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Microscale is key to model current and future Maritime Antarctic vegetation

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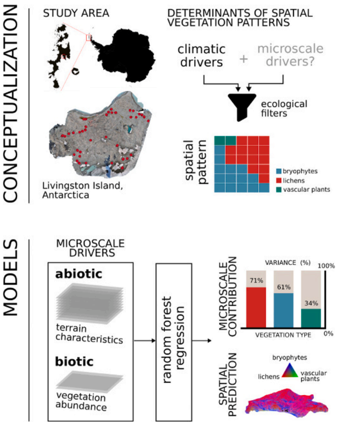
HIGHLIGHTS

- Microscale explained >60 % of lichens and bryophytes cover.
- Niche analysis suggested their likely preference for specific microscale niches.
- Including microscale in climate change ecological models is critical.

GRAPHICAL ABSTRACT



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ABSTRACT

Despite being one of the most pristine regions in the world, Antarctica is currently also one of the most vulnerable to climate change. Antarctic vegetation comprises mostly lichens and bryophytes, complemented in some milder regions of Maritime Antarctica by two vascular plant species. Shifts in the spatial patterns of these three main vegetation groups have already been observed in response to climate change, highlighting the urgent need for the development of comprehensive large-scale ecological models of the effects of climate change.

Besides climate, Antarctic terrestrial vegetation is also strongly influenced by non-climatic microscale conditions related to abiotic and biotic factors. Nevertheless, the quantification of their importance in determining vegetation patterns remains unclear. The objective of this work was to quantify the importance of abiotic and biotic microscale conditions in determining the spatial cover patterns of the major functional types, lichens,

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vascular plants and bryophytes, explicitly determining the likely confinement of each functional type to the microscale conditions, i.e., their ecological niche.

Microscale explained >60 % of the spatial variation of lichens and bryophytes and 30 % of vascular plants, with the niche analysis suggesting that each of the three functional types may be likely confined to specific microscale conditions in the studied gradient. Models indicate that the main microscale ecological filters are abiotic but show the potential benefits of including biotic variables and point to the need for further clarification of vegetation biotic interactions' role in these ecosystems. Altogether, these results point to the need for the inclusion of microscale drivers in ecological models to track and forecast climate change effects, as they are crucial to explain present vegetation patterns in response to climate, and for the interpretation of ecological model results under a climate change perspective.

1. Introduction

Antarctica hosts some of Earth's most pristine ecosystems, a result of its geographic isolation and extreme climate (Gross, 2022). Over millennia, the harsh climatic conditions shaped simplified ecosystems, where species live at the edge of survival in a fragile equilibrium that may be disrupted even by small microclimatic changes (Lenne et al., 2010; Robinson et al., 2003). Antarctic vegetation is mostly composed of lichens and bryophytes, complemented in some of the milder regions of the Antarctic Peninsula by two vascular plant species (Convey et al., 2014). Shifts in the spatial patterns of these three main functional types have already been observed in response to climate change (Cannone et al., 2022; Guglielmin et al., 2014; Miranda et al., 2020; Robinson et al., 2018). Given this fragile ecosystem equilibrium, it is urgent to understand and model the effects of climate change at the regional scale. These models are crucial to signal risk areas where more in-depth research should be done and to help design better conservation strategies.

Antarctica's remote location and extreme conditions have limited the number of regional and long-term ecological data sets (Brabyn et al., 2006; Cannone, 2006; Cannone et al., 2016; Cannone et al., 2022; Colesie et al., 2022; Fowbert and Smith, 1994; Parnikoza et al., 2009). The absence of these has hindered our capacity of building good ecological predictive models, halting a comprehensive view on the possible ongoing and future large-scale impacts of climate change (Koerich et al., 2022). Remote sensing data from UAS or satellites has recently emerged as a valuable tool to expand spatial and temporal data (Turner, 2014). Though these techniques are still limited in distinguishing smaller life forms, they have enabled progress into a better understanding of the spatial and temporal patterns of the main vegetation functional types, lichens, bryophytes and vascular plants, of terrestrial Antarctica (Casanovas et al., 2015; Colesie et al., 2022; Miranda et al., 2020; Sotille et al., 2022; Sotille et al., 2020; Turner et al., 2018) and similar Arctic ecosystems (Huemmrich et al., 2013; Langford et al., 2016). While coarser in detail, the information retrieved can be a priceless contribution to signal areas undergoing change, where on-site more detailed measurements (e.g., community composition) should be done to validate and complement this information, enabling a more thorough understanding of the patterns of change, and to extrapolate from point data to regional scales (Turner, 2014).

In addition to climate, Antarctic terrestrial vegetation is thought to be strongly influenced by non-climatic microscale conditions related to abiotic and biotic factors. Small variations in abiotic microscale terrain characteristics may dictate variations in, for instance, water availability, wind exposure, snow accumulation, or solar radiation, which can result in different community patterns and ultimately shifts from moss or plant, to lichen dominated communities (Andrade et al., 2018; Lucieer et al., 2014; Schwarz et al., 1992; Seppelt and Ashton, 1978). In addition, recent studies in Antarctica have suggested that biotic interactions also play an important role at the microscale in soil microorganisms (Caruso et al., 2019; Caruso et al., 2013; Lee et al., 2019), suggesting they could also play an important role in determining vegetation patterns. Quantifying the contribution of abiotic and biotic microscale conditions in determining the spatial patterns of different functional types is therefore crucial. This should include to what extent the different functional types are more likely to be linked to specific microscale abiotic and biotic conditions, i.e., their niche along a microscale gradient, as this is key to understand their response under climate change (Cramer et al., 2022). Nevertheless, the role these biotic and abiotic microscale drivers may play in determining vegetation patterns remains unclear.

The objective of this work was to quantify the importance of abiotic and biotic microscale conditions in determining the cover spatial patterns of the major functional types, lichens, vascular plants and bryophytes, explicitly determining the likely confinement of each functional type to the microscale conditions, i.e., their ecological niche. The research was designed from an ecological modelling perspective. Sampling was done along a topoclimatic gradient, here determined by altitude and distance to the coast. These have been previously identified as inducing sharper shifts in Antarctic vegetation than latitudinal climatic gradients (Cannone, 2006) and are logistically more feasible. The use of a classification into three functional types refers to the simplest classification that can be performed in image analysis from remote sensing products, warranting at least the separation of these three ecologically different groups. This ensures the applicability of this methodology across different spatial scales of image-based modelling analysis, favouring the spatial and temporal cover as a tool to signal areas where mode detailed analysis should be performed. Furthermore, this approach based on vegetation functional types has long been recognized to enhance process-based biogeography modelling (Prentice et al., 1992) and as an essential part of dynamic global vegetation modelling, namely to analyse climate impacts on vegetation structure (Prentice and Cowling, 2013). Given that microscale drivers are known to induce shifts in these vegetation functional types in Antarctica (Andrade et al., 2018; Lucieer et al., 2014; Schwarz et al., 1992; Seppelt and Ashton, 1978), and that shifts resulting from microscale variation along small topoclimatic gradients has shown to be bigger than that associated with large latitudinal gradients in Antarctica (Cannone, 2006), we hypothesize that microscale abiotic and biotic characteristics will determine a large part of the spatial patterns of vegetation functional types. Vegetation cover was modelled with microscale drivers (abiotic only and all [biotic + abiotic]) to understand how much variance they account for. The most important drivers were afterwards used to determine the functional types' microscale niche.

