Cover page

Incorporating biotic interactions to better model current and future vegetation of Maritime Antarctic

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Summary

Maritime Antarctica harsh abiotic conditions forged simple terrestrial ecosystems, mostly constituted by bryophytes, lichens and vascular plants. Though biotic interactions are thought to, together with abiotic factors, help shape this ecosystem, influencing species' distribution and, indirectly, mediating its response to climate, their importance is still fairly unknown. We modelled current and future abundance patterns of bryophytes, lichens and vascular plants, accounting with biotic interactions and abiotic drivers along a climatic gradient in Maritime Antarctica. Influence of regional climate and other drivers was modelled using structural equation models, with and without biotic interactions. Models with biotic interactions performed better; the one offering higher ecological support was used to estimate current and future spatial distributions of vegetation. Results suggests that plants are confined to lower elevations, negatively impacting bryophytes and lichens, whereas at higher elevations both climate and other drivers influence bryophytes and lichens. Our findings strongly support the use of biotic interactions to predict the spatial distribution of Antarctic vegetation.

Keywords

Antarctic ecology; Climate change; Antarctic vegetation; Plant–climate interactions; Plant–plant interactions

Introduction

In the South Shetland Islands, Maritime Antarctic, adverse abiotic conditions, recent deglaciation history and isolation from main dispersal centres shaped simplified ecosystems [1], to the point where cryptogamic communities of bryophytes and lichens [2,3], complemented in some areas by up to two vascular plant species [4,5], constitute the bulk of its terrestrial vegetation [6,7]. The spatial patterns of Antarctic vegetation composition and floristic characteristics has multiple known drivers. These include spatial variations in the environmental conditions at the microscale, namely topographic features and soil conditions [8,9]. Also, marine vertebrate colonies are known sources of nitrogen pollution, which in turn drive changes in vegetation spatial patterns related to increased nutrient availability [10,11]. Added to these drivers, this area experienced a warming trend of ~1.2ºC since the 1950s to the end of the century, and more recently, a cooling trend [12,13], urging the need for climate change research in the region. Climate impacts, reflected by changes in temperature, water availability and expansion of ice-free areas, are already leading to drastic shifts in these species groups [14,15], influencing growth rates, colonization success, growing seasons, among others [1,3].

Still, terrestrial vegetation is also influenced by biotic interactions. Interspecific (biotic) interactions are ubiquitous in nature and known drivers of species distribution [16] and communities structure [17]. Despite recent evidence [18-20] showing that, even under extreme environmental conditions, biotic interactions play a relevant role in determining several terrestrial Antarctic taxa distribution and abundance [18,19,21], the general belief is that these are overshadowed by abiotic drivers. Thus, biotic interactions role and relation to climate change is yet to be quantified, and models dealing with species distribution and abundance have largely failed to incorporate them [22]. Nevertheless, achieving better predictions for Maritime Antarctic terrestrial vegetation, now and under future climate change, will necessarily require incorporating biotic interactions into distribution models [23,24].

In this study, and for the first time for Maritime Antarctica, we integrated climate (and other environmental drivers) and biotic interactions to estimate present and future abundance and spatial distribution patterns of the three main Maritime Antarctic terrestrial vegetation species groups: bryophytes, lichens and vascular plants. Our main hypothesis was that the abundances of the three species groups would be better explained when biotic interactions were included, though we expect abiotic drivers to exert the strongest control. To test this, we performed structural equation modelling (SEM) to assess whether inclusion of pathways between species groups (biotic interactions) resulted in a better fitting SEM. A well-fitted SEM allows to quantitatively evaluate the strength and pathways of the direct effects of abiotic drivers and its indirect effects *via* biotic interactions between the three groups. As an example of applications, the SEM combining both a satisfactory goodness-of-fit and best ecological support was used afterwards to produce spatial abundance predictions of the vegetation across the ice-free areas of the South Shetlands, both for present and future environmental conditions.

Results

Species groups structure and their main abiotic drivers

Our data showed that in the studied area of the South Shetlands, lichens were the dominant species group, with an average absolute abundance of 58 (of a maximum of 100), followed by bryophytes (32) and vascular plants (11). Lichens abundance increased along the elevation and distance to the coast spatial gradient, while both bryophytes and vascular plants abundance declined along these gradients (Figure S3). From the initial set of 30 environmental variables, seven were selected from their higher and significant correlation coefficients with each species groups abundances (Figure S3) and were afterwards used in the linear models. From the linear regressions (Table S3-5), temperature (mean diurnal temperature range), elevation and slope revealed to be the main drivers of the three species groups (Table 1). Lichens and plants were driven by elevation, positively in the case of lichens ($AdjR^2$ = 48%), and negatively in the case of vascular plants ($AdjR^2$ = 16%), whereas bryophytes were negatively driven by both slope and mean diurnal temperature range ($AdjR^2$ = 37%). These three abiotic drivers (elevation, slope and mean diurnal temperature range) were then used as abiotic predictors in the structural equation models (Figure S4).

