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Research article

Proximity to seabird colonies and water availability shape moss distributions in Antarctica

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Understanding species distributions across Antarctica is crucial for biodiversity conservation under climate change, but continental-scale analyses of key terrestrial species remain scarce. Here, we modelled distributions of 28 moss species across Antarctica using log-Gaussian Cox process models and environmental covariates including topographic wetness index, distance to seabird colonies, and temperature. Broad-scale distributions were primarily driven by proximity to seabird colonies, while species exhibited distinct responses to water availability and temperature. Species exclusive to maritime Antarctica showed negative relationships with a topographic wetness index, whereas continent-wide species responded positively to water accumulation potential, reflecting regional differences in water availability and habitat preferences. Bias-corrected predictions revealed highest moss diversity in coastal regions, with inland areas supporting ecologically distinct assemblages. Our Bayesian modelling approach provides a foundation for forecasting biodiversity responses to environmental change in data-poor systems, offering critical insights for evidence-based conservation planning under increasing anthropogenic pressures.

Keywords: Antarctic ecology, Bayesian modelling, biogeography, bryophytes, species distribution modelling

Introduction

Antarctica is one of the last wilderness regions on the planet, but its biodiversity faces increasingly diverse threats, from global climate change to expanding human activity on the continent (Leihy et al. 2020, Chown et al. 2022). Our understanding of how biodiversity responds to environmental change remains, however, somewhat restricted to well-studied regions and taxa (Hortal et al. 2015, Meyer et al. 2015).

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Data limitations from key, but inaccessible regions, such as Antarctica, have long compromised the application of conventional ecological models in these systems, including models projecting biodiversity change (Hortal et al. 2015, Hughes et al. 2021, Koerich et al. 2023). Nevertheless, information about species distributions is increasingly demanded in biodiversity assessments (Araújo et al. 2019) and necessary to support biodiversity conservation under the Antarctic Treaty (Patterson et al. 2025).

Mosses Bryophyta, excluding liverworts and hornworts) are one of the most dominant forms of vegetation in Antarctica (Lüttge et al. 2011) and serve as ideal sentinel organisms for studying ecosystem health and biodiversity shifts (Walshaw et al. 2024). Operating at the edge of their physiological limits on the continent, these plants respond markedly even to minimal environmental changes, making them highly effective indicators for detecting shifts in Antarctic ecosystems (Robinson et al. 2003). Mosses also play an important role in Antarctic ecosystems by altering soil physicochemical properties and enhancing microbial communities (Ball et al. 2022), and describing their distribution is key to understanding Antarctic terrestrial ecosystems. Correctly assessing their distribution, however, requires careful consideration of the continent's unique environmental constraints and the adaptations of these organisms. Only between 0.2 and 0.5% of the continent is ice-free, and negative temperatures, high aridity, and limited sunlight restrict mosses' presence even further in these already fragmented patches (Robinson et al. 2003, Cary et al. 2010, Convey et al. 2014, Wauchope et al. 2019). Scarce water availability and temperature gradients also drive a marked decrease in vegetation cover and biodiversity from the maritime Antarctic (land north of the Gressitt Line; Fig. 1) into the main body of the continent. These gradients result in the maritime Antarctic (referred to here as maritime-only species) hosting considerably more moss species, and in greater abundance, than the continental region (maritime-and-continental) (Câmara et al. 2021).

The vast scale of Antarctica, combined with its sparse biological presence (vegetation cover estimated at just 44 km^2 out of 12 million km^2; Walshaw et al. (2024)), makes assessing large-scale patterns of species distribution especially challenging. Moreover, harsh environmental conditions render data collection logistically challenging, therefore species distribution data are often limited, spatially biased, and mostly opportunistic presence-only records (Chown et al. 2015, Koerich et al. 2023, Patterson et al. 2025). Understanding species distributions across Antarctica's vast territory, where most of the terrestrial environments have not, and will likely not be extensively surveyed (Patterson et al. 2025), presents a substantial challenge for conservation. Only a few studies implement species distribution models (SDMs) and are