2. Material and methods

2.1. Study area

The study took place in the area surrounding the Juan Carlos I Spanish Antarctic station. The station is located in Hurd Peninsula (Fig. 1), on the southeastern coast of Livingston Island, South Shetlands Archipelago, Maritime Antarctic. The annual mean air (2 m) and close to soil (20 cm) temperatures in the last 22 years were −2.1 °C and −0.03 °C, respectively (mean calculated from monthly average values for the period of 1998–2020), (AEMET, 2023). The average annual precipitation was 419 mm and the average wind speed was 3.58 m/s predominantly blowing from NNE or SSW (approximately 11 and 12 %

each).

The moderately mild summers in the study area enable the development of a relatively dense vegetation cover. On lower wet beach terraces mosses dominate, namely *Sanionia uncinata* (Hedw.) Loeske, *Brachythecium austro-salebrosum* (C. Müll.) Kindb. and *Bryum pseudotriquetrum* (Hedw.) Gaertn., Meyer & Scherb., whereas drier and more elevated beaches are predominantly colonized by *Usnea aurantiaco-atra* (Jacq.) Bory if stable pebbles are present, or by the moss *Polytrichum piliferum* Hedw. if the substrate is sandy. Moving uphill and inland, a dense mixed mat of lichens and mosses can be seen. If a soil substrate is present, the most frequent species are *Stereocaulon alpinum* Laur., *Sphaerophorus globosus* (Huds.) Vain., *Cladonia* spp., *S. uncinata*, *Polytrichum alpinum* Hedw. And *Tortula* spp. The two vascular plants, *Deschampsia antarctica* Desv, and *Colobanthus quitensis* (Kunth) Bartl., constitute a very small fraction of the vegetation in the whole study area, and can mostly be observed in these mats. As the substrate is increasingly composed of small stable loose rocks, *Usnea antarctica* Du Rietz, and *U. aurantiaco-atra* dominate. With increasing altitude *U. aurantiaco-atra* and *Himantormia lugubris* (Hue) Lamb become the dominant lichen species, growing together with the mosses *Andreaea gainii* Card. and *A. regularis* C. Müll.

2.2. Experimental design

As the primary interest of the work is to understand the contribution of microscale abiotic and biotic drivers under a climate change perspective, 37 locations were chosen along elevational and distance to coast gradients in the study area, used here as a proxy of a spatial climatic gradient. Both variables have previously shown to depict shifts in vegetation patterns in response to climatic conditions (Cannone, 2006). Elevation ranged between 2.7 m and 270.6 m altitude, while distance from coast spanned from 42 to 967 m. To comply with the rough terrain conditions and with The Protocol on Environmental Protection to the Antarctic Treaty (https://www.ats.aq/e/protocol.html), these spatial altitudinal and distance to coast gradients were distributed along existing trails. This ensured safety conditions for accessing sampling sites, and that sampling impacts due to trampling between sites were kept to the minimum. Sampling locations are located 50 m apart from each other along the trails, and this distance was increased if altitude or distance to coast were similar between adjacent locations, or when no flat surfaces were available. At each sampling location, five random samples were taken to encompass the microscale variation due to abiotic terrain morphology and/or biotic conditions, resulting in a total of 185 individual sampling sites. These 185 sites were used in the statistical analysis as independent samples to understand the influence of microscale variation.

To understand the influence of microscale drivers on the spatial vegetation patterns, the work followed five steps: 1) estimation of vegetation cover; 2) extraction of microscale abiotic terrain morphology data; 3) multicollinearity diagnosis of abiotic variables; 4) modelling procedures; 5) determination of microscale niche.

2.2.1. Estimation of vegetation cover

Sampling was done in February 2019 and January and February 2020 using an image-based ecological standard sampling methodology (Concostrina-Zubiri et al., 2014). This methodology allows for a faster on-site sampling procedure and enables future calibration with UAS and satellite images for upscaling the spatial extent of the studies. At each sampling site, a quadrat of 30 cm side was randomly placed on ground surface, ensuring it had an inclination lower than 20°. The quadrat was photographed (average quadrat image resolution of 0.1 mm) for posterior functional type cover determination and the GPS coordinates were taken. A total of 185 images were analysed.

In the lab, images were rectified for distortion using Darktable 4.0, to ensure a correct dimensioning of the sampling square in the image. Afterwards, using ImageJ software (1.53 K), the square was size calibrated, and a grid of 3 cm quadrats was superimposed on the image to divide the 30 cm square into 100 small grid cells. The presence of each functional type, lichens, bryophytes and vascular plants, inside the grid was recorded (Fig. 2). Image was zoomed in, and each 3 cm^2 quadrat cell was inspected for the presence of the three different functional types, including those growing on soil, over other vegetation, on rock surfaces