Structural equation modelling

The initial SEM (Figure S4), with the main abiotic drivers of each respective species group and excluding the biotic interactions, performed poorly ([RMSEA] = 0.22, X^2 = 55.26, df = 8, P = 0.000). The inclusion of the biotic interactions pathways generally resulted in a better fitting model. Ten models performed well (within indices cut-offs), all differing less than 5% in the average R^2 across species groups (Table S6). From these models, model XI (Figure 1; goodness-of-fit [RMSEA] = 0.06, $X^2 = 8.01$, df = 5, P = 0.156) showed the strongest ecological support, and was selected for the subsequent analysis. All pathways in this model were significant and explained 43%, 61% and 16% of the variance of bryophytes, vascular plants, and lichens, respectively. This represented an increase of 5%, 13% and 1% in the variance of each group respectively, in comparison to the initial model without biotic interactions, confirming the *a priori* expectations of our theoretical framework. Each species group responded independently to the set of abiotic variables present in the model, showing that their covariance is not due to similar responses to the abiotic factors, and that processes other than abiotic filtering may be responsible.

Biotic interactions mediate abiotic effects

Total abiotic and biotic net effects (sum of all direct and indirect effects of all environmental variables and of all biotic interactions on each group, respectively) help disclosure the importance of the bulk of all biotic interactions on bryophytes, lichens and vascular plants abundance, in comparison to net abiotic effects (Table 2). For bryophytes, total biotic net effects explained 28% of bryophytes abundance patterns, less than half of the abiotic effects. For lichens, biotic net effects explained 43% of its abundance, similar to those of net abiotic drivers. For vascular plants, total biotic net effects were not calculated as the SEM does not contemplate any effect of bryophytes or lichens on this group.

The important role of biotic interactions can also be seen by its part in mediating individual indirect effects of abiotic drivers. These not only exacerbated abiotic direct effects but also clarified the indirect abiotic effects that would have been unquantified otherwise (Table 3). The biotic interactions increased the positive effect of elevation on lichens abundance by 17%, while also mediating an indirect effect on bryophytes abundance. Similarly, these interactions also mediated the indirect abiotic effects of both elevation on bryophytes and slope and mean diurnal temperature range on lichens.

Incorporating biotic interactions to predict present and future spatial vegetation abundance patterns

Model XI was applied to estimate present and future (for 2100) vegetation abundance for the current ice-free areas of the South Shetlands (as no reliable bed elevation model is available for areas currently glaciated), and where the environmental conditions are within the range of the modelled climatic envelope (Figure 2a and 2b). Overall, for both current and future (2100) conditions, the SEM estimated high abundance values for bryophytes on the western side of both Livingston Island (Byers Peninsula) and King George Island (Fields Peninsula), while for lichens, high abundance values are seen across the entire archipelago, particularly at higher elevations (Figure 2a). Contrarily, vascular plants estimated abundance values were low across the entire archipelago. The average estimated abundance values, for present conditions, fell within the range of those sampled (Figure 2c), particularly for bryophytes and vascular plants. When comparing the outcomes of models between present and future conditions, average abundance values were very similar (-6,3% for lichens, -2,9 for bryophytes and 0% for vascular plants). Thus, the predictions based on our models indicate only minor changes in abundance and spatial patterns of the three species groups (Figure 2b). These spatial explicit models can also be used to zoom in specific areas. For illustration purposes, we depicted the variation of the three species groups across a distance to coast and elevation transect, in Hurd Peninsula, Livingston Island (Figure 2d). Plants decrease in abundance along the spatial gradient, until complete absence at higher elevations. This pattern is also observed when projecting for future environmental conditions. Lichens abundance increase along the gradient, although showing an overall decline when comparing present and future conditions. Finally, bryophytes do not exhibit such a clear shift along the elevation gradient but do show a clear mean increase in predicted future abundance when compared to present conditions, particularly at lower elevations.

Discussion

Results supported our initial hypothesis that biotic interactions must be included to better estimate present abundance patterns and to improve future predictions of Maritime Antarctic vegetation spatial distribution. According to our model, the presence of vascular plants negatively impacts bryophyte and lichen communities. Similarly, bryophytes also negatively impact lichens. Furthermore, while abiotic factors are the key drivers for bryophyte and vascular plant communities, such is not the case for lichens, as biotic and abiotic factors contributed equally to their abundance. The best structural equation model (highest fitting and ecological support) was used to, for the first time, map current and future spatial vegetation patterns across most of the South Shetlands Archipelago. Even if limited by available background information of orography and ice-cover extent, it is possible to infer that, under climate change, vegetation will be promoted and expand. This is mostly based on the observation that new ice-free areas are likely to have, in the future, climate conditions that allow colonization by bryophytes and lichens (Figures 2a-b).

Our results revealed that the incorporation of biotic interactions resulted in better-fitting SEMs compared to the one without interactions. All SEMs except one performed better than the SEM without biotic interactions (Table S6), thus confirming, with empirical data, that biotic interactions help shape the distribution of each species group. Although challenging, inclusion of biotic interactions is key to improve distribution models under climate change scenarios [23,25]. This is now confirmed also for Maritime Antarctica, and follows other recent studies for continental Antarctica, where biotic effects were identified as just as important [18,19,26], if not prevalent [21], drivers of several terrestrial communities. Thus, the inclusion of biotic interactions was shown to be a crucial step towards a better comprehension of the spatial abundance patterns of Maritime Antarctica vegetation.

