	0	0	0	0	0	0	0	0	1
Jul/17	0	0	0	1	2	0	0	0	0	0	17	0	0	0	0	0	0	0	0	0
Aug/17	0	0	0	0	0	0	0	0	0	0	11	0	0	0	0	0	0	0	0	0
Sep/17	0	0	0	0	0	0	0	0	0	0	13	0	0	0	0	0	0	0	0	0
Oct/17	0	0	0	0	6	0	0	5	0	0	8	0	0	0	0	0	0	0	0	1
Nov/17	0	20	2	1	17	3	3	18	4	3	18	0	10	4	2	9	1	1	10	15
Dec/17	0	3	2	5	4	4	6	4	6	2	20	0	16	14	7	14	13	7	20	26
Jan/18	0	0	0	0	0	0	0	0	0	0	13	0	0	0	0	1	1	0	2	5
Total	1	173	74	87	123	64	74	134	68	76	320	3	113	89	37	114	96	32	117	162

Table 5. Effect of soil texture (PCA1t and PCA2t) and soil fertility (PCA1f and PCA2f) on plant coverage (*mod 1*). Air temperature and plant coverage as explanatory variables for temperature in the soil profile in different pedoenvironments (*mod1, mod2, mod 3*).

Models	**Response variable**	**Soil texture**				**Soil fertility**			
		PCA1t		**PCA2t**		**PCA1f**		**PCA2f**	
	Plant coverage	F	P	F	P	F	P	F	P
Mod1	Coverage	101.4	<0.001	51.13	<0.001	94.95	<0.001	36.47	<0.001
	Pedoenvironment	28.04	<0.001	58.37	<0.001	23.37	<0.001	51.88	<0.001

	Temperature in the soil profile (°C)	**Air temperature (°C)**		**Plant coverage (%)**	
		F	P	F	P
Mod2	Temperature (10 cm)	157.9	<0.001	189.9	<0.001
	Pedoenvironment	258.2	<0.001	255.7	<0.001
Mod3	Temperature (20 cm)	33.08	<0.001	33.08	<0.001
	Pedoenvironment	17.18	<0.001	17.18	<0.001
Mod4	Temperature (30 cm)	5.13	0.15	1.97	0.17
	Pedoenvironment	40.8	<0.001	36.8	<0.001

Figure captions

Fig. 1. a: Location and general aspects of the three study areas; b-d: profiles with vertical insertion of sensors, b: Moss carpet community (MCC); c: Fruticose lichen community (FLC); d: Moss turf community (MTC).

Fig. 2. Plan coverage in the three pedoenvironments studied. The pedoenvironments studied present the following plant communities: Moss carpet community (MCC), fruticose lichen community (FLC), and moss turf community (MTC). Different letters in each soil parameter indicate significant differences (Tukey, $p < 0.05$).

Fig. 3. Soil properties pattern in the pedoenvironments studied following plant communities: Moss carpet community (MCC), fruticose lichen community (FLC), and moss turf community (MTC). For analysis, available: total N, available P, K, Ca, Mg, Fe, Cu, Mn, Zn, P-rem, exchangeable acidity (H + Al), pH (H2O), organic matter (OM), sum of exchangeable bases (SB); effective cation exchange capacity (t), basis saturation index (V) and effective cation exchange capacity to pH=7 (T), and the soil texture as coarse sand (Sand_c), fine sand (Sand_t), clay and silt contents were included. Different letters in each soil parameter indicate significant differences (Dunn test, $p < 0.05$).

Fig. 4. Principal Component Analysis (PCA) for the soil parameters of the three studied areas. For analysis, available: total N, available P, K, Ca, Mg, Fe, Cu, Mn, Zn. P-rem, exchangeable acidity (H + Al), pH (H_2O), organic matter (OM), sum of exchangeable bases (SB); effective cation exchange capacity (t), basis saturation index (V) and effective cation exchange capacity to pH=7 (T), and the soil texture as coarse sand (Sand_c), fine sand (Sand_f), clay and silt contents were included. The pedoenvironments studied present the following plant communities: Moss carpet community (MCC), fruticose lichen community (FLC), and moss turf community (MTC).

Fig. 1.

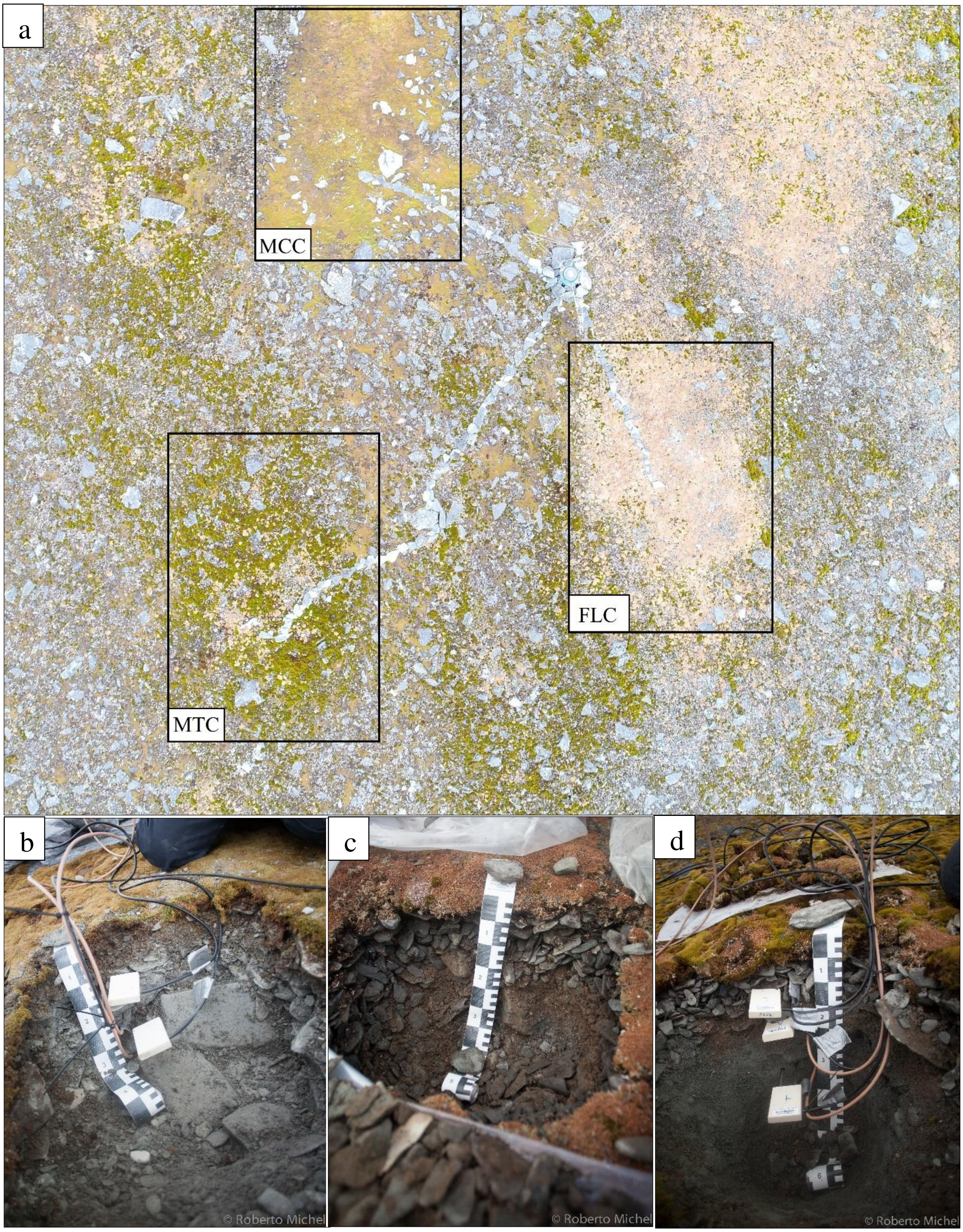
a
MCC
FLC
MTC
b
c
d
© Roberto Michel
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Fig. 2