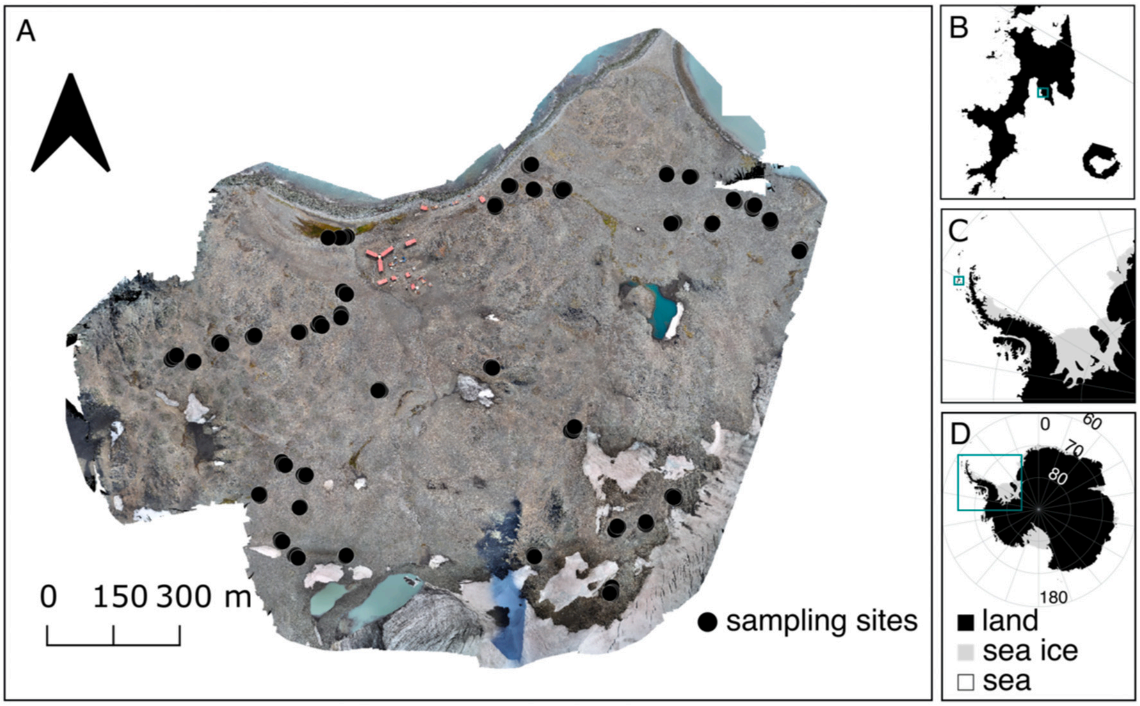

Fig. 1. Orthophotomosaic of the study area with sampling sites (A) and its location in Hurd Peninsula, Livingston Island (B), Antarctic Peninsula (C) and Antarctica (D). Straight grey lines indicate longitude (degrees) at a 20° interval, curved grey lines indicate latitude at 10° interval (A, B and C).

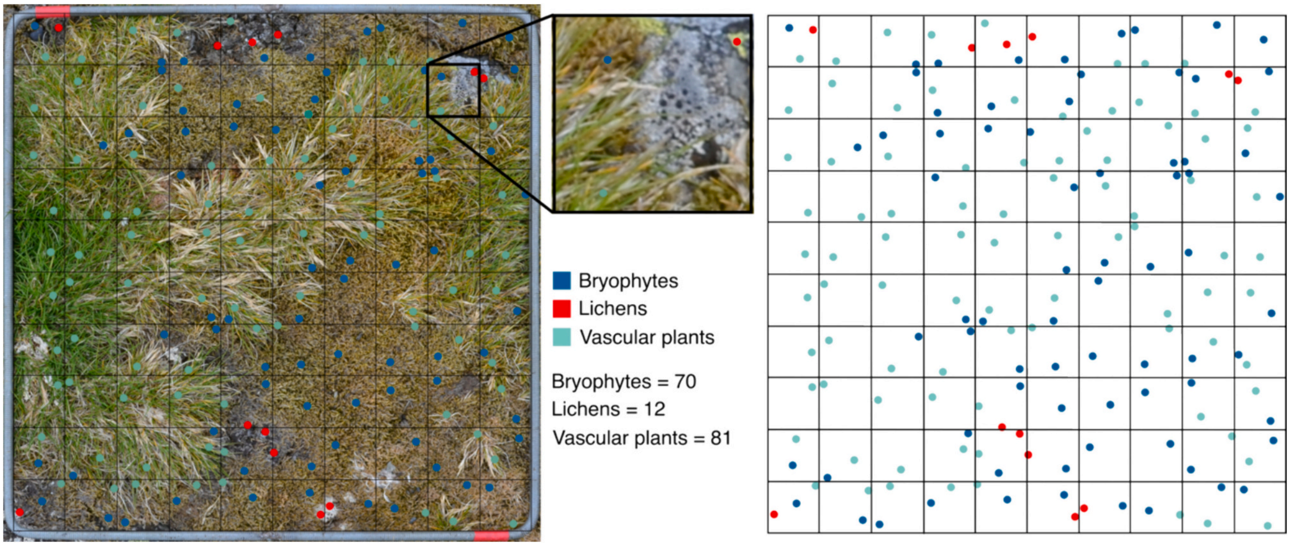

Fig. 2. Scheme depicting an example of how estimation of vegetation cover was done. A grid of 100 × 3 cm^2 squares was superimposed over the sampling image and the presence of each functional type inside each square was registered. The cover of each functional type corresponds to the sum of all squares where each group is present.

or on loose rocks. A dot placed at the centre of the thallus of one species of each of three functional types, marked each taxa presence in each 3 cm^2 cell of the grid. This was done a single time per cell (i.e., maximum frequency for each functional type inside each 3 cm^2 quadrat cell is one), even if more than one species of each functional type was present, or if different individuals were found. This procedure was repeated for the 100 cells of each of quadrat. The results for each sampling site were exported as a csv file, containing the identified functional type observed in each cell of the grid. Cover of each functional type corresponds to the sum of grid cells where they were present (maximum cover of 100 in each sampling site for each functional type). Cover was used in absolute values, unless otherwise indicated.

2.2.2. *Microscale topographic data*

An ultra-high-resolution Digital Surface Model (DSM) with a pixel size of 2 cm was obtained for the study area using an unmanned aerial system (UAS). The images were captured by a DJI Phantom 4 Pro drone, equipped with a high-resolution camera (12.4 mp resolution). The drone flew over the study area at an altitude of 70 m in terrain following mode, capturing images at regular intervals. The images were processed using the Pix4D software, which generated the DSM for the study area (RMSE = 0.075 m). Seven ground control points measured with a differential GPS (Trimble R6) were used for the DSM correction. Since the area shows only very low vegetation and is mostly bare ground, the DSM can be interpreted as a Digital Elevation Model, except for the rare snow patches, which show some noise but don't affect analytical results. The DSM was resampled to 50 cm and was used to calculate 30 terrain attributes related to morphometry, hydrology, and lighting. These indices were chosen as they portray an array of terrain characteristics that may reflect important ecological conditions, like water accumulation, slope or potential solar radiation. These are important drivers of Antarctic terrestrial vegetation (Andrade et al., 2018; Lucieer et al., 2014; Schwarz et al., 1992; Seppelt and Ashton, 1978). The description of all the indices (and software used) can be found in table S1 (Supplementary Material). In addition to these 30 indices, we also used distance to coast. This was included as a proxy for the potential deposition of minerals and organic matter originating in the sea and transferred as aerosols or by sea birds and mammals (Nędzarek, 2008).

Prior to index extraction, quadrat photographs were georeferenced and overlayed on the mosaic image used to build the DEM. If slightly deviated, quadrat position was corrected using the "freehand raster georeferencer" plugin in QGIS 3.28.3. Altitude was included in the set of variables to represent the macroscale variation related to the spatial climatic gradient but was not included in the models. Microscale environmental variables calculated correspond to the mean value of each index in the area occupied by the sampling quadrat.

2.2.3. *Statistical analysis*

Regression models were implemented in R statistical software (R Core Team, 2023) to predict each functional type cover based on microscale variables. Random forest (RF) regressions were chosen as a flexible nonparametric approach that accurately depicts interactions and non-linear ecological relationships between response and predictor variables (Cutler et al., 2007). Though random forest regressions are not much affected by collinearity (Dormann et al., 2013), redundant abiotic microscale variables were removed prior to model construction. Collinearity diagnosis was performed by calculating the variable inflation factor (VIF) using the "vifstep" function in the "usdm" library through a stepwise procedure, excluding variables with a VIF > 5.