According to the stress-gradient hypothesis, the importance of positive (i.e., facilitation) species interactions in plant communities increase with increasing abiotic stress [27]. In fact, recent works in Maritime Antarctica show support for this hypothesis, pointing to the existence of facilitation processes between bryophytes, lichens and vascular plants [28,29]. Nevertheless, recent developments propose that facilitation may collapse and switch to competition at the extremes of the stress gradient [30,31]. In other high latitude regions, cases of competition, commensalism and mutualism were documented for the three species groups considered here [32,33]. The type and mechanisms of biotic interactions in structuring Maritime Antarctica and similar terrestrial ecosystems thus remain poorly understood. For that reason, no *a-priori* structural biotic relationship between the three species groups was tried. Rather, we opted to test all possible interaction pathways, calculating 25 SEMs. From the ten

SEMs that passed the goodness-of-fit cut-offs, we selected the model with the strongest ecological support (Model XI – Figure 1). It is known that, when environmental conditions allow for their coexistence, vascular plants can have a competitive edge over bryophytes and lichens, and bryophytes over lichens [32,34]. In fact, this negative effect of plants and bryophytes on lichens was visible in all significant pathways of the 24 SEMs with biotic interactions. In the Artic [35,36], under warmer temperatures, an increase in vascular plants abundance was accompanied by a decline in lichens. Similar declining trends were observed for bryophytes cover in the Antarctic Peninsula, in response to increased *C. quitensis* cover [37], and in the Arctic for lichens, in response to increased bryophytes cover [38]. Additionally, a study conducted along elevation gradients within the Arctic circle found a similar trend in relation to these three species groups distribution, with vascular plants dominating just above the tree line and lichens and bryophytes peaking only at higher elevations, where plants competitive strength is lowest [39]. While contradicting the positive nursing effects seen in other studies [28,29] in the same region, and not allowing to discriminate the underlaying mechanisms behind these interactions, our results clearly point to the existence of negative effects between the three species groups. Despite scarce to date, field and laboratory manipulative experiments may help shed light on the underlaying mechanisms that determine the hierarchical relationships between these three species groups in Maritime Antarctica [22,40]. This would be an important step to analyse structural relationships in Maritime Antarctic ecosystems and to disclose the validity of the stress-gradient hypothesis in regions positioned at the extremes of the stress gradient.

Our model (Figure 1) also revealed the prominence of abiotic drivers for bryophytes and vascular plants communities (Table 2). For both species groups, regional climate (temperature seasonality) and altitude, a proxy of local climate conditions, namely temperature, explained the biggest portion of the spatial abundance patterns variance, with neither mean or seasonal temperature and precipitation variables being selected to the final SEM. Other temperature and precipitation-related variables could have been selected, although with less statistical significance. Thus, we can conclude that temperature, driven by regional and terrain factors, play a role influencing Maritime Antarctica vegetation directly and indirectly. This supports the view that abiotic factors, in low-diversity ecosystems like the Antarctic region, are in fact the most important ecological filter [1,7,41], at least for bryophytes and vascular plants. Remarkably, that was not the case for lichens, for which our model revealed both biotic and abiotic factors share similar importance in determining their abundance. Numerous biotic factors driving lichen communities are documented [42]. At high-latitudes however, the importance of these interactions in shaping lichen communities is still poorly understood [22]. In a study conducted in the Antarctic Peninsula [18], biotic interactions importance for lichens, bundled together with other multicellular taxa, was exceed by the importance of abiotic factors. Similar results were found in an arctic–alpine landscape [43], where cover of three vascular plants were used as biotic predictors and amounted for less than the abiotic predictors. Our results show that for lichens, as an independent group in this region of Antarctica, the opposite is seen. We consider two potential reasons for this difference: 1) Model XI revealed negative effects of both plant and bryophyte on lichens (weighting biotic interactions importance for lichens abundance); 2) as stated before, lichens can be outcompeted by the two remaining species groups, potentially due to shading, physical displacement, between other factors. In fact, our data showed that in plant or bryophyte-dominated communities, lichens decline in abundance (Figure S3). Future studies should further investigate this pattern in other high latitude regions (i.e., sub-Artic, Artic and continental Antarctica), enlarging the climate gradient.

The addition of biotic interactions in the chosen model also helped unravel potential indirect impacts from environmental drivers not affecting the vegetation group directly, but rather by a chain of effects through other species group. Although unexplored, some studies have already pointed to the important role of these indirect effects of abiotic drivers mediated by biotic interactions [18,44], which can potentially enhance or downplay climate change effects on Maritime Antarctic vegetation. Studies conducted in Maritime Antarctica [14,45] suggest that plants are promoted under a climate change scenario, which according to our results will indirectly and negatively impact bryophytes and lichens communities.