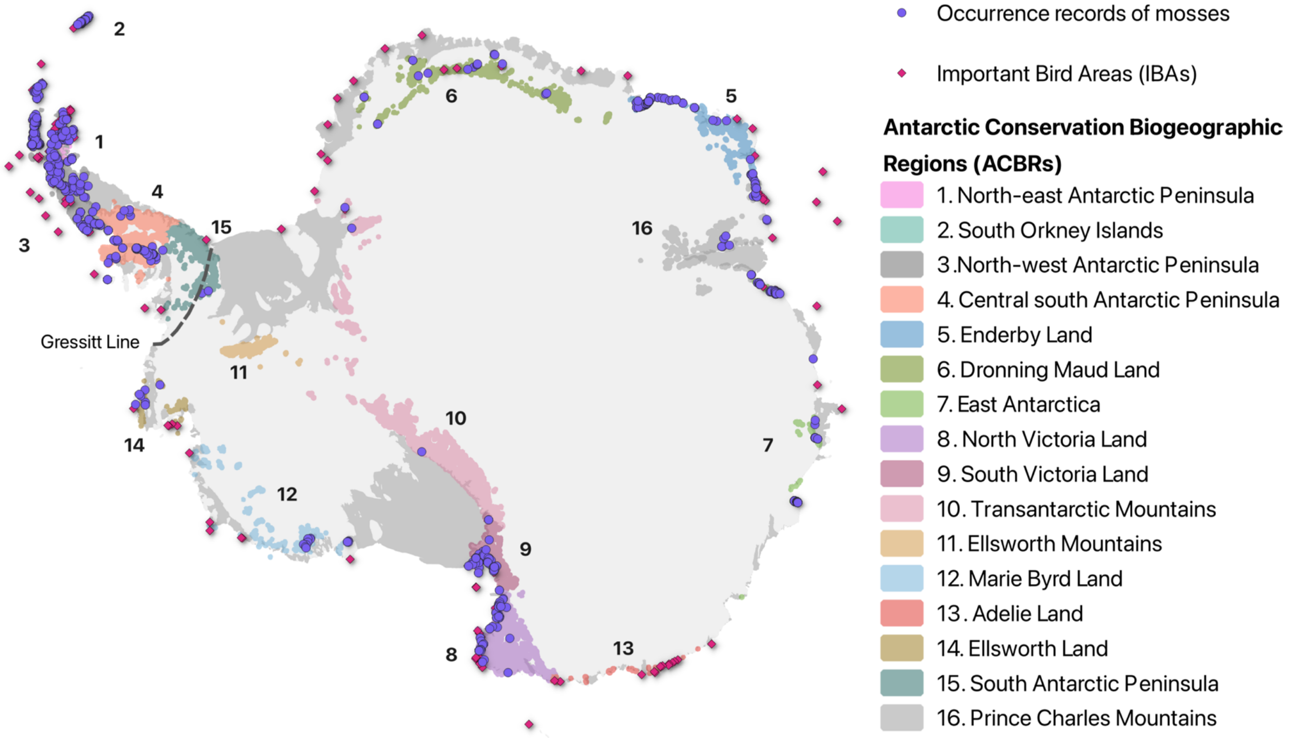

Figure 1. Occurrence records of mosses (purple circles) included in the study (moss species with over 50 occurrences) across the continent and different Antarctic Conservation Biogeographic Regions (ACBRs) as defined by Terauds et al. (2012). ACBRs also demonstrate a rough outline of the location of ice-free areas in Antarctica. Pink diamonds show the distribution of important bird areas (IBAs), and the grey dashed line represents the Gressitt Line, which biogeographically separates maritime Antarctica (maritime-only) from the main body of continental Antarctica (maritime-and-continental species).

focused on invasive species or small-scale correlative modelling in specific regions (Lee et al. 2013, Pertierra et al. 2017, Contador et al. 2020, Patterson et al. 2025). This current paucity of SDMs for terrestrial Antarctica limits our understanding of how key terrestrial taxa, such as mosses, respond to current environmental conditions and to a changing climate. Establishing a continent-wide baseline understanding of moss relationships with their environment is therefore crucial for forecasting changes not only in moss communities, but also in the broader terrestrial ecosystems they help sustain and regulate.

Recent methodological advances in species distribution modelling offer new opportunities to leverage existing data in a statistically robust manner. Spatially explicit Bayesian SDMs have demonstrated efficacy in handling scenarios characterised by sparse, clustered data, as they allow for the incorporation of spatial autocorrelation as a random effect within a mixed-effects framework (Redding et al. 2017). Among these, log-Gaussian Cox process (LGCP) models stand out as a special case of a point process model that uses the coordinates of presence-only data directly in a regression (Warton and Shepherd 2010). This approach addresses two critical challenges in Antarctic biodiversity research: it eliminates the need for generating pseudo-absences, a debatable technique in presence-only modelling (Acevedo et al. 2012, Hijmans 2012, Jiménez-Valverde et al. 2013, Warren et al. 2020), and accounts for the spatial non-independence within species occurrences (i.e. spatial autocorrelation) (Renner et al. 2015). Accompanied by model-based bias correction (Warton et al. 2013) and assessment of uncertainty in predictions, these models can bring valuable insights into the drivers of mosses distributions in the continent using the limited, but existing data.

In this study, we implemented an LGCP model for the first assessment of large-scale environmental drivers of moss distributions in Antarctica. Our analyses showed that proximity to seabird colonies, combined with water availability alone, are the main environmental drivers shaping moss presence across Antarctica. Our study also demonstrated important regional differences in species' responses to water availability and temperature. We produced bias-corrected distribution maps for 28 moss species, identifying richness hotspots across the continent as well as under-sampled regions with possible suitable habitats for mosses.

Material and methods

Species data and covariates

We extracted georeferenced presence-only moss species data from the Biodiversity of Ice-free Antarctica Database (Terauds et al. 2025), removing genus-level records and those without dates. We verified species taxonomic status using Tropicos (tropicos.org) and corrected non-accepted names using the Bryophyte Nomenclature catalogue (bryonames.org). We selected species with more than 50 occurrences for modelling (28 species) to ensure enough data for model training, categorising them as either maritime-only or maritime-and-continental to investigate potential biogeographical differences related to the Gressitt Line, a strong biogeographical barrier on the continent (Fig. 1).

We used environmental covariates in our models that are known to influence Antarctic moss distributions, including temperature, proximity to seabird colonies, and topographic features (Bokhorst et al. 2019, Yin et al. 2023, Rocha et al. 2024). Temperature data were extracted from the AntAir ICE dataset at 1-km^2 resolution (Nielsen et al. 2023), from which we calculated average cell mean and maximum temperatures (2003–2021, °C) and cumulative days above 0°C in the season. As Antarctic vegetation correlates with important bird areas (IBAs) (Harris et al. 2015) due to nutrients from guano (Cocks et al. 1998, Walshaw et al. 2024), we included distance to IBAs (km). To account for sampling bias towards accessible areas near research stations (Patterson et al. 2025), we calculated distance to scientific stations (km) from the Council of Managers of National Antarctic Programs data (COMNAP 2017, ver. 2.0.0). We then included this covariate in the model, and our predictions were made both including this covariate (non-bias-corrected predictions) and with it set to 0 (bias-corrected predictions) to remove the effect of different visitation rates of different locations, as recommended by Warton et al. (2013). In other words, we conditioned the bias-corrected predictions to a common level of observer bias (i.e. distance from scientific stations set to zero; Warton et al. (2013)). We applied log transformations to both distance measures before analysis.

Topographic features can be important in describing moss habitat preferences, as they can capture the amount of sunlight mosses are exposed to and water accumulation due to terrain features (Kopecký et al. 2021, Collart et al. 2023, Rocha et al. 2024). Topographic variables were derived from the 100-m Reference Elevation Model of Antarctica (REMA; Howat et al. 2022). We calculated aspect and slope using QGIS (ver. 3.28.5), converting them to northness as a proxy for sun exposure (Amatulli et al. 2018). A topographic wetness index (TWI) was derived to estimate relative soil moisture following Kopecký et al. (2021), using the Freeman FD8 flow algorithm (Qin et al. 2007) and a local slope gradient approach (Haralick 1983). These calculations were done in SAGA 7.8.2 (QGIS 3.28.5). TWI calculation estimates the catchment water supply and drainage driven by terrain features. Lower TWI values are typically found at ridges and steep slopes with small contributing areas, while higher TWI values represent flatter areas and depressions where water tends to accumulate. However, TWI in Antarctica should be interpreted with care, as the primary water sources are melting snow, glaciers, and lakes that are unevenly distributed across the landscape (Stichbury et al. 2011). As such, we interpret TWI here as a proxy for relative wetness influenced by Antarctic topography and acknowledge that it does not capture all possible sources of water in the continent. To preserve ice-free area characteristics, we first calculated these metrics at 100-m resolution, masked them to rock outcrops (Gerrish et al. 2020), then upscaled to 1-km^2 to match the temperature layers using the 'terra' R package (Hijmans 2024).

We standardised all covariates except the sampling bias covariate, which we scaled but did not centre to maintain interpretability of other coefficients as partial effects without sampling bias. After checking for multicollinearity using variance inflation factors (VIFs) with the 'usdm' R package (Naimi et al. 2014), we removed mean temperature (VIF > 10). The final set of covariates included maximum temperature, sum of days above zero degrees, northness, TWI, distance to scientific stations, and distance to IBAs.