The resulting non-collinear abiotic microscale variables (Table 1) were used to build the RF models using "randomForest" function of the library with same name. In this model implementation, abiotic variables can potentially affect the spatial cover patterns of the three functional types at the microscale (hereafter referred to as abiotic model). Nevertheless, biotic interactions, i.e., interaction between different functional types, either positive, or negative, can also influence the spatial cover patterns at the considered microscale. For that reason, a second set of RF models was built including the cover of the other functional types as biotic variables (hereafter referred to as all). Models were built for each functional type separately. Random splitting of data into training and testing was set to 80/20 ratio. To keep the underlying spatial vegetation structure resulting from the altitudinal gradient, splitting was done taking this structure into account. Eleven equal classes of altitude were created at a 25 m interval, and random splitting of data into 80/20 ratio was applied accounting with these altitudinal classes. This process was repeated 100 times, and each splitting was used to run a model to account for the possible effect of random splitting of data. RF models were built using 1000 trees and 7 variables randomly sampled at each split. Variable importance in each model was assessed using the "varImp" function of "caret" library. For each RF regression model the Root Mean Square Error (RMSE), cross validation correlation (spearman correlation coefficient between observed and predicted values in the testing set) and

Table 1
Description of microscale variables included in the random forest models. For the complete set of variables considered see Supplementary material Table S1.

Variable	Code	Description
Aspect	Asp	Mean facing direction of each sampling quadrant recoded into 8 cardinal positions: N [337.5°, 22.5° [NE [22.5°, 67.5°[E [67.5°, 112.5°[SE [112.5°, 157.5°[S [157.5°, 202.5°[SW [202.5°, 247.5°[W [245.5°, 292.5°[NW [292.5°, 337.5°[.
Channel Network distance	ChanNetDis	Distance from a given point in the terrain to the nearest channel or stream.
Convergence index	Conv	Indicates convergent (channels) and divergent areas (ridges), calculated by the agreement of aspect direction of surrounding cells.
Cross sectional curvature	CrosSecCurv	The tangential curvature intersecting with the plane defined by the surface normal and a tangent to the contour - perpendicular to maximum gradient direction
Distance to coast	DistCoast	Shortest linear distance to the nearest coastline.
Hillshading	HillSh	Shaded relief, varying from 0 (complete shadow) to 255 (complete sun).
Mass balance index	MassBalInd	Geomorphometric variable used to determine patterns of soil deposition and erosion. Negative values represent net deposited areas like cavities and valleys, while positive values represent erosion areas such as convex hill slopes.
Mean solar radiation	MeanSol20205	Mean incoming solar radiation in the month of May 2020.
Minimum curvature	MinCurv	Minimum measured curvature in direction perpendicular to the direction of maximum curvature.
Morphometric features	MorfFt	Classification of landforms based on the relationship of a cell to its neighbours in terms of convexity and concavity. Landforms: 6-peaks, 5-ridges, 4-passes, 1-planes, 3-channels, and 2-pits.
Plan curvature	PlanCurv	Horizontal curvature of the surface. Positive curvature values indicate cell convexity and negative values indicate concave cell, with respect to surrounding cells.
Profile curvature	ProfCurv	Vertical curvature of the surface, i.e. parallel to the direction of the maximum slope. Negative values indicate convex surface, zero a linear surface, and positive a concave surface.
Slope	Slope	Mean terrain inclination recoded into 4 classes: flat [0°, 5°[; ramp[5°, 20°[; steep [20°, 45°[; very steep]45°, 90°[.
Terrain ruggedness index	TerRugInd	Quantitative measurement of terrain heterogeneity calculated by summarizing the difference between the focus pixel and the surrounding pixels. This results in a unitless index that ranges from 0 to infinity, with higher values indicating greater topographic complexity.
Topographic wetness	TopWet	Mean terrain driven variation in soil moisture. Cells with negative values represent areas with the steepest slope, ex. ridges or crests, positive values represent areas with increased accumulated runoff potential.
Total catchment area	TotCatAre	Same as flow accumulation, corresponding to the total area contributing for water accumulation to a specific location or point on a landscape.
Valley depth	ValDepth	Measures the depth of a valley or depression relative to the surrounding terrain.
Wind effect	WindEffct	Represents the relative exposure of a given area to wind. Values below 1 indicate wind shadowed areas whereas values above 1 indicate areas exposed to wind, all about the specified wind direction.
Wind exposition	WindExp	Relative exposure of a given area to wind from different directions, with higher values indicating greater exposure.

the coefficient of determination (R^2), depicting the percentage of variance explained were used to evaluate its performance. Partial response plots of the top five most important variables were built using the “partial” function of the “pdp” library. Top five abiotic predictors and its description can be found in Table 1.

The five most important variables in the RF models were used to determine each functional type microscale niche. The subset of the top five predictors for each functional type was used to produce a Principal Component Analysis (PCA) using the “dudi.pca” function from “ade4” library, after scaling the variables using “scale” function. The Outlying Mean Index analysis (OMI) was used afterwards to measure niche positioning. OMI corresponds to the distance between mean microscale habitat of each functional type in the PCA and the mean microscale habitat for the whole area (Dolédec et al., 2000). An OMI deviation from mean values indicates a likely confinement to specific conditions, i.e., specialized niche; while those closer to the mean indicate generalists. The OMI analysis was performed for the three functional types using the function “niche” from “ade4” library. This library was also used to calculate the mean and standard deviation of the weight distribution of each functional type in the two OMI axes and to evaluate significant differences from the mean, using the “sco.distri” and the “rtest” functions, respectively. This analysis followed the methodology of Kleyer et al. (2012).

Finally, the best microscale model with the top five predictors was used to predict the spatial cover for each functional type for the whole study area. A grid of 50 cm was first overlayed in the study area, and the average of top five microscale variables for each functional type was computed for each cell of the grid. A simplified version of the random forest models containing only the top five predictors were used to predict the cover of each functional type for each cell of the 50 cm resolution grid. The best random forest model corresponded to the model with the highest R^2. If both abiotic and all models R^2 were similar, the model chosen was that were sum of predictors importance was higher. The cover of each functional type was afterwards used to make a composite raster image, each vegetation corresponding to an RGB band: Red – lichens; Green – vascular plants; Blue – bryophytes. The composite image was merged with the digital surface model to produce a 3D representation using the ArcScene module of ArcGIS Pro.

3. Results

3.1. Patterns of vegetation cover along the altitudinal gradient

Lichens represented 60 % of the vegetation, bryophytes made up 32 % and vascular plants averaged only 4 % (Fig. 3 A). As expected, the altitudinal gradient corresponded to shifts in the vegetation dominance patterns (Fig. 3 B). Bryophytes dominated below 50 m, decreasing with altitude, while lichens represented most of the vegetation above 50 m, increasing its proportion with altitude. Above 250 m altitude both lichens and bryophytes average relative cover were close to 50 %. Vascular plants relative cover decreased also with altitude, occurring predominantly bellow 50 m and being absent above 150 m altitude.