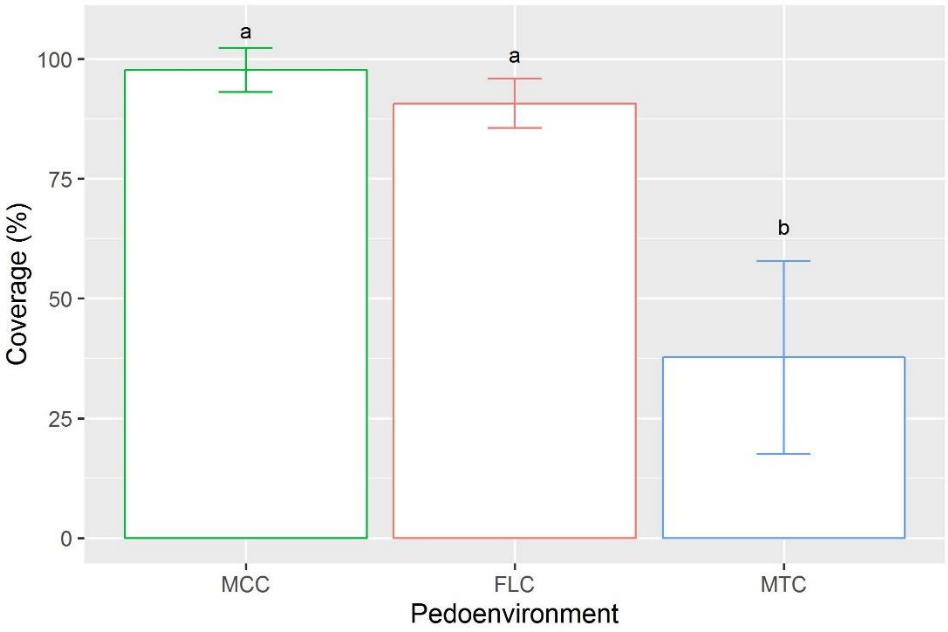


Fig. 3

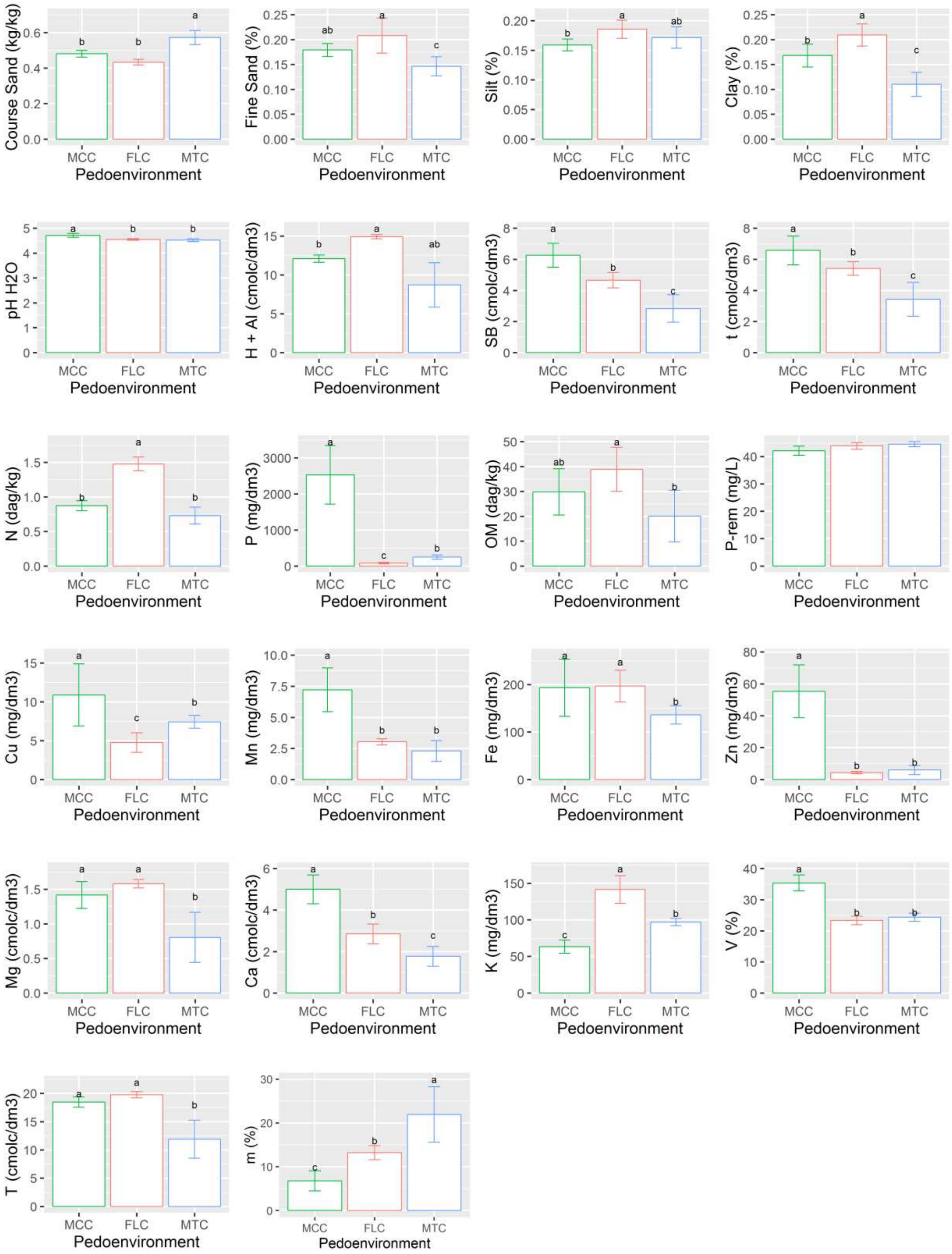
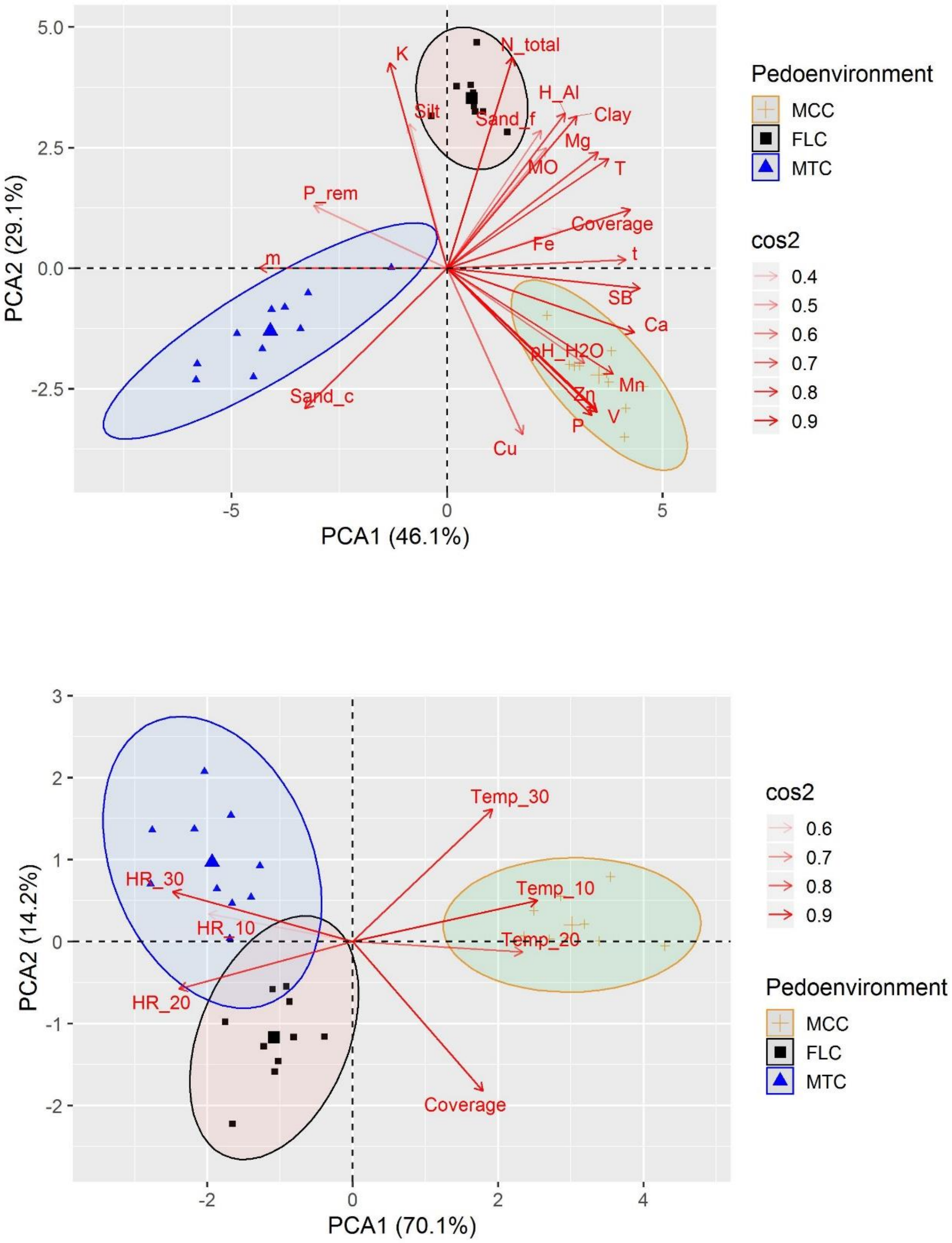