Antarctica holds some of the most simplified ecosystems on Earth. For that reason, even small variations in the abundance and/or distribution of the three major species groups, due to changes in climate conditions, may imply a disproportionate increase in the biotic complexity of these systems [46]. Colonization by new species [47,48] is also likely to occur under changing climate conditions. As every added species can bring in a new set of interactions, this will most likely imply a shift from a primarily abiotic driven system to one with increased biotic complexity (e.g., novel, altered, or lost intra or inter-taxon interactions) with the potential to disrupt current biological composition and ecosystem structure [46,49]. Together with future climate change effects, an increased species pool may disrupt vegetation spatial patterns and consequently the current interspecific dynamics, both in direction and intensity, established between species groups. As climate change effects are mediated by biotic interactions [50], any changes in the biotic complexity of Maritime Antarctic ecosystems will lead to changes in the way climate change will impact Maritime Antarctic ecosystems, either through positive or negative feedbacks, potentially leading to greater changes in the spatial patterns of the vegetation than expected if climatic drivers would be considered alone. Furthermore, shifts in more dominant community groups are expected to drive changes in ecosystem functions and services [51-53]. As these three species groups dominate across terrestrial Maritime Antarctic, biotic interactions will not only be key drivers of the vegetation spatial abundance patterns but also key drivers of changes to the ecosystem functioning itself.

Predicting future vegetation patterns is a crucial step in planning and designing more efficient conservation strategies [54,55]. Model XI was thus used to build spatial explicit estimations of vegetation abundance patterns, for present and under future climate change (Figures 2a-b). Yet, the low spatial resolution of the environmental variables used, together with the uncertainty associated to future projections, demand a cautious interpretation. As such, this exercise was meant to explore its potential as an Antarctic conservation planning tool and not to produce *de-facto* maps for Maritime Antarctic vegetation. Overall, the estimated distribution patterns (Figure 2a), for current conditions, were similar to known patterns from past field surveys [6,56-58]. This corroborates the greater potential to achieve more reliable spatial models when biotic and abiotic effects are considered together. Incorporating biotic and abiotic effects is thus an important step towards producing more accurate maps under future climate change scenarios, which so far have been almost exclusively focused on the dominant role of climate change [22,23].

Although the constrains of environmental data seemed to have not limited the quality of the estimations for current conditions, that was not the case for the predictions of future vegetation patterns. In the last decades, an expansion trend in the spatial distribution of the South Shetlands terrestrial vegetation has been observed in response to ameliorated environmental conditions and increasing ice-free areas [14,45]. However, such spatial trend is not observable in our estimations for 2100 (Figure 2b), as the present ice-free extension was maintained due to the low reliability of future deglaciation predictions and elevation values (and all remaining terrain variables calculated from it) were maintained due to unreliable future bed elevation models. Furthermore, the mean diurnal temperature range is only predicted to slightly change across the Archipelago. Altogether, the uncertainty in relation to future ice-free areas and the lack of variation in the environmental variables included in model XI hinders future predictions of the three species groups. It is thus clear that, for improved future estimations, more accurate and reliable predictions of future glacier loss and consequent bed terrain models are required [59]. Furthermore, better quality environmental data is also necessary for future predictions, as the incorporation of micro- climate and -terrain data is key to improve predictive spatial models [60-62]. The empirical data collected here reenforces this need, as clear abundance shifts in the three species groups were seen even across short spatial gradients (Figure S3). These shifts cannot be accurately explained with existing environmental datasets, which are only provided in coarser resolution. Future efforts should thus target the creation of enhanced spatial resolution environmental data that can help disclose small-scale climatic change and terrain features (e.g. areas of water accumulation in terrain depressions) leading, for example, to hotspots for bryophytes establishment at higher elevations [56]. Such bryophytes hotspot can be seen in Figure 2d, where the declined trend of bryophytes with elevation was inverted due to the characteristic flat-topped hill of Reina Sofia Mountain. Despite these limitations, predictive spatial models are a fundamental tool to better understand Maritime Antarctic ecosystems response to climate change impacts. Thus, its urgent to promote bridges between remote sensing disciplines and field-based measurements to improve environmental management conservation efforts in the region [63,64].

In conclusion, we found that adding biotic interactions was a vital step to explain the spatial abundance patterns of these three main species groups of Maritime Antarctic terrestrial vegetation. This was particularly evident for lichens, for whom biotic and abiotic effects had the same importance. Incorporating biotic interactions allowed to produce spatial explicit estimations for the current abundance of the three species groups, under present environmental conditions, that closely resemble those observed in the field. These predictive spatial models incorporating biotic interactions, if accompanied by improved environmental data spatial resolution, will boost our understanding of future climate change impacts, thus acting as a powerful conservation tool for Antarctica.