3.2. Microscale predictors of each functional type cover

The collinearity diagnosis performed prior to model construction eliminated 13 abiotic microscale variables. After this step, 17 abiotic

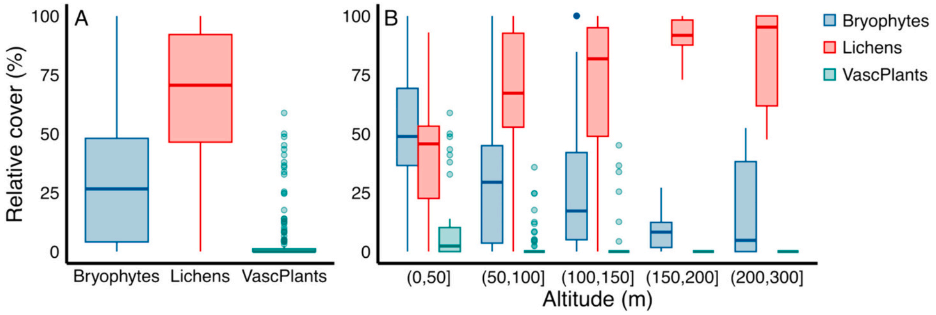

Fig. 3. Variation of relative cover of bryophytes, lichens, and vascular plants (VascPlants) in the whole study area (A) and by altitudinal class (B). Boxes represent the 25th and 75th percentile, whiskers minimum and maximum values, horizontal line the median and dots the potential outliers.

microscale variables were kept in the RF models. Both for the abiotic and all model sets, 100 models were run differing in the random split of training and testing datasets (summary of the median model evaluation and variable importance is shown in Table S2 from the Supplementary materials). The overall median contribution of microscale for models trained only with abiotic variables differed between functional types (Fig. 4 A). While for lichens and bryophytes microscale explained >60 % of variance in the cover patterns (median R^2 of 0.67 and 0.61, RMSE of 17.8 and 23.0, respectively), for vascular plants, the variance explained dropped to half that value (median R^2 of 0.30, RMSE 15.5). The inclusion of biotic variables in lichens and vascular plants models increased the median variation explained by microscale in 4 % but had no effect on the bryophytes' models. Fig. 4 B shows the top five variables explaining the cover patterns of each functional type. In total, they comprise a set of 7 abiotic microscale variables both for abiotic and for all models. Though many of the most important variables are common, the distribution of importance scores varied with functional type. Overall, importance scores were higher in bryophytes models and lower in vascular plants models, and very similar between abiotic and all models. In all models, abiotic variables were more important than biotic variables.

The most important variables explaining the spatial patterns of bryophytes and lichens cover were wind exposition, valley depth, channel network distance, distance to coast and topographic wetness in abiotic models. For bryophytes, topographic wetness was replaced by a biotic variable in all models, lichen cover, while bryophyte cover replaced wind exposition in lichens models. Vascular plants abiotic models shared wind exposition, distance to coast and channel network distance with the other functional types, and plan curvature and convergence completed the top five variable set. In vascular plants all models, convergence was replaced by lichen cover.

The partial dependence of each functional type cover to microscale variables is shown in Fig. 5. Wind exposition has a marked effect on the three functional types, but that effect is different for each of them. Lichens cover increases under low wind exposition and remains unaffected under intermediate and high wind exposition. Conversely bryophytes cover does not change under low wind exposition but decreases sharply under medium wind exposition and remains more or less constant at high wind exposition levels. Vascular plants are only negatively affected at high wind exposition values. Valley depth or depressions have also marked opposing effects in lichens and bryophytes (not an important driver for vascular plants) but also within a certain threshold, after which this microscale driver effect stops. Bryophytes cover increases until a valley depth of 5 m, while lichens cover declines until a valley depth of around 7.5 m. Channel network distance influences all functional types cover, though more moderately, and also only up to a certain level. Up to a distance close to 5 m from channels, it exerts opposite effects on lichens and bryophytes, more markedly disfavouring bryophytes. Vascular plants cover is positively influenced, but only above a distance of around 22 m. Distance to coast also affects the three functional types, but with contrasting effects on lichens and vascular plants (positive and negative, respectively), but only until around 200 m from the coast. Its negative effect on bryophytes is very small and only between close to 500 and 600 m. The topographic wetness index effect is also only seen around specific conditions. Bryophytes cover decreases slightly in areas of transition between dry areas to areas of increased accumulated runoff but returns to original cover values at the narrow upper end of this transition towards wetter conditions. At this narrow upper end of the transition, lichens cover declines sharply. Plan curvature has an important negative influence on vascular plants cover but only on surfaces were the curvature perpendicular to the direction of the maximum slope changes from concave to flat.

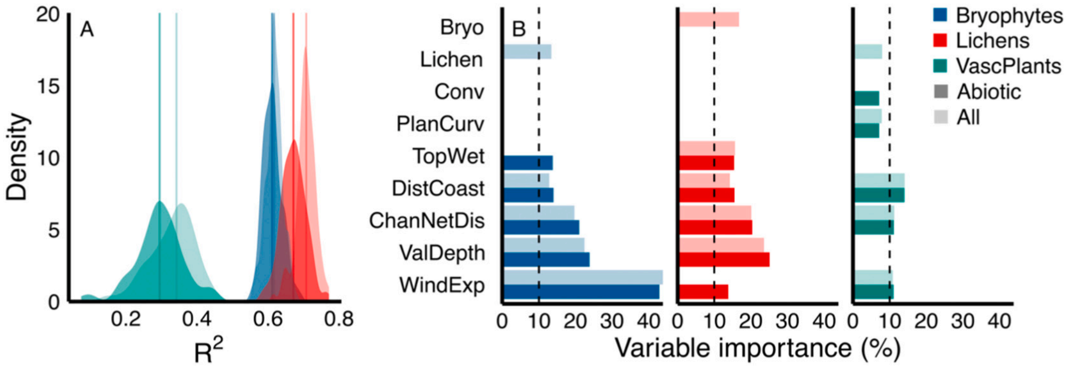

Fig. 4. Random Forest regression prediction of vegetation cover by microscale variables: A) distribution of the coefficient of determination, R^2, from 100 models with different random training/test splitting, vertical lines show median value; B) median variable importance (%) of the top five predictors. Colours correspond to the functional type: blue - bryophytes, red - lichens, green - vascular plants. Color shade indicates type of microscale variables included in the model: dark - abiotic; light - all (abiotic + biotic). The top five abiotic microscale variables in the models were: Conv; PlanCurv; TopWet; DistCoast; ChanNetDis; ValDepth; WindExp. Biotic variables included in the models were Lichen and Bryo (bryophytes). For abiotic variable acronyms and description see Table 1.