Course Sand (kg/kg)
0.0
0.2
0.4
0.6
b
b
a
Fine Sand (%)
0.00
0.05
0.10
0.15
0.20
0.25
ab
a
c
Silt (%)
0.00
0.05
0.10
0.15
0.20
b
a
ab
Clay (%)
0.00
0.05
0.10
0.15
0.20
0.25
b
a
c
pH H2O
0
1
2
3
4
5
a
b
b
H + Al (cmolc/dm3)
0
5
10
15
b
a
ab
SB (cmolc/dm3)
0
2
4
6
8
a
b
c
t (cmolc/dm3)
0
2
4
6
8
a
b
c
N (dag/kg)
0.0
0.5
1.0
1.5
b
a
b
P (mg/dm3)
0
1000
2000
3000
a
c
b
OM (dag/kg)
0
10
20
30
40
50
ab
a
b
P-rem (mg/L)
0
10
20
30
40
Cu (mg/dm3)
0
5
10
15
a
c
b
Mn (mg/dm3)
0.0
2.5
5.0
7.5
10.0
a
b
b
Fe (mg/dm3)
0
100
200
a
a
b
Zn (mg/dm3)
0
20
40
60
80
a
b
b
Mg (cmolc/dm3)
0.0
0.5
1.0
1.5
a
a
b
Ca (cmolc/dm3)
0
2
4
6
a
b
c
K (mg/dm3)
0
50
100
150
c
a
b
V (%)
0
10
20
30
40
a
b
b
T (cmolc/dm3)
0
5
10
15
20
a
a
b
m (%)
0
10
20
30
c
b
a
MCC
FLC
MTC
Pedoenvironment

Fig. 4



PCA1 (46.1%)
PCA2 (29.1%)
5.0
2.5
0.0
-2.5
-5
0
5
K
N_total
H_Al
Silt
Sand_f
Clay
Mg
MO
T
P_rem
Coverage
Fe
t
m
SB
Ca
pH_H2O
Mn
Zn
V
P
Sand_c
Cu
Pedoenvironment
MCC
FLC
MTC
cos2
0.4
0.5
0.6
0.7
0.8
0.9
PCA1 (70.1%)
PCA2 (14.2%)
3
2
1
0
-1
-2
-2
0
2
4
Temp_30
Temp_10
Temp_20
HR_30
HR_10
HR_20
Coverage
cos2
0.6
0.7
0.8
0.9
Pedoenvironment
MCC
FLC
MTC

Supplementary data

Table A.1. List of species identified in the three study areas.

Family	**Group**	**Species**	**Abbreviation**	**N. of plots***
Amblystegiaceae	moss	*Sanionia georgicouncinata* (Müll. Hal.) Ochyra & Hedenäs	San_g	10
	moss	*Sanionia uncinata* (Hedw.) Loeske	San_u	9
Bryaceae	moss	*Pohlia cruda* (Hedw.) Lindb.	Poh_c	1
Dicranaceae	moss	*Chorisodontium aciphyllum* (Hook. f. & Wilson) Broth.	Cho_a	19
Polytrichaceae	moss	*Polytrichastrum alpinum* (Hedw.) G.L. Sm.	Pol_a	2
Cephaloziellaceae	liverwort	*Cephaloziela varians*	Cep_v	2
-	liverwort	Not id hepatic		1
Cladoniaceae	lichen	*Cladonia metacorallifera* Asahina	Cla_m	9
	lichen	*Cladonia rangiferina* (L.) Weber ex F.H. Wigg.	Cla_r	10
Ochrolechiaceae	lichen	*Ochrolechia frigida* (Sw.) Lynge	Och_f	8
Pannariaceae	lichen	*Psoroma cinnamomeum* Malme	Pso_c	2
		Psoroma hypnorum	Pso_h	9
Parmeliaceae	lichen	*Usnea antarctica*	Usn_a	16
	lichen	*Usnea aurantiacoatra* (Jacq.) Bory	Usn_aa	6
	lichen	*Cornicularia aculeata (Schreb.) Ach.*	Cor_a	13
Sphaerophoraceae	lichen	*Sphaerophorus globosus (Huds.) Vain*	Sph_g	19
Not defined	lichen	*Cystocoleus niger (*Huds.) Har.	Cys_n	12

Table A.2. List of species found in each area and their respective relative frequency (F), coverage (C) and Ecological Significance Index (ESI).