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Authors contribution

B.R.: Conceptualization, Formal analysis, Investigation, Methodology, Roles/Writing - original draft. P.Pinho: Conceptualization, Formal analysis, Methodology, Writing - review & editing. P.G.: Formal analysis, Writing - review & editing. L.C-Z.: Methodology, Writing - review & editing. G.V.: Writing - review & editing. P.Pina: Writing - review & editing. C.B.: Conceptualization, Methodology, Writing - review & editing. P.M.: Conceptualization, Formal analysis, Funding acquisition, Investigation, Methodology, Writing - review & editing. All authors contributed critically to the drafts and gave final approval for publication.

Declaration of interests

The authors declare no competing interests.

Main figure titles and legends

Figure 1. Structural equation model (SEM) overview

SEM (Model XI) showing the absolute standardized path coefficients (ranging from 0 to 1), explaining Antarctic terrestrial vegetation (bryophytes, lichens and vascular plants) abundance in response to abiotic drivers (elevation, slope and mean diurnal temperature range) and accounting with the biotic interactions between species groups. Overall goodness-of-fit statistics: $\chi^2 = 8.01$, df = 5, p = 0.16, robust Tucker

Lewis index (TLI) = 0.98, robust comparative fit index (CFI) = 0.99, robust root mean square error of approximation (RMSEA) = 0.06 (0.000–0.13), standardized root mean Square Residual (SRMR) = 0.04. Arrow widths are proportional to the standardized path coefficients presented. The R^2 next to each response variable indicates the proportion of variance explained. *p < 0.05; **p < 0.01; ***p < 0.001. See also Figure S3, S4 and Table S6.

Figure 2. Estimated vegetation abundances

Estimated **A)** present and **B)** future vegetation abundance maps for the three species groups (bryophytes, lichens and plants) in the South Shetlands, Maritime Antarctic. Abundance was estimated using the Model XI to model the response to abiotic drivers and integrating the biotic interactions described above. Future climate conditions are projected for 2100 under the most pessimistic CMIP6 emissions scenario (SSP5-8.5). Present and future vegetation abundance estimations are spatially limited to current ice-free areas of the archipelago and where the environmental conditions match those within the modelled climatic envelope (i.e., where values for abiotic variables used are withing the range used to build the model). White areas represent the current extent of glaciers in the Islands. Larger sized, higher resolution, versions of the maps are available in Figure S5. **C)** Distribution of sampled and estimated present and future abundance values of the three species groups, considering only current ice-free areas. Boxes display first to third interquartile ranges, black lines the median, dots the average, and whiskers the maximum and minimum abundance values. **D)** Abundance changes along a distance to the coast and elevation spatial gradient, based on present and future estimated abundance values of the three species groups in Hurd Peninsula, Livingston Island, depicted here to illustrate the application of this methodology. See also Figure S5.

Main tables and corresponding titles and legends

Table 1. Most important drivers of vegetation abundance

Summary of the best linear model selected for each response variable, unveiling the key abiotic drivers of the three species groups. The sign of the coefficients of the selected predictors, in each model, are indicated. The proportion of variance (%) explained by the regional climate and terrain variables was calculated using a variance decomposition analysis based on each model. *p < 0.05; **p < 0.01; ***p < 0.001. See also Figure S3 and Tables S3 to S5.

	Regional climatic		Terrain	
	Mean diurnal temperature range	Slope	Elevation	Adj. R^2
Bryophytes	42% (-)***	58% (-)***		0.37
Lichens			100% (-)***	0.48
Plants			100% (-)***	0.16

Table 2. Quantification of biotic and abiotic factors

Total net effects of abiotic and biotic factors on the abundance of bryophytes, lichens and plants. Values represent the absolute standardized path coefficients (ranging from 0 to 1).

	Abiotic	**Biotic**

Bryophytes	0.66	0.28
Lichens	0.47	0.43
Plants	0.40	-

Table 3. Quantification of direct, indirect and total abiotic effects

Direct, indirect and total effects of elevation, slope and mean diurnal temperature range (BIO2) on bryophytes and lichens via biotic interactions with plants and bryophytes. Effects represent the absolute standardized path coefficients (ranging from 0 to 1). *p < 0.05; **p < 0.01; ***p < 0.001.

	Bryophytes			**Lichens**			**Plants**		
	Direct	Indirect	Total	Direct	Indirect	Total	Direct	Indirect	Total
Elevation	0	0.11**	0.11**	0.47***	0.17***	0.64***	-0.4***	0	-0.4***
Slope	-0.34***	0	-0.34***	0	0.04*	0.04*	0	0	0
BIO2	-0.45***	0	-0.45***	0	0.06*	0.06*	0	0	0

STAR Methods text

Resource availability

Lead contact

Further information and requests for resources and reagents should be directed to and will be fulfilled by the lead contact, Dr. Pedro Pinho (paplopes@fc.ul.pt).

Materials availability

This study did not generate new unique reagents.