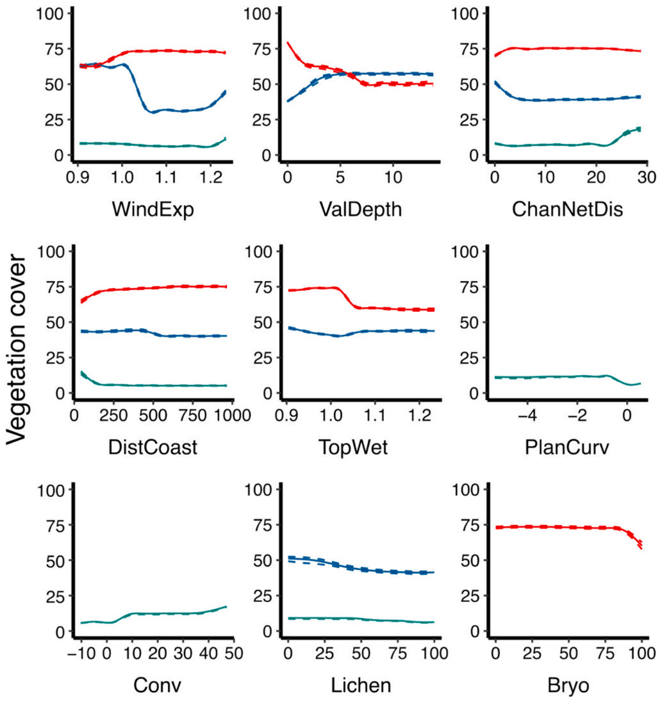

Fig. 5. Partial response of bryophytes (blue), lichens (red) and vascular plants (green) cover to the top five microscale variables from random forest regression analyses. The filled lines represent a loess function applied to the median of the partial predictions of 100 models with different random training/test splitting, and 25 and 75 quantiles is represented with the dashed lines. Median variable importance of the models can be seen in Fig. 4. Response to bryophytes (Bryo) and lichen (Lichen) result from models where all (abiotic and biotic variables) are included. The remaining partial responses result from models where only abiotic variables were included (abiotic). The top five microscale abiotic variables shown were: Conv; PlanCurv; TopWet; ChanNetDis; ValDepth; DistCoast; WindExp. For abiotic variable acronyms and description see Table 1.

Convergence impacted vascular plants cover but only under specific thresholds. Plant cover increases in the transition between flat to convergent cells, and again under intermediate convergence conditions. Concerning the biotic variables, bryophytes negatively affected lichens but only when its cover is very high (>80). On the other hand, lichens had an overall weak negative effect on bryophyte and vascular plants cover.

3.3. Analysis of vegetation microscale abiotic niches

The first two axes of the OMI analysis performed with the ensemble of the top five most important abiotic variables accounted for 66.5 % and 31.9 % of the explained variance in niches, thus subsequent analyses focus only on these two axes (total of 98.4 %, Fig. 6). These two axes were used to represent the microscale abiotic niche breadth of the three functional types (Fig. 6 B). The OMI of the three functional types were significantly different from the mean OMI value (all with $p = 0.001$), indicating that they show a strong preference for specific microscale conditions, i.e., relatively specialized niches, in this microscale environmental space. The positive scores on OMI1 corresponded to sites with higher runoff accumulation (topographic wetness), located in valleys or depressions (high valley depth values), and negative scores to sites located closer to ridge tops, more wind exposed and more distant from terrain channels. This first microscale gradient did not have the same impact on the three functional types. Lichens had a narrower niche (specialist), positioned mostly on the side of the gradient located closer to ridge tops under more exposed wind conditions, corresponding this position to its peak cover along this axis. Vascular plants had the same average niche position but with a wider niche breadth (more generalist in this gradient), also with its peak cover on this side of the gradient. Bryophytes niche average position occurred in sites with higher runoff accumulation, on valley or depression bottoms, which corresponded also to its peak cover, though its niche breadth extends over the entire gradient (generalist). The second OMI axis appears to represent a gradient from sites with sidewardly concave surfaces (positive scores) and intermediate convergent conditions (i.e., halfway between plan surface and channels), to sites distant from the coast and with flat surfaces (negative scores). Vascular plants average niche position and peak cover along this axis was located closer to the sea with a narrow niche breadth (specialist), and clearly shows an absence of vascular plants on the other side of the gradient. On the other hand, lichens and bryophytes average niche was positioned on the middle part of this axis, but while bryophytes peak cover was on the side of the gradient more distanced from the coast, lichens peak cover was in the middle of the gradient. The overall cover patterns give some clues about the possible role of biotic interactions. In the first OMI axis, as lichen cover peaks on positive side of the gradient under intermediate conditions, the cover of bryophytes and vascular plants drops abruptly. As we move to the negative side of this gradient on valley bottoms or terrain depressions, bryophytes cover peaks, while the other vegetation patterns decrease for close to zero. On the second OMI axis, as vascular plants cover peaks, both bryophytes and lichens cover drop, and as vascular plants start to disappear, lichens and bryophytes increase.

The microscale niche is visible in the spatial prediction of vegetation cover for the whole study area (Fig. 7). The best simplified random forest model was used to predict the cover of each functional type in the study area at 50 cm interval (Fig. 7). Best model for bryophytes had only abiotic microscale variables, while for lichens and vascular plants the best model had both abiotic and biotic variables (See Table S3 of supplementary material for details on model). The spatial prediction clearly shows the areas where each functional type dominates, and where their niches overlap. Lichens dominate in peaks and ridges more exposed to wind. Vascular plants are more abundant closer to the sea, when terrain is flat to slightly concave, and in areas with higher water drainage. Finally, bryophytes are more abundant in areas with higher moisture, on valley bottoms or terrain depressions, and closer to water channels.

4. Discussion

4.1. Microscale is a key determinant of the spatial vegetation patterns

Overall, results suggest that including microscale drivers in ecological models to track and forecast climate change effects is critical. In fact, microscale variables explained >60 % of the spatial variation of the main vegetation components (lichens and bryophytes) and the niche analysis suggested that each of the three functional types dominate under specific microscale conditions in the studied gradient. This explicit quantification of microscale importance in determining spatial vegetation patterns and the range of microscale conditions that each functional type is more likely to occur along this gradient is important to understand the vegetation response under climate change.