Modelling

We modelled bryophyte distributions using an LGCP, treating species presence data as point events in an inhomogeneous Poisson point process. This approach avoids selecting pseudo-absences since the response variable is evaluated throughout a continuous spatial field (Krainski et al. 2019). The LGCP model also incorporates spatial autocorrelation as a Gaussian random field (GRF) to account for non-independence between occurrences.

We fit the expected counts per area of bryophytes ($\lambda\left(s\right)$) as:

$$\log\left(\lambda\left(s\right)\right) = \beta_0 + \beta X\left(s\right) + f\left(s\right)$$

where β_0 is the intercept, β represents species' responses to environmental variables $X\left(s\right)$, and $f\left(s\right)$ is a spatial random field estimated with a Matérn covariance function.

GRFs underlying $f\left(s\right)$ are computationally demanding, therefore we chose the integrated nested Laplace approximation (INLA) method, which uses a stochastic partial differential equation (SPDE) approach to estimate the GRF via a discrete triangulated mesh (Rue et al. 2009, Lindgren et al. 2011). We implemented this approach using the 'R-INLA' and 'inlabru' R packages (Rue et al. 2009, Bachl et al. 2019). We tested model sensitivity to mesh resolution and SPDE priors (Supporting information). As the sensitivity analysis showed no significant effects of mesh choice on intercept and minimal differences on the deviance information criteria (DIC), while choice of priors had significant effects on both, the final models used the same mesh but species-specific priors (Supporting information).

Spatial predictions and model evaluation

To predict moss presence, we defined a spatial grid around half the size of the spatial range shown in the models (30 km) to aggregate predictions. To generate this spatial grid, we used a 1-km buffer around the ice-free areas (thus reducing the complexity of the boundary) to delineate them as possible suitable habitats for mosses in Antarctica. We chose to simplify the boundary to allow model convergence, as geometrically complex boundaries increase the complexity of the mesh (Ribeiro et al. 2023). Then, we used the fitted models to predict the presence of mosses in each grid cell. We predicted both the detected presence of mosses (i.e. not correcting for the uneven sampling effort; non-bias-corrected predictions) and the expected habitat suitability (bias-corrected predictions) across the continent, by setting the covariate related to the sampling effort (distance to scientific stations) to zero. Since the intensity $\lambda\left(s\right)$ represents expected abundance per area rather than probability of occurrence (Renner et al. 2015), we converted it to probability of presence $\left(Y\right)$ using $Y = 1 - e^{-\lambda\left(s\right)}$, transforming unbounded intensity values to probabilities between 0 and 1. The non-bias-corrected predictions served two purposes: as a baseline to assess sampling bias influence on inferred distributions, and for model evaluation. We used non-bias-corrected predictions for evaluation because they represent the model's performance against the actual (biased) sampling locations where ground-truth data exist, providing a more direct assessment of predictive accuracy. In contrast, ecological interpretation of ecological relationships and distributional patterns relied on bias-corrected predictions, as these are predictions without the effect of geographical sampling bias.

We mapped predicted moss richness across Antarctica from both bias-corrected and non-bias-corrected predictions. From the non-bias-corrected predictions, we assessed residuals to check for any remaining spatial structure that the LGCP did not capture. Specifically, we computed posterior residuals, which provide a diagnostic check on model assumptions (Baddeley et al. 2005). We then visualised the residuals using a spatial field of raw and Pearson residuals to identify any regions where the observed data deviated significantly from model predictions (Baddeley et al. 2005). For each -km^2 ice-free cell, we classified Pearson residuals as significant underprediction (> 1.0), significant overprediction (< −1.0), or non-significant deviation (−1.0 to 1.0; i.e. good model fit). We then created a categorical map to visualize areas where multiple species (1–2, and 3+ species) showed consistent patterns of over- or underprediction. We also used a scoring rule metric, the strictly proper continuous ranked probability score (CRPS), to assess the accuracy of predictions by assigning a numerical penalty to each prediction–observation pair (Jordan et al. 2019). The lower the CRPS value, the better the predictive performance of the model is. We calculated CRPS using the 'scoringRules' package in R (Jordan et al. 2019) and using the aggregated predictions in grid cells described above. We also overlapped our predictions with the Plantarctica vegetation map (Walshaw et al. 2024), which is derived from Sentinel-2 satellite imagery, to assess agreement between spatial predictions. Our predictions and Plantarctica have significant differences in spatial resolutions (1-km^2 and 10-m^2 grid cell resolution, respectively), and Plantarctica is also only a detection of green vegetation (thus, no species-level information). Regardless, this dataset served as independent validation data to evaluate the correspondence between our predicted distributions and areas with detected presence or absence of vegetation.

To examine the isolated effect of individual covariates while controlling for other model components, we employed a component-wise evaluation function available in 'inlabru'. From this approach, we were able to plot partial responses of species to individual covariates and assess diversity and community patterns across the range of each environmental covariate being evaluated. For each environmental covariate, we generated predictions from single-species models across the observed range of that covariate and created a community matrix of predicted occurrence probabilities for all species. We then performed unconstrained distance-based redundancy analysis (dbRDA) using Aitchison distance, which is appropriate for compositional data (Aitchison 1982), and plotted species scores in ordination space to visualise their contributions to compositional patterns along environmental gradients. To examine spatial patterns in community composition, we applied the full model (i.e. individual species models with all the covariates) to make bias-corrected predictions of species occurrences across Antarctica. From these predictions, we created a community matrix of predicted probabilities and performed a dbRDA on this matrix using Aitchison distance. To visualise the continental-scale community patterns, we encoded the first three dbRDA axes into RGB colour values to represent the multivariate community ordination in geographic space. This colour mapping allows visualisation of how communities' composition varies across the Antarctic landscape based on their positions in ordination space, with the RGB values directly corresponding to the communities' positions along the first three dbRDA axes.

Results

Species-specific responses to environmental drivers

Species presence was strongly influenced by proximity to IBAs (significant for 27/28 species), scientific stations, and relative wetness (TWI; 25/28 species) (Fig. 2). Maximum temperature and northness showed more variable relationships (positive for 12/28 and 16/28 species, respectively), and sum of degree days above zero had the least influence (11/28 species). Maritime-only species consistently showed negative relationships with TWI, and maritime-and-continental species had mixed associations with TWI. For maximum temperature, most maritime-only species showed no relationship, whereas maritime-and-continental species exhibited positive relationships. The opposite pattern emerged for northness and sum of degree days, with more maritime-only species showing negative relationships while most maritime-and-continental species were unaffected. For example, the maritime-only species *Chorisodontium aciphyllum* and *Polytrichum strictum* exhibited similar responses to shared covariates, contrasting with the endemic continental-only species *Coscinodon lawianus* (Fig. 3). All species showed expected negative relationships with distance to scientific stations. Only one species had no relationship with distance to IBAs, and only *C. lawianus* showed a positive response to increasing distances from IBAs (Fig. 3C); all remaining species showed negative relationships.