Data and code availability

Data and code availability statement:

1. Vegetation groups abundance data reported in this paper has been deposited in Dryad, as of the date of publication. The reference to it location is provided in Science Data Bank [65].
2. All original code has been deposited at GitHub and is publicly available, as of the date of publication. A link to the script is provided in the key resources table.
3. Any additional information required to reanalyse the data reported in this paper is available from the lead contact upon request

Experimental Model and Subject Details

Study area

The sampling for this study was conducted in Livingston and Nelson Islands, South Shetlands, off the northwest tip of the Antarctic Peninsula. The Köppen-Geiger climate system classifies the South Shetlands archipelago's climate as polar tundra, averaging annual air temperature at sea-level of −2 °C and an annual precipitation range between 350 and 500 mm [66]. Bryophytes and lichens are the main species groups in the islands, with 106 and 360 known species, respectively, with only sparse occurrences of two vascular plant species [67,68]. The three main species groups were surveyed along elevation and coast-inland gradients (Figures S1-2), in four ice-free areas encompassing different ground features [69,70]: (1) Byers Peninsula, (2) Hannah Point and (3) Hurd Peninsula, in Livingston Island and (4) Rip Point in Nelson Island. Sampling followed coastal-inland and elevation gradients, from the coastline (2 m elevation and 12 m from the nearest coastline) to the highest accessible ice-free area (370 m elevation and 947 m from the nearest coastline). A sampling site was defined as a patch with the presence of at least one of the three species groups targeted (bryophytes, lichens and vascular plants), of variable dimension, along which the survey of the species groups was conducted (Figures S1-2). Although not measured in this study, the Antarctic coast-inland and elevation gradients along which the 30 sampling sites are distributed across (Table S1) represent sharp climatic gradients due to the lapse rate in temperature [71]. Previous research has shown that Antarctic vegetation distribution patterns are more influenced by coastal–inland and elevation gradients than by a 400 km latitudinal gradient across continental Antarctica [72], thus supporting our sampling design. Thus, this spatial gradient was intended to depict the shifts in the three species groups associated with the spatial climate gradients, and thus encompassing bryophyte dominated communities, lichen dominated communities, communities with vascular plants, and the possible transitions between these in response to the shifts in climatic conditions.

Method details

Vegetation sampling

The abundance of bryophytes, lichens and vascular plants was determined in 30 sampling sites (Figure S1) in February 2019, and January and February 2020. Sampling site selection was done following an elevation stratification along the four areas in Livingston and Nelson Islands. A total of 6 sampling sites were randomly chosen from 5 elevation classes of increasing range to better capture vegetation shifts, which were greater at lower elevations ([0 – 23 m], [24 – 46 m], [47 – 92 m], [93 – 184 m] and [185 – 367 m]), distributed equally among the four areas when possible. In each site, and following an adaptation of the standard sampling methodology used to access biocrust abundance in arid ecosystems [73,74], five quadrats of 30 x 30 cm were randomly placed to assess the vegetation abundance (resulting in a total of 150 quadrats), ensuring that ground surface was close to horizontal (maximum slope was 20º). The quadrat was photographed perpendicularly to the ground surface. The slope of each quadrat was measured, and the coordinates were taken. This image-based method is less invasive (i.e., less time spent in the field and less disturbance), following the Antarctic Treaty recommendations, and has the potential for future upscaling with UAS imagery. For that reason, micro-vegetation groups, e.g. cyanobacteria, are not included in this study, as they are not identifiable at this image resolution. Nevertheless, we are confident that these three species groups represent the main flora of Maritime Antarctic, thus encompassing the complexity of its vegetation. The abundance of each species group was posteriorly determined through image analyses. Images were first corrected for distortion, using Adobe Photoshop 23.0. Afterwards, with Image J software [75], a grid of 3 cm side small cells was superimposed on the image to divide the 30 cm square into 100 small cells. The presence of the three species groups inside each grid cell was recorded. The abundance of each species group, in each quadrat, corresponds to the sum of all cells where that group was recorded (e.g. up to a maximum abundance of 100 in each quadrat). The five quadrats were treated as independent samples.

Environmental data

A set of 30 regional climatic, terrain morphometry, hydrology and lighting, and natural pollution environmental variables were retrieved, as these are known to be important drivers of Antarctic vegetation patterns or their proxies [11,14]. These were collected at the best spatial resolution available in the data repositories. Climate variables are here referred to as regional climatic due to their coarse spatial resolution (30 seconds or ~1 km). Although this is the best spatial resolution available, it is still not optimal and thus the limitations that can arise from it are considered in the discussion. A set of 19 regional climatic variables were retrieved from WorldClim dataset [76,77], corresponding to the period of 1970-2000 (see Table S1 for details on each variable). We opted for the bioclimatic variables instead of raw temperature and precipitation variables, as the former are biologically potentially more meaningful and often used in species distributions models [78]. To model future vegetation patterns in response to future regional climatic projections, we retrieved the same bioclimatic variables, at the same spatial resolution, for the period 2081-2100. These are based on eight CMIP6 models [79] within the more catastrophic emissions scenario (SSP5-8.5), a follow up of the CMIP5, RCP8.5 scenario [80].