Community	Species	F	C	ESI
Moss carpet	*Sanionia georgicouncinata*	100	5	600
Moss carpet	*Pohlia cruda*	10	0.2	12
Moss carpet	*Ochrolechia frigida*	10	0.1	11
Fruticose lichen	*Sphaerophorus globosus*	100	4.2	520
Fruticose lichen	*Chorisodontium aciphyllum*	100	1.3	230
Fruticose lichen	*Cladonia rangiferina*	80	1	160
Fruticose lichen	*Usnea antarctica*	80	0.9	152
Fruticose lichen	*Cystocoleus niger*	60	0.9	114
Fruticose lichen	*Cladonia metacoraliphera*	60	0.6	96
Fruticose lichen	*Usnea aurantiacoatra*	60	0.6	96
Fruticose lichen	*Cornicularia aculeata*	50	0.5	75
Fruticose lichen	*Sanionia uncinata*	40	0.7	68
Fruticose lichen	*Psoroma hypnorum*	40	0.4	56
Fruticose lichen	*Ochrolechia frigida*	30	0.3	39
Fruticose lichen	*Psoroma cinnamomeum*	20	0.2	24

Moss turf	*Chorisodontium aciphyllum*	90	3.5	405
Moss turf	*Sphaerophorus globosus*	90	1.5	225
Moss turf	*Usnea antarctica*	80	1	160
Moss turf	*Cornicularia aculeata*	80	0.8	144
Moss turf	*Cystocoleus niger*	60	0.6	96
Moss turf	*Sanionia uncinata*	50	0.8	90
Moss turf	*Psoroma hypnorum*	50	0.6	80
Moss turf	*Ochrolechia frigida*	40	0.4	56
Moss turf	*Cladonia metacoraliphera*	30	0.3	39
Moss turf	*Cephaloziela varians*	20	0.6	32
Moss turf	*Cladonia rangiferina*	20	0.3	26
Moss turf	*Polytrichastrum alpinum*	20	0.2	24

Table A.3. Morphological and physical properties of studied profiles from Stinker Point.

Depth (cm)	**Transition**	**Gravel (%)**	**CS**	**FS**	**Silt**	**Clay**	**Class**
			(%)				
Moss carpet community *Sanionia georgico uncinata*							
A 0-5	clear flat	32.34	47.4	29.6	12.9	10.1	Sandy-loam
B 5-10	diffuse flat	71.91	60.6	18.4	12.8	8.2	Sandy-loam
BR 10-	diffuse flat	78.90	57.7	18.6	18.1	5.6	Loam
Fruticose lichen community *Sphaerophorus globosus*							
A 0-15	clear flat	96.81	54.9	20.9	11.2	13.1	Sandy-loam
B 15-30	clear flat	84.84	44.1	18.4	18.6	18.9	Sandy-loam
Moss turf community *Chorisodonthium acyphillum*							
Pav 0-10	clear flat	93.88	50.3	21.5	19.4	8.9	Sandy-loam
AB 10-	clear flat	72.28	60.5	14.8	16.8	7.9	Loam
B 17-40+	clear flat	36.88	36.4	18.0	39.5	6.1	Loam

Table A.4. Chemical properties of studied profiles from Stinker Point.

Depth (cm)	pH H2O	P	K	Na	Ca^{2+}	Mg^{2+}	H + Al	SB	(t)	T	V	m	ISNa	OM	P-rem	Cu	Mn	Fe	Zn	N
			----mg/dm³----					----cmol$_c$/dm³ ----				-----%-----		dag/kg	Mg/L			----mg/dm³----		dag/k
Moss carpet community *Sanionia georgico uncinata*																				
A 0-5	4.81	4547.2	48	181.1	5.15	1.37	10.4	7.43	7.73	17.83	41.7	3.9	4.42	10.11	38.9	12.73	8.4	175.2	63.42	0.196
B 5-10	5.24	6761.8	38	192.1	4.49	0.83	7.1	6.25	6.25	13.35	46.8	0.0	6.26	2.61	46.3	22.91	11.6	364.9	81.18	0.385
BR 10-30	5.16	880.2	65	71.4	3.03	0.28	5.6	3.79	4.29	9.39	40.4	11.7	3.31	1.3	48.2	5.47	0.9	144.2	3.2	0.298
Fruticose lichen community *Sphaerophorus globosus*																				
A 0-15	4.64	1019.9	76	108.3	3.82	1.38	8.1	5.87	6.37	13.97	42.0	7.8	3.37	2.61	38.6	7.06	6.2	165.2	8.16	0.215
B 15-30	5.21	6880.9	35	175.7	8.19	1.29	8.6	10.33	10.33	18.93	54.6	0.0	4.04	4.17	32.9	42.30	15.0	176.0	112.38	0.140
Moss turf community *Chorisodontium aciphyllum*																				
A 0-10	5.35	5894.0	76	215.6	6.63	1.47	6.6	9.23	9.23	15.83	58.3	0.0	5.92	1.43	44.1	30.24	16.4	296.5	84.78	0.196
AB 10-17	5.54	5644.5	56	235.5	4.55	0.73	4.0	6.45	6.45	10.45	61.7	0.0	9.80	1.3	42.5	43.62	13.1	327.6	90.30	0.329
B 17-40+	5.3	1217.1	55	55.5	2.83	0.36	4.5	3.57	4.07	8.07	44.2	12.3	2.99	1.43	47.5	9.53	1.6	169.5	6.37	0.215

Table A. 5. Annual means of temperature between different depths by sites, in the period from January 30, 2016 to December, and throughout the year 2017.