The Matérn correlation model range varied across species, with mean correlation distances between 66 and 84 km for most species. Exceptions were for *Hennediella heimii*, *Polytrichum strictum*, *Sanionia georgicouncinata*, *Sanionia uncinata*, and *Syntrichia princeps*, which showed ranges exceeding 100 km (Fig. 2). High variation around mean range values was observed across species. Including covariates in the model substantially reduced correlation distances from hundreds to less than hundreds of kilometres, as observed from models without covariates (Supporting information).

Species-specific model predictions and performance

Most models predicted occurrence counts similar to input occurrences and showed CRPS scores close to 0, indicating good predictive performance (Supporting information). *Bryum pseudotriquetrum* and *Ceratodon purpureus*, the species with the most occurrences, showed the poorest predictive performance, but scores remained low. Spatial Pearson residuals are near zero for most species in most locations (Fig. 4), indicating good model fit. Most deviations between predicted and observed data are overpredictions of species (Fig. 4A) found in different regions across the continent (Fig. 4B), indicating areas where there are spatial structures not captured by our models. Residuals for individual species revealed overprediction for most maritime-only species in continental locations and some underpredictions in maritime Antarctica (Supporting information). For maritime-and-continental species, overprediction occurred primarily in mountain ranges of the Ross Sea region, Queen Maud Land, and parts of East Antarctica, with underpredictions mostly in the Antarctic Peninsula. Bias-corrected predictions showed approximately 10-fold increases in predicted counts for most species. Individual maps of predicted presence probabilities, standard deviation of predictions, and spatial Pearson residuals are available in the Supporting information for each species.

Spatial patterns of mosses in Antarctica

Non-bias-corrected predictions showed higher species richness in the Antarctic Peninsula, South Victoria Land (Ross Sea region), and East Antarctica (Supporting information), with the remainder of the continent showing very low predicted richness or no presence. Bias-corrected predictions substantially expanded expected presence and richness across the continent (Fig. 5), with increased richness in previously identified regions and additional expected presences in Dronning Maud Land, the Transantarctic Mountains, and Prince Charles Mountains. Comparisons with Plantarctica (Walshaw et al. 2024) showed congruence between our predictions and detected vegetation, especially for bias-corrected predictions (Supporting information). Prediction incongruence occurred primarily in the Transantarctic Mountains (region not covered by Walshaw et al. (2024)), North Victoria Land, Dronning Maud Land, and Ellsworth Mountains, where our models predicted wider regions of probable vegetation.

Figure 2. Estimated intercepts and slopes (posterior mean and respective 95% credible intervals (CI)) of the 28 species distribution models, as well as the range of the spatial random field estimated with a Matérn covariance function. Maritime-only species are represented in blue, while orange represents maritime-and-continental species. Whether the 95% CI crosses zero or not is represented by darker and lighter colours, respectively. The range of the Matérn covariance function for each species shows the decay in spatial correlation with distance for each species, indicating the strength of spatial dependence in species occurrences. Species acronyms: ADep: *Andreaea depressinervis*, AGai: *Andreaea gainii*, AReg: *Andreaea regularis*, BAmb: *Bryum amblyodon*, BArg: *Bryum argenteum*, BAus: *Brachythecium austrosalebrosum*, BDry: *Blindia dryptodontoides*, BPat: *Bartramia patens*, BPse: *Bryum pseudotriquetrum*, CAci: *Chorisodontium aciphyllum*, CLaw: *Coscinodon lawianus*, CPur: *Ceratodon purpureus*, DBra: *Didymodon brachyphyllus*, DCap: *Distichium capillaceum*, HHei: *Hennediella heimii*, PAlp: *Polytrichastrum alpinum*, PCru: *Pohlia cruda*, PNut: *Pohlia nutans*, PPil: *Polytrichum piliferum*, PStr: *Polytrichum strictum*, SAnt: *Schistidium antarctici*, SFil: *Syntrichia filaris*, SGeo: *Sanionia georgicouncinata*, SGla: *Sarconeurum glaciale*, SPri: *Syntrichia princeps*, SSax: *Syntrichia saxicola*, SUnc: *Sanionia uncinata*, WFon: *Warnstorfia fontinaliopsis*.

Unconstrained redundancy analysis (dbRDA) of bias-corrected predicted species presences revealed differences in community composition between coastal and inland assemblages (Fig. 6B). Maritime-and-continental species showed broader dispersion in ordination space, while maritime-only species displayed more clustered patterns (Fig. 6A), indicating similar habitat preferences or environmental requirements. The clear separation between some maritime-and-continental species suggests distinct environmental requirements. Partial model predictions for distance to IBAs, maximum temperature, and TWI reinforced the different responses of maritime-only versus maritime-and-continental species while also showing species richness patterns along these gradients (Supporting information). Species richness declined with