To characterize the terrain morphometry, hydrology and lighting variability across the study area, ten variables were retrieved (see Table S2 for details on each variable): Elevation, slope, standard curvature, flow accumulation, topographic wetness index, potential solar radiation, distance to the coast, the area occupied by sea, area occupied by ice and ice-free areas at 11 buffers of different sizes. Elevation was retrieved both from the Reference Elevation Model of Antarctica (REMA), with a 2 m resolution[81]. Elevation is a widely used ecological proxy for changes in temperature and precipitation [82-84]. Slope was calculated using the same digital elevation model, and used here as a terrain morphometry driver, as slope could determine humidity conditions [85,86] through a gradient or steepness (e.g. steeper slopes may indicate less water retention, and thus drier conditions at the site level). The standard curvature, by combining both the profile and planform curvature can similarly help determine moisture conditions [86], by affecting the acceleration and deceleration of water flow and influencing flow convergence and divergence. Flow accumulation was calculated from the D8 flow direction method [87], which in turn was calculated from the digital elevation model. It can be used to identify potential stream channels and areas with higher probability for water accumulation. Monthly total potential solar radiation (PSR) was calculated also using REMA. PSR is known to influence climatic conditions at the microscale [88]. Distance to coast (linear distance to shoreline) and ice-free areas and areas occupied by sea, and ice (in 11 buffers of different sizes ranging from 4 to 4096 m, in increasing buffers of doubled size) around each quadrat, were chosen also as climate proxies. Proximity to the sea influences air relative humidity, an important driver for lichens and bryophytes [89,90]. Ice-free areas available for colonization, can also have an important role in determining vegetation patterns [67]. Proximity to glaciers is also known to influence the climatic conditions [91,92], thus with potential to be an important driver determining vegetation composition. Sea, ice-free and ice extent rasters were retrieved from the SCAR Antarctic Digital Database.

Finally, one natural pollution environmental driver was considered (see Table S2). Known maritime vertebrates colonies were either drawn manually as polygons whenever its presence was recorded during field work or retrieved from existing online databases [93], with distance to colonies determined afterwards. All data was retrieved at the quadrat level and analysed with ESRI ArcGis Pro 3.2 software. For environmental variables distribution see Figure S6.

Quantification and statistical analysis

All statistical analyses were conducted using R software [94]. Vegetation species groups mean abundance, standard deviation, and interquartile range were calculated based on absolute abundances, per quadrat (N=150). The first step was to reduce the number of environmental variables for the sake of better clarity and methodological flow. We started by determining the correlations coefficients between environmental variables and the absolute abundance of each vegetation group using Spearman correlation coefficients. Environmental variables not significantly correlated with any of the groups were excluded (considered significant for $p < 0.05$). From the 11 buffers of area occupied by sea, area occupied by ice and ice-free areas, only the buffer with highest average significant correlation coefficient with the three species groups was kept. A threshold of > 0.7 in the correlation coefficient was then used to identify collinear variables. Whenever collinearity was detected among environmental variables, the one with the highest average significant correlation coefficient with the three species groups was kept. It is important to note that, for this reason, several climate variables were excluded from further analysis although presenting only slightly lower correlation values with the three vegetation groups. Finally, the four environmental variables best correlated with each species group were selected for modelling. Correlation coefficients between each species group and the set of four best environmental variables can be seen in Figure S3.

Linear regressions were then used to determine the main abiotic drivers of abundance of the three different species groups along the elevation and distance to the coast gradients. We followed a thorough approach, modelling each species group with all the possible combinations of their respective four best environmental variables, based on the step performed previously. We first evaluated the individual response of each species group with the set of regional climatic, terrain, and natural pollution variables.

Prior to modelling, normality of response variables and linearity of the relationships between response variables and predictors were tested. The abundances of the three species groups were not normally distributed and the relationships between these and the set of environmental variables tested were not linear. For that reason, we log transformed (natural logarithm) both the response variables and predictors prior to modelling. Selection of the best model for each species group was based on the highest adjusted R^2 ($AdjR^2$) value and significance (considered significant for $p < 0.05$), while ensuring a parsimonious model. For that, all possible models were built and ranked per number of predictors and $AdjR^2$ value (Table S3-5). The model with the highest $AdjR^2$ on each level of predictors were compared, starting from the most parsimonious model (with just one predictor). The model for which including one extra predictor resulted in an $AdjR^2$ increment of more than 5% was selected. The proportion of variance in the abundance of each species group, explained by their respective best environmental predictors, was calculated using a variance decomposition analysis based on each model (Table S6). One regional climate (mean diurnal temperature range) and two terrain variables (elevation and slope) arose as the best predictors of the three species groups. Models were performed with the *lm* function from the stats package [94].