	Temperature (ºC)					
	2016			2017		
	10cm	20cm	30cm	10cm	20cm	30cm
MCC	-0.4	0.6	-0.7	-0.8	-1.0	-1.1
FLC	-1.3	-1.4	-1.4	-1.2	-1.4	-1.4
MTC	-1.2	-1.3	-1.3	-1.2	-1.4	-1.3

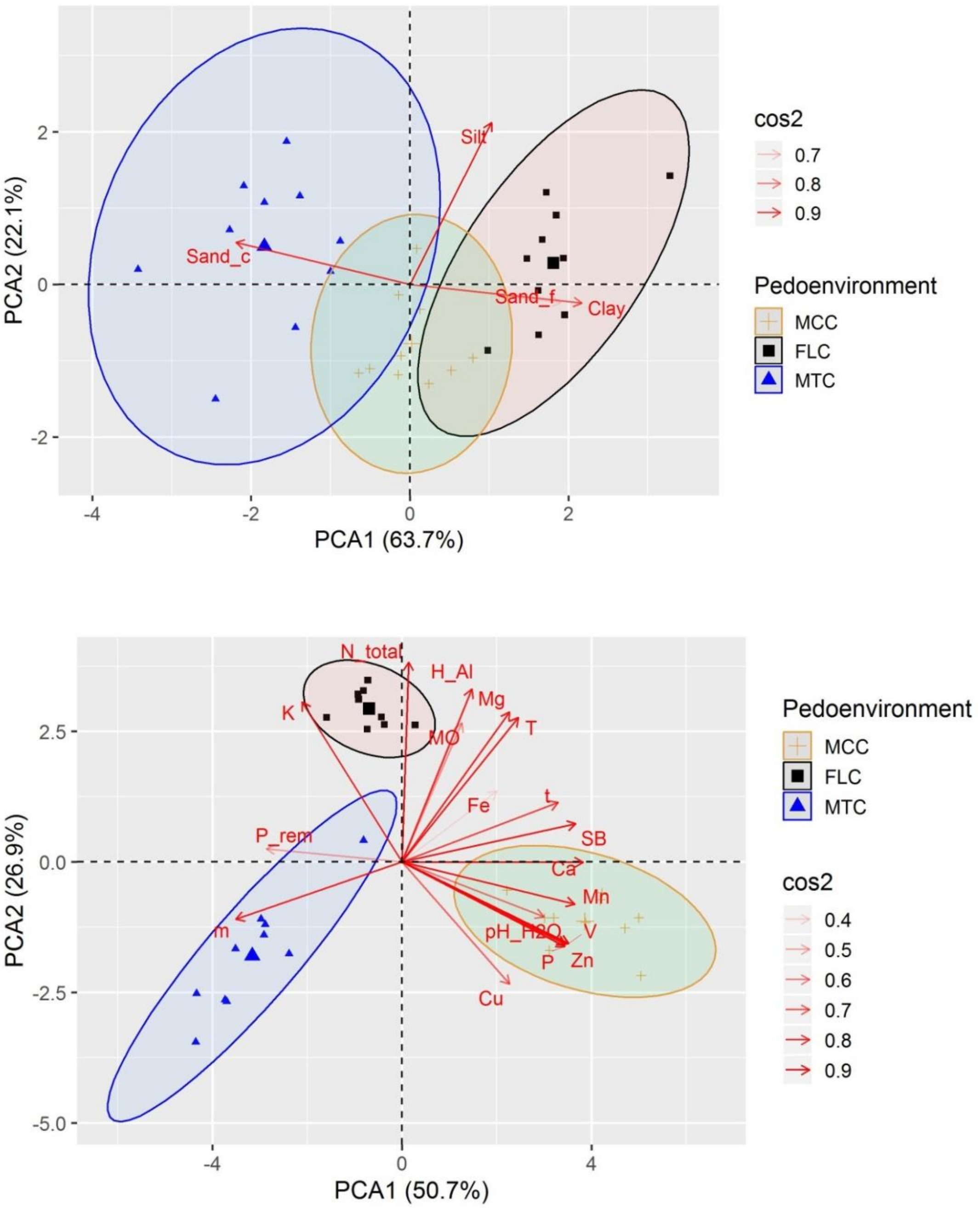


Fig. A.3. Principal Component Analysis (PCA) for the physical (biplot above) and chemical (biplot below) properties of the three studied pedoenvironments. For analysis, available: total N, available P, K, Ca, Mg, Fe, Cu, Mn, Zn. P-rem, exchangeable acidity (H + Al), pH (H_2O), organic matter (OM), sum of exchangeable bases (SB); effective cation exchange capacity (t), basis saturation index (V) and effective cation exchange capacity to pH=7 (T); and the soil texture as coarse sand (Sand_c). fine sand (Sand_f). clay and silt contents were included. The pedoenvironments studied present the following plant communities: Moss carpet community (MCC), fruticose lichen community (FLC), and moss turf community (MTC).

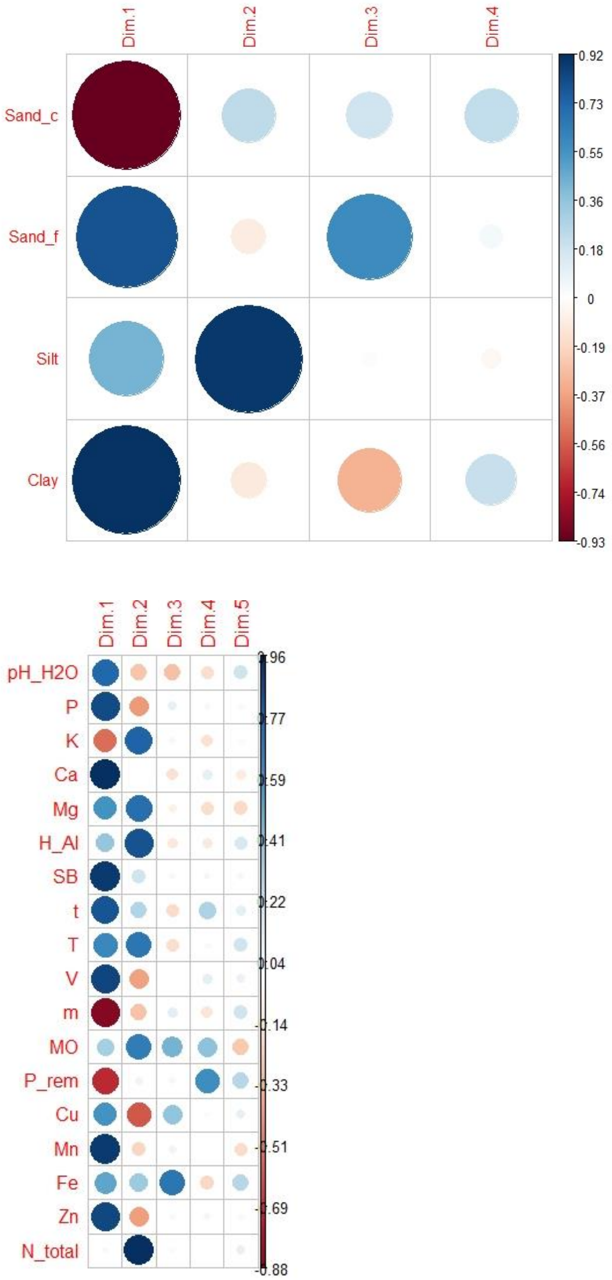


Fig. A.4. Significance levels are based on Spearman correlation coefficients between physical (above) and chemical (below) properties and principal components of both PCA1 and PCA2 from 30 different plots of the three studied pedoenvironments. Factors that significantly correlated with PCA axes are highlighted in big circles in PCA1 and PCA2. For analysis, nutrients, exchangeable acidity (H^+Al), pH, organic matter (OM), potential cation exchange capacity (T), remaining phosphorus (P-Rem), percentage of bases saturation (V), 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.