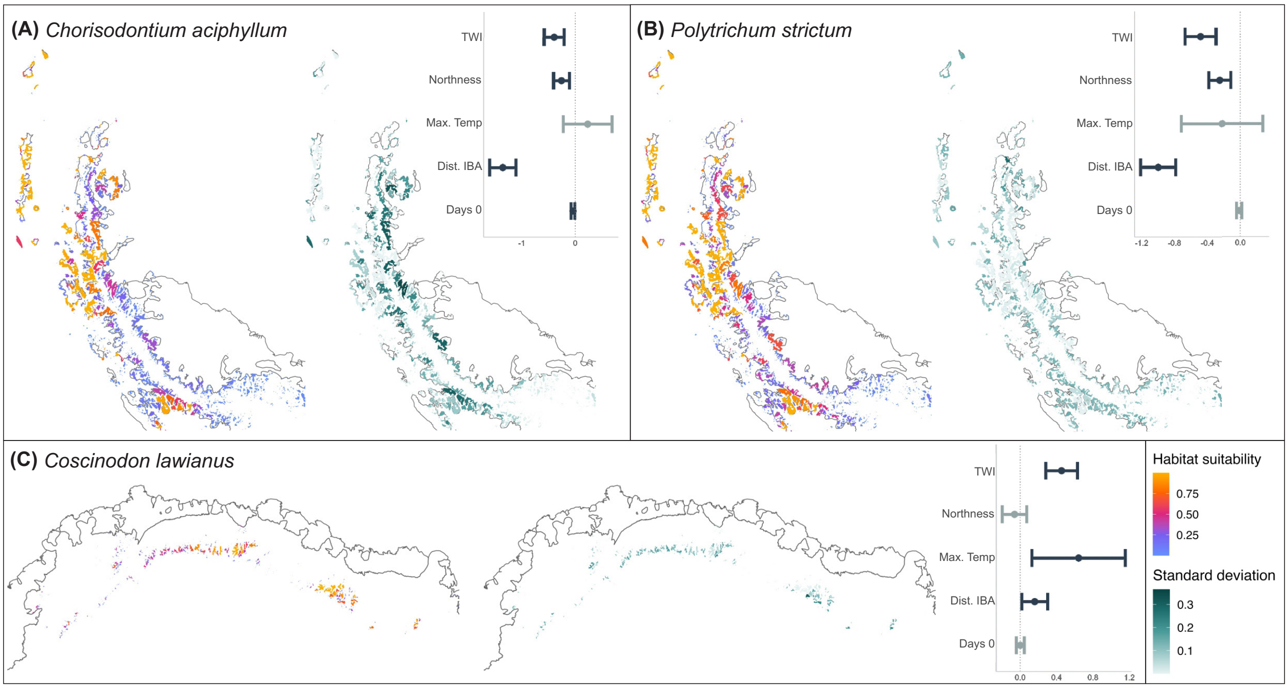

Figure 3. Bias-corrected predicted habitat suitability for two maritime-only species, (A) *Chorisodontium aciphyllum* and (B) *Polytrichum strictum*, and one continental-only species, (C) *Conscinodon lawianus*. The region depicted is the Dronning Maud Land, ACBR 6. Standard deviation of predicted habitat suitability is shown for each species, as well as the estimated slopes of each species (top right corner of each panel; posterior mean and respective 95% credible intervals). Colours of the bars represent whether the 95% CI crosses zero (grey) or not (dark blue). Covariates acronyms: TWI: topographic wetness index, Max. Temp: maximum temperature, Dist. IBA: distance to important bird areas, and Days 0: sum of days above zero in the season.

increasing distance to IBAs, increased with temperature, and remained relatively stable across TWI values. The dbRDA results suggested these three covariates moderately drive community composition, with certain species characterizing different ends of the community gradient.

Discussion

By conducting a continent-wide assessment of one of Antarctica's main vegetation groups, we revealed that moss distributions across Antarctica are primarily driven by proximity to seabird colonies and water availability, and detected important distinctions between maritime and continental assemblages. At the continental scale, moss community distributions were found to be linked to IBAs, relative wetness of the terrain, northness, and temperature. Regions with highest predicted presences are the Antarctica Peninsula, South Victoria Land, and East Antarctica, with predictions identifying possible suitable habitats in understudied regions (e.g. Ellsworth Mountains and Dronning Maud Land). Maritime-only species exhibited similar responses among themselves, as did continental-only species, reinforcing the biogeographic distinction between these communities. Despite sparse data, our models effectively revealed interspecific responses to the environment and overall patterns of diversity in the continent. Model overpredictions in remote regions highlight strong sampling bias and should be interpreted with care. Our approach complements vegetation mapping efforts using remote sensing (Walshaw et al. 2024) and broad-scale diversity analyses (Anderson et al. 2024) by revealing species-specific environmental responses. This study demonstrates that model-based assessments of biodiversity in Antarctica are possible and provide valuable insights when applied with care, but challenges remain and emphasise the need for continued refinement of data collection and modelling approaches.

Broad-scale biogeographical patterns of mosses in Antarctica

We found consistent effects of distance to IBAs on moss presence in Antarctica, with increasing distances from colonies associated with decreasing moss presence and richness, confirming patterns reported by other studies (Cocks et al. 1998, Gray et al. 2020, Walshaw et al. 2024). Antarctic soils are often nutrient-poor, and mosses derive nutrients from seabirds' guano (Yin et al. 2023), with declining gradients of ammonium concentrations in moss as the distance from colonies increases (Bokhorst et al. 2019). An experimental study demonstrated that bryophyte communities are more strongly influenced by increasing nutrient levels than by water availability, and communities are likely to thrive under wetter conditions only if sufficient nutrients are available (Wasley et al. 2006). Seabirds contribute not only

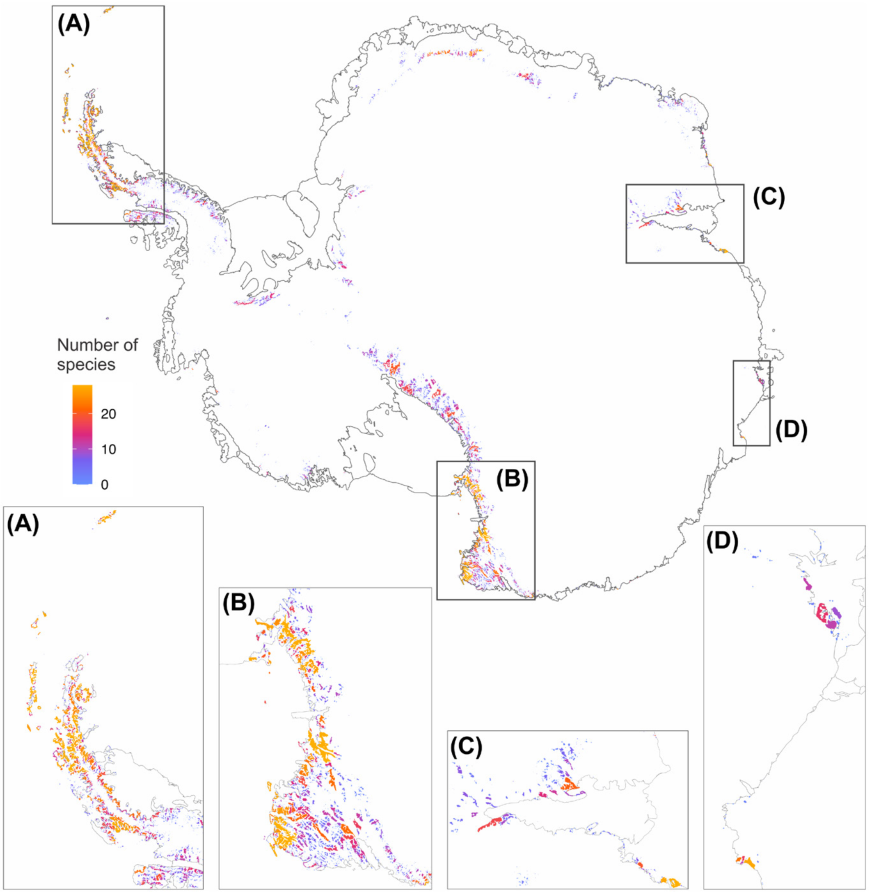

Figure 4. Number of bryophyte species predicted by the models across the continent, based on bias-corrected predictions of probability of presence taken from individual models. Insets on the map zoom in on (A) North Antarctic peninsula and South Orkney Islands, (B) South and North Victoria Land (part of the Ross Sea region), (C) Prince Charles Mountains, and (D) East Antarctica.