Though seldomly quantified, the role of the microscale drivers in determining the patterns of Antarctic bryophytes and lichens is widely recognized in this vegetation ecology literature, (Andrade et al., 2018; Lucieer et al., 2014; Schwarz et al., 1992; Seppelt and Ashton, 1978). Here, we corroborate this general assumption, and add that this contribution may sum up to >60 % of the spatial variance in their cover patterns along an altitudinal gradient. Nevertheless, though high for lichens and bryophytes, the contribution was around half that value for vascular plants. Previous studies have shown that vascular plants are usually confined to lower elevation sites, where climate is milder, soil is well drained and nutrient availability is higher (Leishman and Wild, 2001). Here, the most important microscale driver of vascular plant cover was distance to coast, which may indirectly reflect the importance

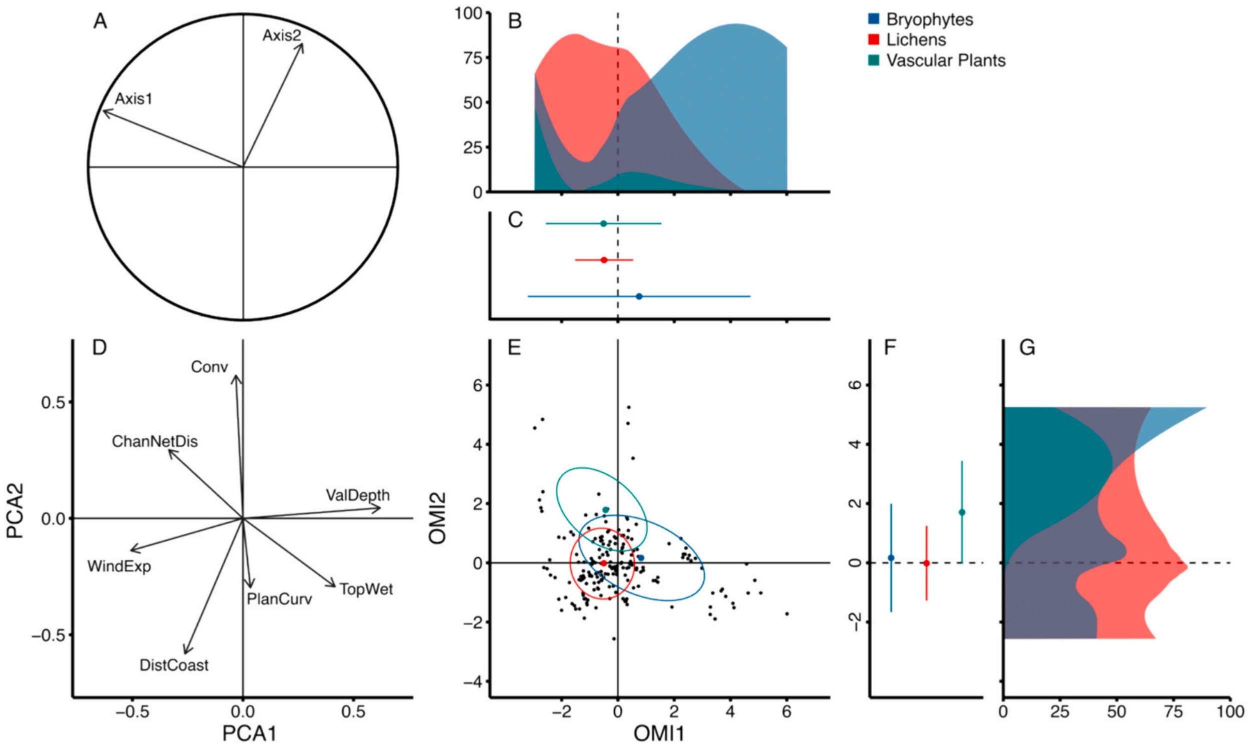

Fig. 6. Microscale niche of the vegetation. (A) Projection of the first two PCA axes of the environmental variables on the first two axes of the Outlying Mean Index analysis (OMI). (B &G) Loess regression of the cover of each functional type along the axes of the OMI analysis. (C & F) Realized niche position (point) and breadth (line) along the OMI axes for each functional type. Points show deviation from the mean habitat condition (niche breadth = 0) within the study area for each functional type, and the lines length represents the range of habitat conditions (described by the abiotic microscale variables). (D) Canonical weights of the environmental variables. (E) Ordination diagrams showing samples (black dots) and vegetation average position (coloured dots) and niche (ellipses) along the microscale abiotic niche space. For abiotic variable acronyms and description see Table 1.

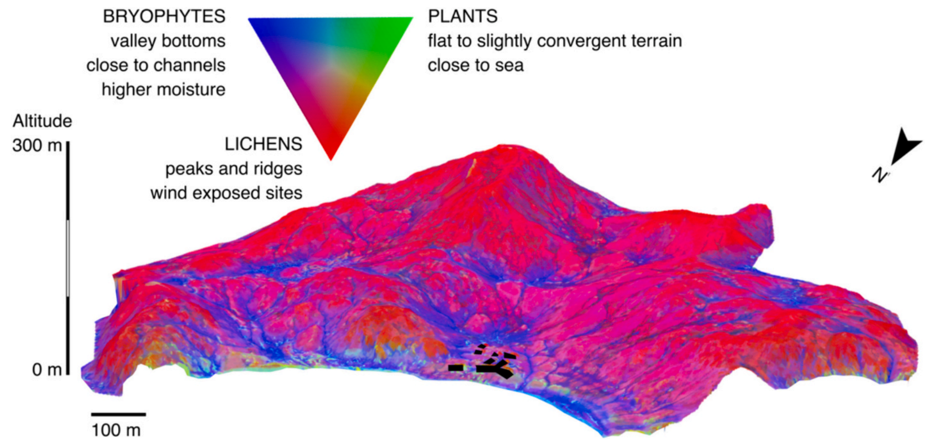

Fig. 7. Prediction of the vegetation spatial cover based on the microscale niche for the area surrounding the Antarctic Spanish base Juan Carlos I. The best simplified random forest model was used to predict the cover of each functional type in the study area at 50 cm interval. RGB color scale shows the composite cover of the three functional types. Areas represented by the colours of each vertex of the triangle represent areas where each functional type dominates, and remaining colours show niche overlap between the three functional types. Areas coloured in black correspond to the station buildings.

of nutrient availability. Sea spray and guano are identified sources of nutrients in soils (Nędzarek, 2008; Łachacz et al., 2018) and research has shown that these influence plant distribution in the Antarctic Peninsula (Ferrari et al., 2021; Park et al., 2012). Future more in-depth local scale studies should contemplate soil nutrient content to further explain vascular plant cover patterns. Still, given that lichens and bryophytes are the bulk components of the vegetation in Antarctica (Convey, 2006), the fact that more than half of the spatial variation in their cover patterns was explained by the selected microscale drivers strongly advocates to the inclusion of this type of microscale drivers in future works.