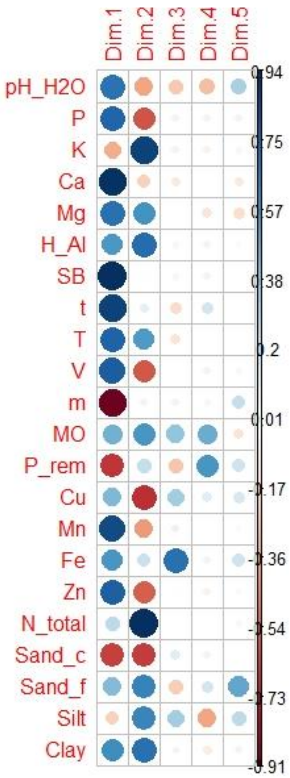


Fig. A.5. Significance levels are based on Spearman correlation coefficients between soil parameters and principal components of both PCA1 and PCA2 from 30 different plots along the pedoenvironmental gradient. Factors that significantly correlated with PCA axes are highlighted in big circles in PCA1 and PCA2. For analysis, nutrients, exchangeable acidity ($H^{+}Al$), pH, organic matter (OM), potential cation exchange capacity (T), remaining phosphorus (P-Rem), percentage of bases saturation (V), 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.

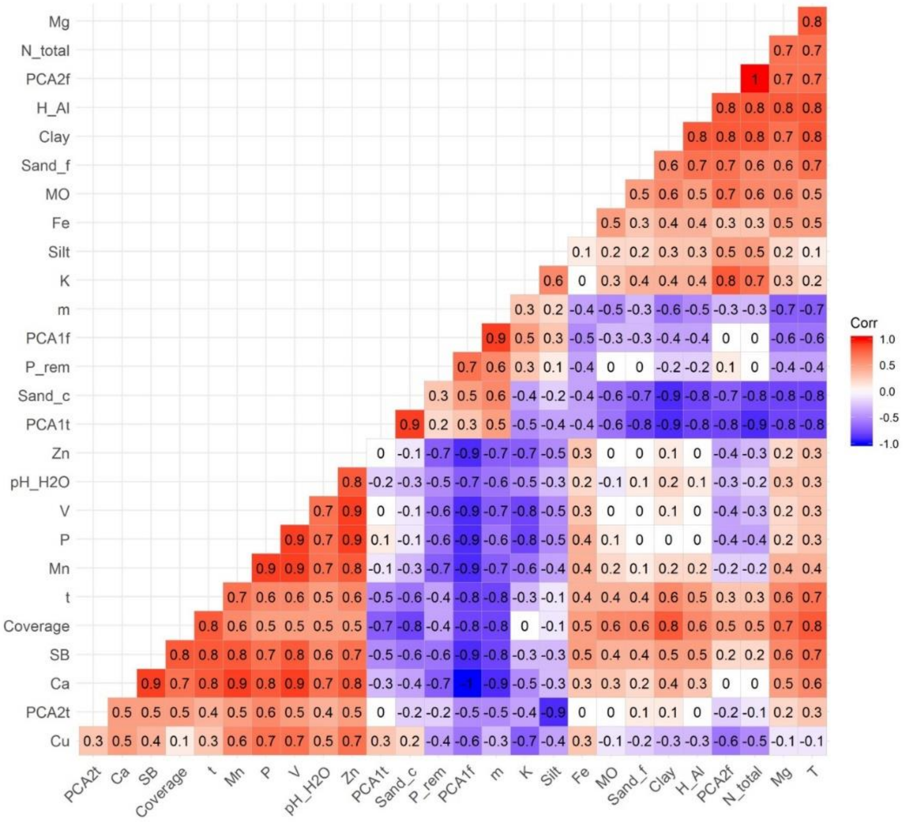


Fig. A.6. Spearman correlation among all individual variables measured in 30 plots along a pedoenvironmental gradient. For analysis, available: nutrients, exchangeable acidity (H + Al), pH (H_2O), organic matter (OM); effective cation exchange capacity (t), potential cation exchange capacity (T), sum of exchangeable bases (SB), remaining phosphorus (P-Rem), percentage of bases saturation (V), and the soil texture as coarse sand (Sand_c), fine sand (Sand_t), clay and silt contents were included. Factors that significantly correlated with PCA axes of texture (PCA1t, PCA2t) and fertility (PCA1f, PCA2f) are highlighted in red color.

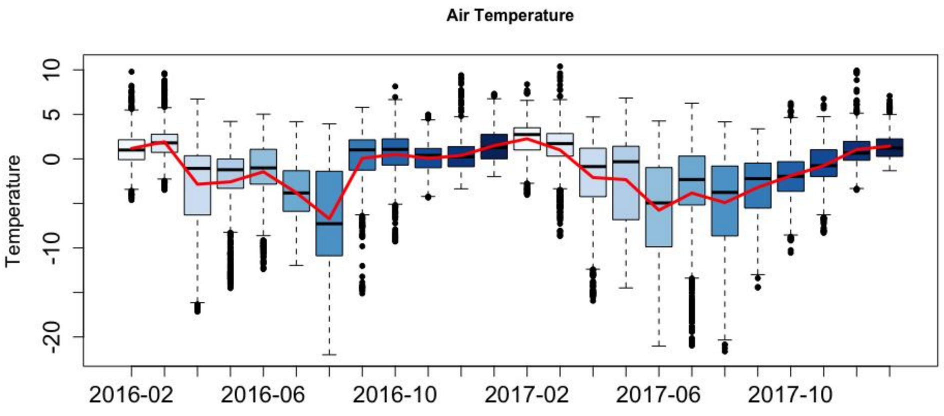


Fig. A.7. Fig. 3. Air temperature (hourly intervals) of Stinker Point, Elephant Island, South Shetlands, Maritime Antarctica (2016–2018). Sensor located at 1 m above soil surface.