to favourable nutrient conditions but also to dispersal of mosses across sites (Parnikoza et al. 2018, Ivanets et al. 2022, Maggio et al. 2022), which is particularly important as sexual reproduction in Antarctic mosses is limited (Skotnicki et al. 2000). Our results support the importance of seabird distributions, past and present, in determining moss distribution patterns and imply that changes in seabird distributions will have cascading impacts on terrestrial biodiversity in Antarctica (Bokhorst et al. 2019).

Species-specific results showed idiosyncratic responses to relative wetness, indicating different habitat preferences of mosses across the continent. Maritime-only species exhibited negative associations with the TWI, which initially appears counterintuitive given their restriction to the wetter region. However, water availability is variable across Antarctica, and the maritime region receives direct precipitation (rain or snow), whereas continental Antarctica primarily relies on meltwater from ice and snowbanks (Cary et al. 2010, Schlensog et al. 2013, Vignon et al. 2021). This latitudinal gradient allows species that do not rely on meltwater to colonise the Antarctic peninsula (Schlensog et al. 2013). For example, *Ceratodon purpureus* relies on precipitation in maritime Antarctica but occupies drier margins of meltwater courses in continental areas (Seppelt et al. 2010, Schlensog et al. 2013). The negative TWI relationship of maritime-only species likely reflects their ability to occupy relatively drier microsites while still having sufficient water in the generally moister maritime region. Their negative relationship with northness further supports this balance between moss metabolism and moisture availability, as south-facing slopes retain more moisture (Collart et al. 2023). Conversely, some maritime-and-continental species responded positively to TWI with no association with northness, aligning with continental Antarctica's extreme aridity. In the Ross Sea Region, the highest moss diversity is indeed associated with moraine or alluvial deposits and relatively high groundwater content (Seppelt et al. 2010, Cannone et al. 2013). Our models demonstrate that mosses prefer habitats where water accumulates in these drier regions, highlighting the crucial role of water availability in shaping the distribution of mosses at both local and continental scales.

Responses to maximum temperature also varied, with maritime-only species mostly unaffected, and maritime-and-continental species showed positive responses. Given continental Antarctica's colder conditions (Convey et al. 2014), habitats providing warmer temperatures appear preferable to

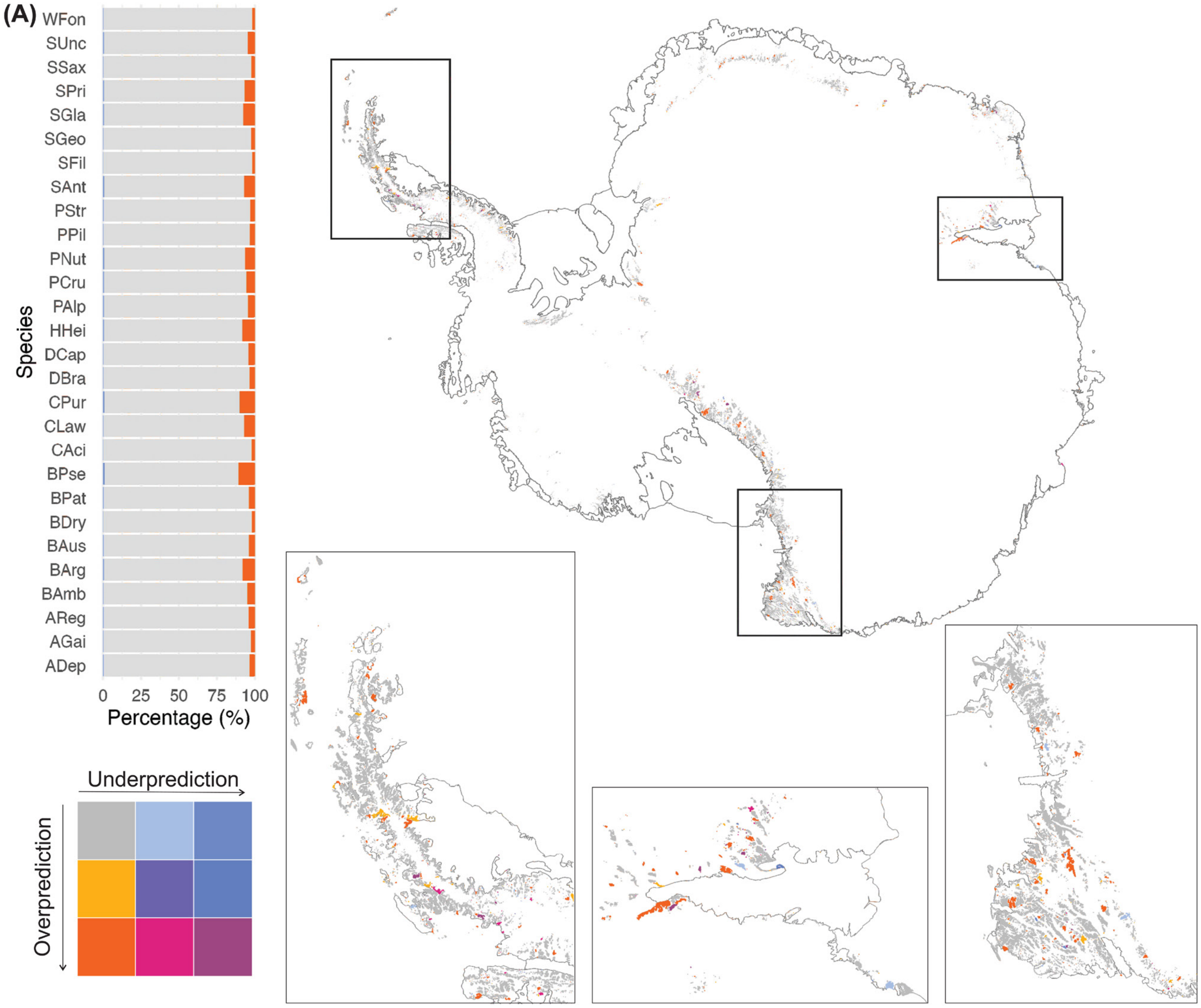

Figure 5. Categorical patterns of spatial Pearson residuals, showing patterns of over- and underpredictions across multiple species in each prediction grid of Antarctica's ice-free areas. (A) Percentage of grid cells for which our models overpredicted (dark orange, Pearson residuals < -1.0), underpredicted (dark blue, Pearson residuals > 1.0), and areas with non-significant residuals (grey, $-1.0 \leq$ residuals ≤ 1.0) for each species (refer to Fig. 2 for species acronyms). (B) Residual pattern map showing regions with non-significant residuals (grey), one or two species being over- or underpredicted (light orange and light blue, respectively), and regions with three or more species being over- or underpredicted (dark orange and dark blue, respectively). Regions where some species are overpredicted while others are underpredicted are shown in purple (1–2 species) or burgundy (3+ species). Pearson residuals were calculated from the non-bias-corrected model predictions.