4.2. *Microscale as an ecological filter*

Our models emphasize that in these extreme environments the main ecological filters are abiotic drivers (Convey et al., 2014; Lee et al., 2019; Weiher and Keddy, 1995), as they were the most important in the models. Yet, the fact that in all vegetation models' biotic variables made the top five most important microscale predictors, within a set of 20 microscale variables, suggests that they represent a significant share among microscale drivers. Like previously suggested for Antarctic soil biota richness, the interactions we found between the cover patterns of the functional types may be underpinning part of the biological complexity in the system (Lee et al., 2019). Our models showed that lichens cover dropped when bryophyte cover was very high, and both vascular plants and bryophyte cover dropped if lichens cover in the plot was above 50 (from a maximum of 100). A manipulative work in the same region focusing on a single lichen species, *Usnea antarctica*, has demonstrated positive interaction effects of this species on other lichen, bryophyte and plant species (Molina-Montenegro et al., 2013). In our work, *U. antarctica* was observed at lower to mid altitudes, dominating with *U. aurantiaco-atra* in mixed mats of lichens and mosses, sometimes in the presence of vascular plants. However, our model of lichens functional type includes not only *U. antarctica*, but several other lichens species, along the entire altitudinal gradient. This may have overshadowed the facilitation effect of *U. antarctica* and explain the negative relationship found with bryophytes and vascular plants. Still, though our results do not allow us to extend our considerations on the type of interactions underlying these relationships, they point to the hypothesis that interactions may play a prominent role in the main cover vegetation patterns. Also, we cannot dismiss the possibility of these relationships between biotic variables being a product of covariation with abiotic variables, since we allowed all vegetation groups to respond to the same set of abiotic variables. Yet, even with these limitations, our results show the potential benefits of including biotic variables as microscale drivers in ecology models to forecast climate change effects and highlight the need for further clarification of vegetation biotic interactions' role in these ecosystems.

The most important microscale abiotic drivers determining the vegetation spatial cover patterns, their covariation and niche positioning and breadth of each functional type along the microscale abiotic gradient that we found is in general accordance with the ecological requirements that have been reported for each functional type. Bryophyte preference for sites with higher moisture is widely recognized (Robinson et al., 2018; Schwarz et al., 1992; Seppelt and Ashton, 1978). Here, bryophytes microscale niche and peak cover was located on valley bottoms or terrain depressions closer to channels, areas with higher terrain driven content in soil moisture. By comparison, lichens are known to dominate in more wind exposed and drier sites, further away from the coast (Seppelt and Ashton, 1978; Williams et al., 2017), a pattern corroborated by our results. Vascular plants are known to occur mostly close to the coast, on flat well drained soils with high nutrient availability (Park et al., 2012; Vera, 2011). Our results confirm vascular plants preferences for tendentially flat, well drained surfaces near the coast, avoiding valley floors or depressions in the proximity of channels, where water availability may be too high.

Furthermore, even though each functional type comprises several species, the niche analysis suggested that each of them is strongly associated to a range of specific microscale conditions. To the best of our knowledge this had not yet been done in Antarctica. In Marion island, a sub-Antarctic island, lichens were considered marginally specialists and bryophytes generalists (Cramer et al., 2022) along a topographic and edaphic gradient. Under the harsher conditions of the Antarctic Peninsula, our results indicate that the three functional types show some habitat preferences, thus pointing to the fact that they are more likely to be restricted to specific microscale environments. This result is highly relevant in a scenario of climate change. Vegetation restraint to particular microscale abiotic and biotic conditions may influence climate change impacts. Microscale niche can hinder their response, e.g. shifts in spatial distribution range, unless these microscale conditions are met; or conversely buffer climate impacts if microscale niches act, for instance, as a refugia for climate change (Scherrer and Körner, 2011).

Microscale importance as an ecological filter is also relevant from an ecological indicator perspective. Models of spatial vegetation patterns along climate gradients can be used to track and predict areas more prone to change (Branquinho et al., 2019; C. and P., 2017; Matos, 2016; Matos et al., 2017; Matos et al., 2015). In Antarctica, vegetation patterns have been used as indicators of snow dynamics (Vieira et al., 2014). The strong associations of microscale drivers with the spatial cover patterns of the Antarctic vegetation emphasize the potential of using the spatial vegetation patterns as ecological indicators of other microscale variables.

4.3. Limitations and uncertainties

The choice of microscale variables should be signalled as a potential limitation and source of uncertainty in our models. Edaphic factors like soil nutrient content are key drivers of Antarctic vegetation (Ferrari et al., 2021; Park et al., 2012), but they were not included in this work as this information is not yet available. As discussed above, the lack of this type of information may have contributed to the underestimation of the role of microscale variables, and resulted in more uncertainty, particularly in the case of vascular plants. In addition, the application of these models in other regions may be limited by the quality of the DEM. Given that ultra-high-resolution imagery is not yet available at the large scale in Antarctica, the DEM of 2 m that became recently available for the continent (Howat et al., 2019) could be used instead. In this scenario, the calculation of microscale variables will imply a more careful interpretation of the results and should be regarded as a source of uncertainty. Finally, our work was limited to a single location, thus it is reasonable to question if microscale contribution could change under, for instance, harsher conditions or a wider macroclimate gradient. Studies in other Antarctic regions are needed to further examine the uncertainties linked the contribution of microscale drivers under different environmental settings.

4.4. Implications for the environment and conclusions

Antarctic ecosystems are frequently seen as an ideal natural laboratory to study climate change effects, given that they are relatively simple and intact ecosystems (Bergstrom et al., 2006). However, forecasting or interpreting spatial or temporal shifts in vegetation patterns due to climate change should consider other complexity levels beyond climate, like microscale topographic or edaphic variation (Cramer et al., 2022; Scherrer and Körner, 2011). We demonstrated that microscale drivers (biotic and abiotic) explained more than half of the spatial vegetation variation for bryophytes and lichens, with these functional types exhibiting clear microscale niches under the studied conditions. This provides a new quantitative understanding on the response relationship between spatial vegetation patterns and terrain microscale drivers and reinforces the need for accounting with this underlying complexity. In the case of plants, the importance of microscale drivers was much lower. Further studies are needed to understand whether other microscale drivers, like nutrient availability, are the main environmental filters, or if macroclimate plays a more prominent role in the spatial patterns of vascular plants cover than microscale. Yet, overall, this work shows that to understand and predict climate change impacts in Antarctica, microscale drivers cannot be ignored.

In conclusion, the overall large microscale contribution, and the range of microscale conditions that each vegetation prefers, show how crucial they are to explain present vegetation patterns in response to climate, and for the interpretation of ecological model results under a climate change perspective. Furthermore, our work also highlights the potential of the methodology to be used in large-scale studies as the use of functional types, rather than the classic species approach revealed successful. All together these are crucial contributions to extend the spatial scope of the ecological models, a much-needed effort to improve our predictions and enlarge our spatial and temporal coverage.

CRediT authorship contribution statement

Paula Matos: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization. **Bernardo Rocha:** Writing – review & editing, Investigation, Formal analysis. **Vasco Miranda:** Writing – review & editing, Investigation, Formal analysis. **Pedro Pina:** Writing – review & editing, Methodology, Formal analysis. **Gabriel Goyanes:** Writing – review & editing, Investigation, Formal analysis. **Gonçalo Vieira:** Writing – review & editing, Methodology, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2024.174171.

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