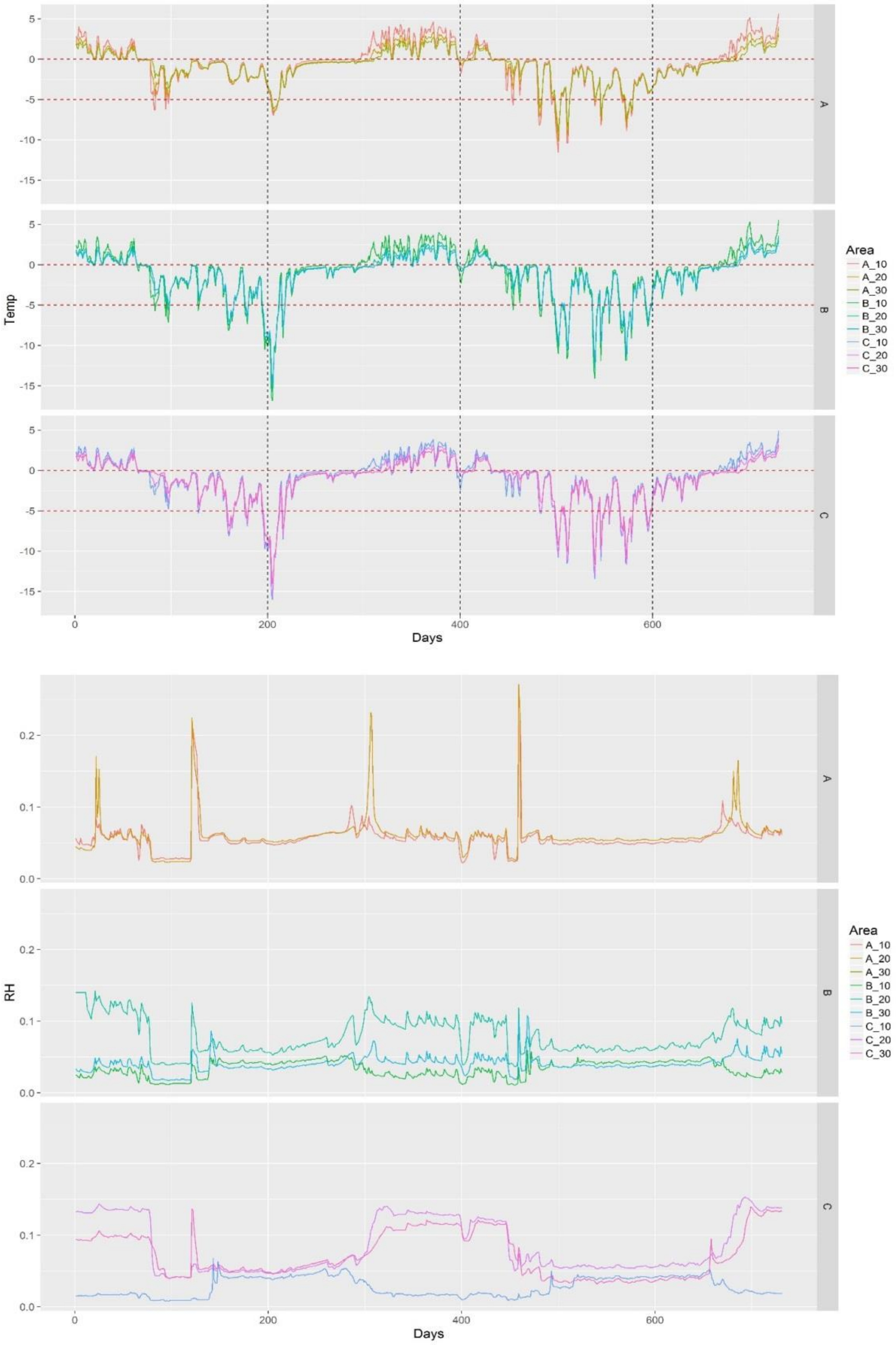


Fig. A.8. Daily mean soil temperatures (A) and relative humidity (B) measured at the soil depth of 10. 20 and 30 cm for the whole two years respectively at A) Moss carpet, B) Fruticose lichen and C) Moss turf community.

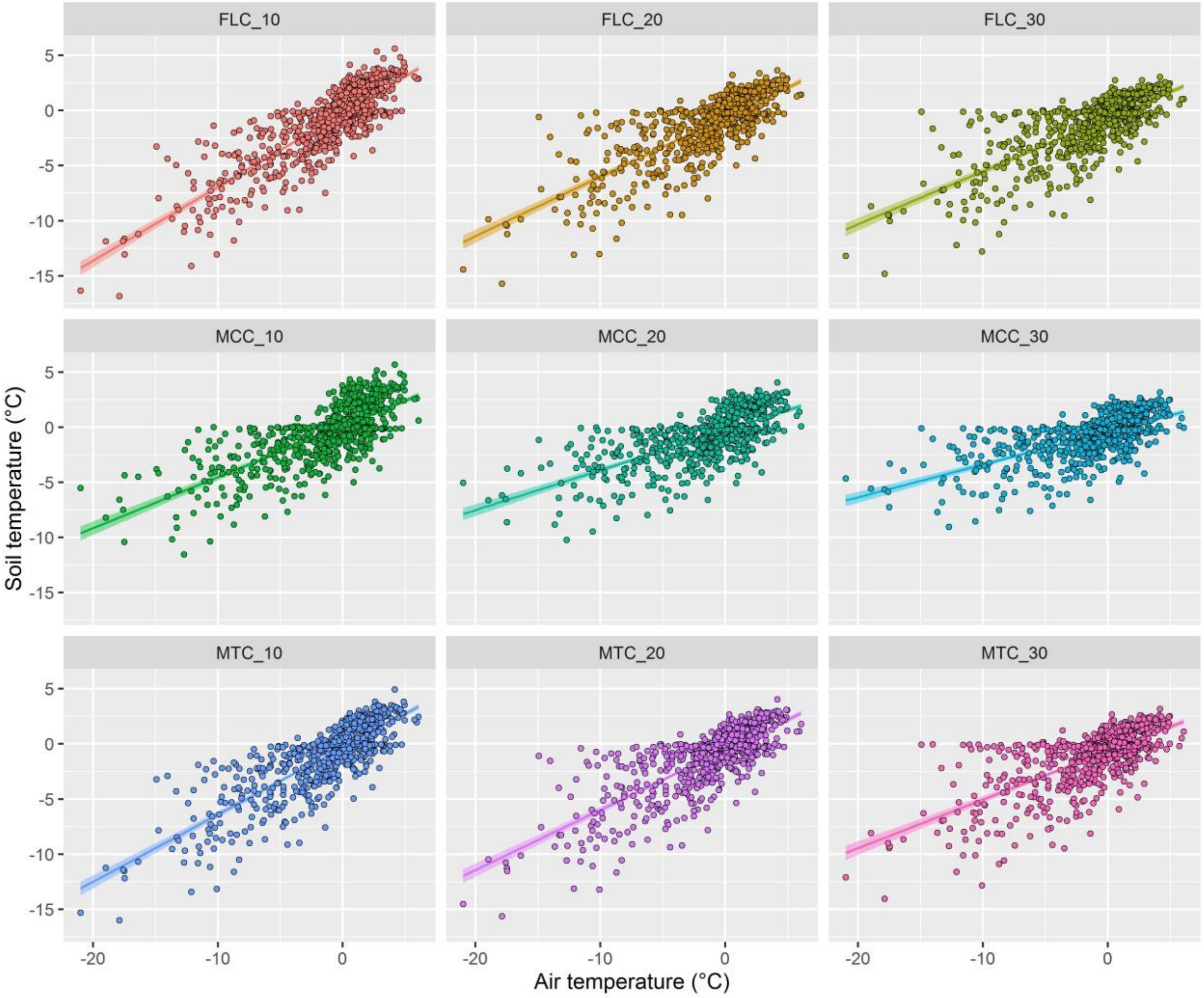


Fig. A.9. Main effects of air temperature on temperature in the soil profile (variable response) using a covariance analysis (ANCOVA). Solid lines represent the fitted values (prediction) of the models, and the shaded area the 95 % confidence interval of the predicted values of each model.