species present in both regions. Temperature regulates many physiological processes in mosses in Antarctica, and optimum temperatures for photosynthesis of Antarctic mosses can exceed 20–30°C (Perera-Castro et al. 2020). Our models, however, predict the probability of presence, not physiological performance. Thus, temperature appears to dictate the presence of maritime-and-continental species in colder regions, while temperatures in maritime regions are sufficient for the presence of maritime-only species.

A better understanding of the ecological differentiation between continental and maritime Antarctic bryophytes emerges by comparing three representative species with contrasting distributions. On the Antarctic Peninsula, the dominant peat-forming mosses *Polytrichum strictum* and *Chorisodontium aciphyllum* frequently co-occur in extensive moss banks (Fenton 2022). With an erect growth form that promotes efficient drainage, these mosses form deep peat on slopes where water accumulation is reduced (Fenton 2022). This is reflected in coefficients showing lower TWI values, indicating adaptation to well-drained habitats. By contrast, *Conscinodon lawianus*, one of Antarctica's two continent-only endemic species, shows a different ecological strategy. Common in Dronning Maud Land, this species occupies diverse dry environments and some wet areas at higher elevations but avoids marine-influenced or seabird-affected locations (Ochyra 2004). Unlike most species we analysed, *C.*

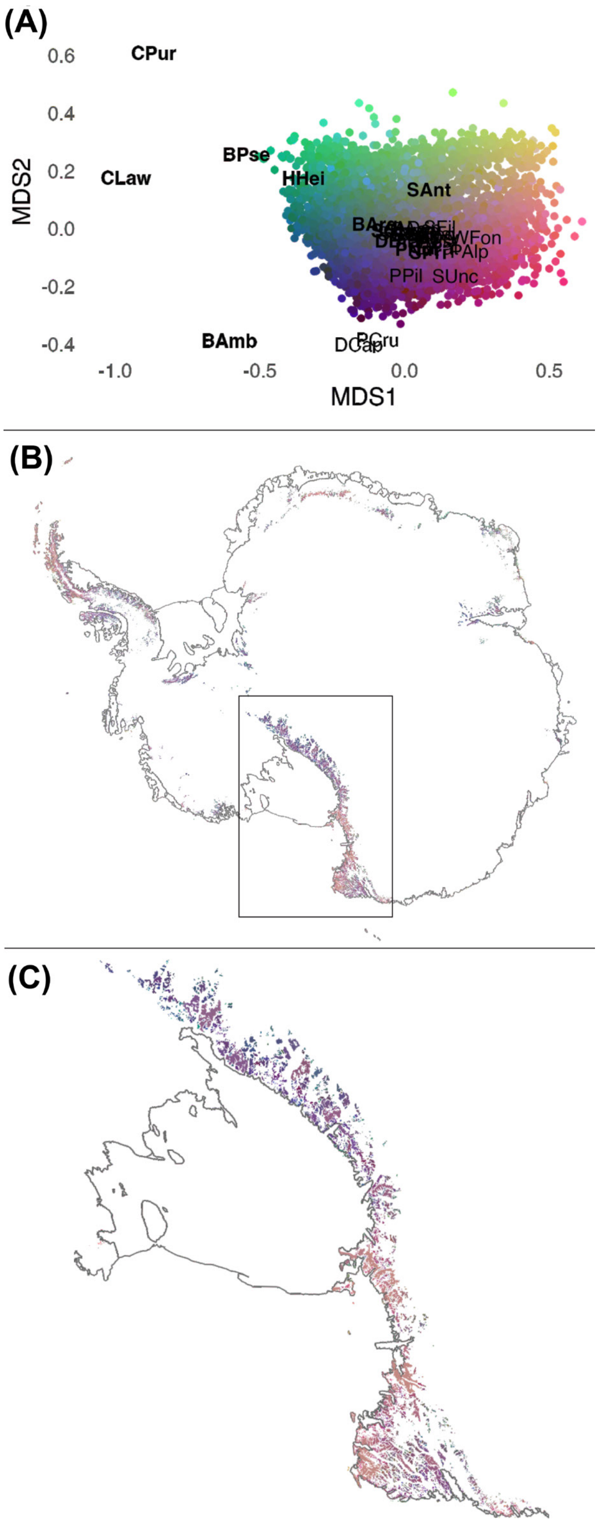

Figure 6. Spatial patterns of bias-corrected predictions (from individual species models) of Antarctic moss community composition. (A) Ordination plot shows community clustering in reduced multivariate space, with labels indicating species (refer to Fig. 2 for species acronyms). Labels indicate species positions in the ordination space (scaled by 10 to improve visualisation). Species in bold are maritime-and-continental species, and non-bold are maritime-only species. (B) Geographic visualization of community composition across Antarctica, with colours representing different community assemblages based on RGB-encoded dbRDA scores (axes 1–3). Inset on the map is shown in (C), Victoria Land and Transantarctic Mountains.

lawianus showed negative association with seabird presence, reflecting adaptation to nutrient-deficient soils at higher elevations lacking marine and biotic influence (Ochyra 2004). These contrasting preferences explain the distinct biogeographic patterns between coastal and inland communities, with *C. lawianus* contributing substantially to distinguishing communities along temperature, distance to IBAs, and TWI gradients.

Our bias-corrected predictions showed higher species richness in coastal regions and highlighted compositional differences between coastal and inland communities. Predicted patterns align with those reported by Anderson et al. (2024) and Walshaw et al. (2024), with highest moss diversity in the South Shetland Islands, followed by areas in the Ross Sea region and East Antarctica. Bias correction expanded predicted richness across multiple locations, including Dronning Maud Land and Transantarctic Mountains, and identified possible suitable habitats in the Ellsworth Mountains, Marie Byrd Land, and around the Hudson Mountains – where moss presence was recently confirmed (Walshaw et al. 2024). Although our models likely overpredict suitable habitats (as indicated by Pearson residuals), accounting for sampling bias helped identify potential habitats in under-explored regions, such as the Hudson Mountains. Our community analysis supports the high species turnover found by Anderson et al. (2024): coastal assemblages appear similar and contain most modelled species, while continental regions support more ecologically distinct communities. This dissimilarity reflects differential responses to environmental variation and is likely reinforced by population isolation due to the fragmented distribution of suitable habitats (Saługa et al. 2022).