To evaluate these three abiotic drivers importance on vegetation patterns and the biotic effects (i.e. *via* interactions between species groups), we fitted a structural equation modelling (SEMs), using the *sem* function from the lavaan package [95]. As in the prior step, response variables and predictors were log transformed prior to modelling. An initial SEM (SEM I), without biotic interactions and therefore focusing only on the relationship between the three abiotic drivers (mean diurnal temperature range, elevation and slope) and the abundance of each species group was tested

(Figure S4). Deriving from this initial model, 24 additional SEMs were tested, by adding pathways representing the biotic interactions between the three species groups, encompassing all possible biotic pathways combinations between them (Figure S4 and Table S6). The importance of each added pathway in each structural equation model was inspected through the model residual covariance matrices and modification of goodness-of-fit indices. This approach allows to test hypothesis about processes with complex casual connections [96], enabling the discrimination of direct and indirect effects of the predictors and the estimation of multiple effects strengths. We assumed that: i) environmental drivers could directly drive the abundance patterns of each species group. ii) biotic interactions also play an important direct role driving their patterns; iii) biotic interactions could indirectly increase environmental drivers effects or unveil potentiating previously unseen effects. SEMs overall goodness-of-fit evaluation was tested based on the following indices cut-offs [97,98]: Satorra-Bentler chi-square statistic and its significance (the model is rejected if p-value < 0.05), robust comparative fit index (CFI > 0.9), robust Tucker Lewis index (TLI > 0.95), robust root mean square error of approximation index (RMSEA < 0.08) and the standardized root mean square residual (SRMR < 0.08). Within each model, estimated standardized path coefficients were used to measure the direct and indirect effects of the exogenous variables [96,99]. Direct pathways coefficients are interpreted as the size of an effect that one variable exerts upon another, represented in a structural model by a single path. Indirect pathways coefficients are interpreted as the size of an effect that one variable exerts upon another through a third intervening variable. Total “net” effects were calculated using composite variables within the SEM [100], by summing the “direct” and “indirect” effects of each environmental driver on each species group. Ten models performed within the indices cut-off, with the average R^2 across the three species groups differing in less than 5% across these SEMs (Table S6). As these models were statistically similar, only the one encompassing the biotic pathways best supported by ecological literature (Model XI) was used to estimate present and future abundance spatial patterns of each species group. These estimations were performed by first retrieving the values of the three abiotic drivers present in Model XI, (ESRI ArcGis Pro 3.2), but only for the areas of the study area with the same environmental envelope as the one used to build the SEM (i.e., where values of the abiotic variables used are within the range used to build the model). In addition, both present and future abundance spatial estimations, were also limited to current ice-free areas of the Archipelago. Net effects were derived from the winning SEM (Model XI) and calculated by adding composite variables to the SEM, thus encompassing the total effect (sum of direct and indirect effects) of all environmental variables on each species group as well of each species group on the remaining groups.

To estimate present and future abundance spatial patterns of each species group, elevation and slope from REMA (2 m resolution) [81], and mean diurnal temperature range (BIO2) rasters where first clipped, using the extract by mask tool, so to range only within the environmental envelop defined and outside the ice-covered areas. Clipped raster pixels values were retrieved using the raster to point tool. Both steps were performed using (ESRI ArcGis Pro 3.2). We then ran the *lavPredictY* function from the laavan package [95], which allowed for the prediction of each species group abundance, under current (from here on referred as current abundance) and future (from here on referred as future abundance) environmental conditions given the values of predictors, and by considering the biotic interactions from the best supported SEM (Model XI). Although we also intended to repeat this step for the SEM where biotic interactions are not considered, the fact that the model performed under all the goodness-of-fit evaluation indices cut-offs prevented us from doing so.

Future vegetation abundance maps were estimated based on the CMIP6 regional climate variables values for the year 2100, under the more pessimist emissions scenario (SSP5-8.5), which considers that current greenhouse gas emissions will be maintained, or even surpassed, over the course of the century. Mean diurnal temperature range (BIO2) raster values were initially averaged to the eight existing CMIP6 models available in the WorldClim database [76]. We are aware that modelling the abundances under several emission scenarios would be a more appropriate approach. However, because the bioclimatic variable used to produce the maps present only a small change even under the more pessimistic scenario, due to the low spatial resolution available, we decided not to replicate the maps for the most optimistic ones. This step was run using the point to raster tool (ESRI ArcGis Pro 3.2). As future elevation is assumed not to vary within the current ice-free areas, the same DEM and slope raster (2 m resolution) values were used for both present and future abundance estimations. Following a conservative approach, for each vegetation map (both present and future scenarios), abundance estimations where spatially limited to the areas inside the modelled environmental envelopes. These were defined based on the range of mean diurnal temperature range BIO2, elevation and slope range found in the sampled sites used to build the model. Estimations are also limited to current ice-free areas of the Archipelago. Despite some works having pointed to a massive ice-free area expansion [15,101,102], there is still a high degree of uncertainty surrounding these estimations for the Maritime Antarctic region. Furthermore, the low resolution and inaccuracy in the bed elevation models [103,104] further exacerbate the uncertainties surrounding the future landscape of Maritime Antarctic. Together, the limitations and uncertainties led to the decision to focus our estimations on the current ice-free areas, though we are aware that these will most likely expand greatly in the future.

Lastly, the abundance of each species group, for both present and future environmental conditions, were used to plot their spatial patterns along a distance to coast and elevation spatial gradient in the Hurd Peninsula, as a conceptual purpose. We prioritized this area as most of the sampling sites are located in this area. Because data fitted in the SEMs was log transformed, species groups abundance values were transformed (inverse of log transformation, i.e., exponential) prior to mapping.

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