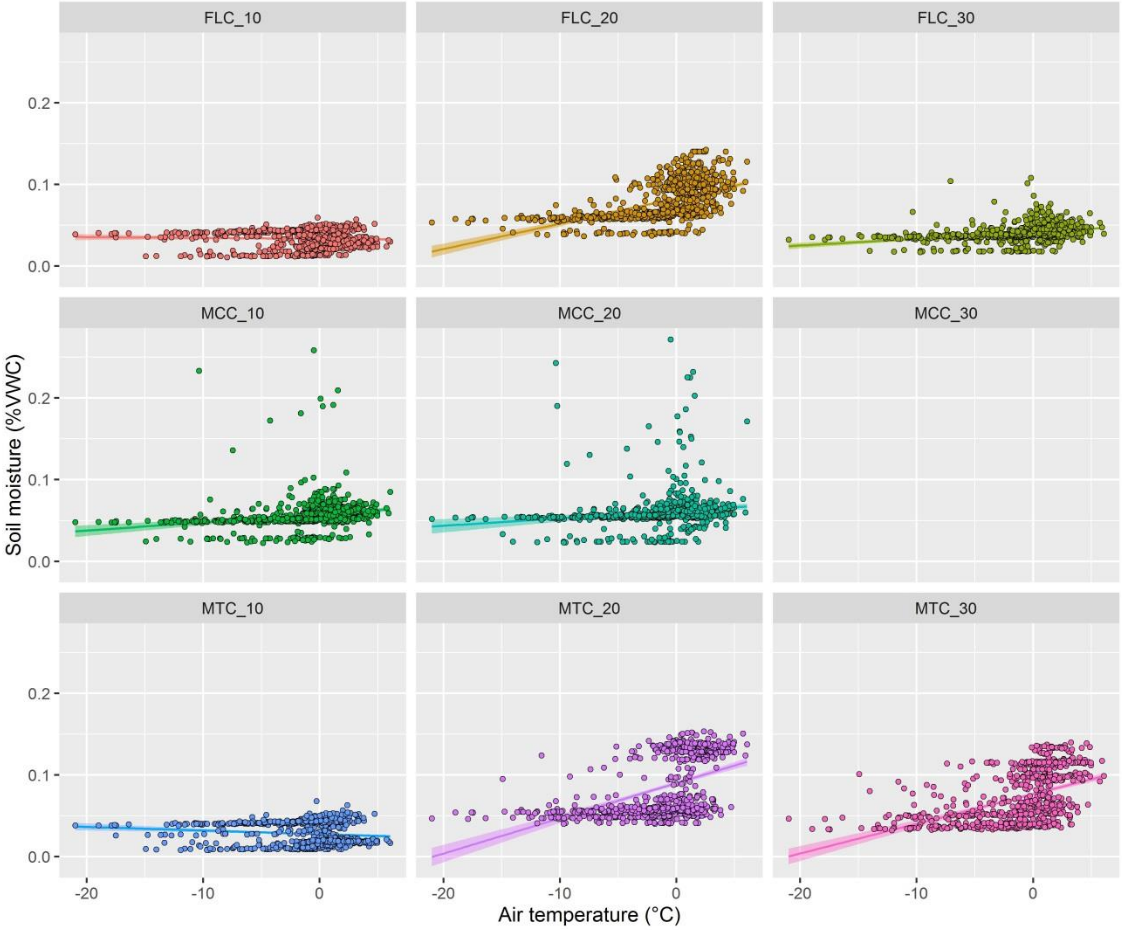


Fig. A.10. Main effects of air temperature on soil moisture (variable response) using a covariance analysis (ANCOVA). Solid lines represent the fitted values (prediction) of the models, and the shaded area the 95 % confidence interval of the predicted values of each model.

CONCLUSÃO GERAL

Os resultados desta pesquisa demonstraram que existe uma alta heterogeneidade pedoambiental em uma fina escala dentro e entre as áreas de degelo das três ilhas estudadas na Antártica Marítima. Assim, observou-se uma diferenciação de hábitats que foi determinada principalmente pela alta variabilidade das propriedades físicas e químicas dos solos, as quais definiram gradientes edáficos contrastantes entre os pedoambientes nas ilhas. Em consequência, demonstrou-se que houve diferenças no padrão de riqueza, composição de espécies e cobertura vegetal de comunidades de plantas não vasculares ao longo dos diferentes gradientes pedoambientais analisados na Antártica Marítima. No entanto, diferenças na riqueza e composição de espécies não foram tão acentuadas quanto o esperado, mostrando altos graus de similaridade entre os diferentes pedoambientes.

A composição de espécies de plantas não vasculares diminui em similaridade com o aumento das diferenças nas propriedades do solo ao longo dos gradientes pedoambientais, promovendo alta diversidade β. Essas variações na Antártica Marítima, também podem ser devido a diferentes processos periglaciais, grau de intemperismo, material parental e influência biológica (especialmente por pinguins e outras aves) que devem ser melhor estudados. A riqueza de espécies e a cobertura vegetal ao longo do gradiente pedoambiental foram diferentes; no entanto, eles compartilham espécies em comum que estão presentes na maioria dos pedoambientes, apesar das diferenças na cobertura vegetal. Observamos que muitos pedoambientes registraram espécies raras que ocorreram apenas sob condições específicas do solo, o que também contribui para a alta troca de espécies entre os pedoambientes e baixa similaridade florística, o que promove a alta diversidade β.

Nós presumimos que a elevação pós-glacial na Antártica Marítima pode promover um gradiente topográfico de influência ornitogênica, responsável por diferenças nas propriedades do solo. Essas diferenças edáficas definiram um gradiente pedoambiental heterogêneo que impulsiona os padrões de diversidade e de cobertura vegetal. Por enquanto, os pedoambientes recém-expostos apresentam menor riqueza de espécies e cobertura vegetal. Além disso, neste estudo também se demonstrou que as propriedades do solo e o padrão de cobertura vegetal ao longo do gradiente pedoambiental, também podem induzir mudanças no regime térmico e higrométrico da camada ativa no solo, promovendo um maior isolamento térmico nos solos com maior cobertura vegetal; e ainda, que existem efeitos da temperatura do ar sobre a temperatura do solo na camada ativa ; Assumimos que outros fatores têm relações próximas para diferentes processos no permafrost que devem ser melhor estudados.

Estes resultados permitem concluir, que a filtragem pedoambiental (filtragem de hábitats) pode determinar diferentes padrões de diversidade e estrutura de comunidades de plantas não vasculares através de diferentes processos em cada uma das ilhas. Pode-se inferir que preditores ambientais (e.x., propriedades físicas e químicas do solo) atuam de forma distinta em cada ilha, e que em cada ilha cada preditor tem importâncias relativas diferentes para explicar variações na diversidade e estrutura das comunidades de plantas não vasculares. Este é um resultado inédito de relevância dentro dos estudos de ecologia de comunidades vegetais na Antártica, uma vez que, os processos que estruturam a vegetação podem ser importantes indicadores na avaliação das mudanças climáticas. Por tanto, o monitoramento destas comunidades vegetais, deve partir de critérios rigorosos para avaliar efeitos de condições ambientais específicas de cada ilha, que além de considerar a alta variabilidade pedoambiental em fina escala, deve considerar também a escala local e regional. Desta forma, recomenda-se ajustar um método de análise e monitoramento que permita diferenciar a sensibilidade destas comunidades aos verdadeiros efeitos das mudanças climáticas globais.