The spatial random field in our models revealed spatial dependency in moss distributions, with most species showing clustering within approximately 100 km. This clustering pattern may arise from dispersal limitation, competition, or unmeasured environmental variation (Ribeiro et al. 2023). Antarctic moss populations are often isolated due to fragmented ice-free areas, past glaciation events, biogeographical barriers, and limited dispersal abilities (Skotnicki et al. 2000, Lee et al. 2022, Saługa et al. 2022). Sexual reproduction is infrequent on the continent, with vegetative dispersal being the primary means of spread (Skotnicki et al. 2000). Although moss spores can theoretically disperse over thousands of kilometres, vegetative propagules disperse more limitedly (Pohjamo et al. 2006, Lönnell et al. 2012). Even with strong winds potentially enabling long-distance dispersal, establishment success, often the limiting step in colonisation (particularly in arid ecosystems) remains very low (Convey et al. 2000, Skotnicki et al. 2000, Wiklund and Rydin 2004, Hurtado et al. 2022). Our results support the hypothesis of limited connectivity between moss patches, consistent with other studies (Anderson et al. 2024). Therefore, predictions of suitable habitats for maritime-only species in continental Antarctica may reflect areas with suitable conditions where successful colonisation depends on both dispersal and establishment. Incorporating dispersal ability in future models will provide improved predictions of moss ranges in Antarctica.

Modelling sparse data: advances, challenges, and future directions

To the best of our knowledge, our study constitutes the first attempt at modelling Antarctic biodiversity while accounting for sampling bias, giving a new ecological understanding of moss distribution patterns across the continent. Including sampling bias proved to be essential as demonstrated by our model coefficients for distance to scientific stations (significant for all species). Comparing our non-bias-corrected and bias-corrected predictions revealed substantial sampling bias, demonstrating that bias-corrected predictions can effectively identify priority areas for future sampling efforts. By accounting for these biases, we were able to identify regions with predicted suitable habitats for mosses that historically have not been extensively surveyed. We recognise that our models may be overestimating moss presence in these areas, either because of extrapolation beyond our training data range, true unsampled suitable habitat, or regions where other limiting factors prevent moss presence. Regardless of the underlying cause, these bias-corrected predicted suitable areas provide valuable targets for field sampling. The confirmation of moss absence in these locations can lead to insights into additional limiting factors constraining moss distributions in Antarctica.

Similarly, although our bias-corrected predictions are more reliable in well-sampled regions (which vary substantially across the continent as reported by Patterson et al. (2025)), our approach generated information about potential limited knowledge on moss habitat drivers in the continent. Our spatial residual analysis highlighted regions where moss distribution patterns were not fully captured by our models, such as the Antarctic Peninsula and Transantarctic Mountains. These spatial structures not captured by our models suggest either unmeasured environmental variables, dispersal limitations, or a scale mismatch between the microhabitats mosses occupy and our coarse-resolution environmental models. Antarctic vegetation occurs from extensive mats to small patches under rocks (Walshaw et al. 2024), with microclimatic conditions critically determining moss distribution (Colesie et al. 2014, Yin et al. 2023). Understanding the role of scale and these other possible ecological and environmental factors in driving our 'model errors' is an interesting venue for future research. By identifying both the strengths and limitations of our modelling approach, our findings provide a crucial baseline for understanding how the environment shapes mosses distributions and shed a light into what remains to be investigated. Approaching sparse data with careful consideration of their limitations and associated uncertainty in model predictions proved to be a valuable framework to better document and protect Antarctic biodiversity. This work demonstrates that spatially explicit Bayesian models can be useful for other under-sampled ecosystems where similar data completeness challenges are present, demonstrating the broader applicability of our modelling approach.

Conclusion

We believe that we have provided the first continent-wide SDMs for terrestrial species in Antarctica. Our study confirms previous assertions that abiotic conditions strongly influence the distribution of organisms in harsh, low-diversity systems such as Antarctica (Convey et al. 2014). However, we also reveal species- and region-specific idiosyncrasies for these Antarctic mosses, emphasising the role of environmental variability in shaping community assembly and diversity. Although limitations in the available data and our predictions persist, improving biodiversity forecasts is only possible through iterative learning and model refinement (Urban et al. 2016, Dietze et al. 2018). The models presented here are transferable to other taxa and regions and serve as a foundation for advancing Antarctic ecological modelling. Forecasts of future changes in these unique ecosystems are urgently needed to inform science-based management of Antarctica's biodiversity under anthropogenic climate change. Our results highlight the utility of Bayesian spatially explicit models in addressing critical gaps in understanding species distributions in a data-poor region. As such, optimizing the use of existing and new data is a promising path forward, and will be key to providing robust forecasts for Antarctic biodiversity (Koerich et al. 2023).

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Author contributions

Gabrielle Koerich: Conceptualization (lead); Formal analysis (lead); Writing – original draft (lead); Writing – review and editing (lead). **Hao Ran Lai**: Formal analysis (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Charles K. Lee**: Supervision (supporting); Writing – review and editing (supporting). **Fraser J. Morgan**: Funding acquisition (lead); Writing – review and editing (supporting). **Jonathan D. Tonkin**: Conceptualization (supporting); Supervision (lead); Writing – review and editing (supporting).

Transparent peer review

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Data availability statement

Data and code are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.wstqjq2zf (Koerich et al. 2025). These data were derived from the following resources with CC BY 4.0 licenses: Automatically extracted rock outcrop dataset for Antarctica (ice-free shapefile) (Gerrish et al. 2020); High resolution vector polylines of the Antarctic coastline (Gerrish et al. 2023); The biodiversity of ice-free Antarctica database (Terauds et al. 2025); Antarctic daily mesoscale air temperature dataset derived from MODIS land and ice surface temperature (Nielsen et al. 2023); Important Bird Areas (Harris et al. 2015); COMNAP Antarctic facilities information (research stations) (COMNAP 2025); Reference Elevation Model of Antarctica (REMA) (Howat et al. 2022); An online, interactive map of the paper results can be visualised here: moss-app-c63b-prod.app.oceanum.io/.

Supporting information

The Supporting information associated with this article is available with the online version.

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