Predicting mire distribution using species distribution models: a case study of the sub-Antarctic Prince Edward Islands

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Abstract

Peatlands, covering approximately one-third of global wetlands, provide various ecological functions but are highly vulnerable to climate change, with their changes in space and time requiring monitoring. The sub-Antarctic Prince Edward Islands (PEIs) are a key conservation area for South Africa, as well as for the preservation of terrestrial ecosystems in the region. Peatlands (mires) found here are threatened by climate change, yet their distribution factors are poorly understood. This study attempted to predict mire distribution on the PEIs using species distribution models (SDMs) employing multiple regression-based and machine-learning models. The random forest model performed best. Key influencing factors were the Normalized Difference Water Index and slope, with low annual mean temperature, with low annual mean temperature, precipitation seasonality and distance from the coast being less influential. Despite moderate predictive ability, the model could only identify general areas of mires, not specific ones. Therefore, this study showed limited support for the use of SDMs in predicting mire distributions on the sub-Antarctic PEIs. It is recommended to refine the criteria used to select environmental factors and enhance the geospatial resolution of the data to improve the predictive accuracy of the models.

Keywords: GIS, machine learning, peatland distribution, random forest, sub-Antarctic

Introduction

Wetlands are a critical global biome and include a variety of permanently or seasonally inundated freshwater habitats, such as lakes, rivers, marshes and coastal and marine areas like estuaries, lagoons, mangroves and reefs (Ramsar Convention on Wetlands 2018). They provide a wide range of ecosystem services, including freshwater purification and provision, food, energy resources, erosion control, habitats for wetland-dependent species and benefits for human well-being and the environment (Millennium Ecosystem Assessment 2005, Amler *et al.* 2015, Ramsar Convention on Wetlands 2018). Mires, a subset of peatlands, are wetlands where vegetation creates peat by depositing organic material at the surface without entirely decomposing, due to deposition occurring at or near the water table (Rydin *et al.* 1999, 2013, Joosten & Clarke 2002, Dartnall & Smith 2012). Accounting for approximately one-third of all wetlands globally (or ~3% of the Earth's surface), mires provide a variety of additional ecological services, such as carbon storage, biomass production, biodiversity conservation and climate regulation (Joosten 2012, Grundling *et al.* 2017, Minasny *et al.* 2019). However, mires are highly dependent on cool and humid climatic conditions, along with low evaporation rates and high effective moisture, making them particularly vulnerable to climate change and other environmental stressors (Yu *et al.* 2009, Essl *et al.* 2012, Harenda *et al.* 2018).

Wetland ecosystems, including mires, are dynamic and sensitive to natural climatic variations. However, anthropogenic activities and climate change have increased the rate of change in wetlands, leading to rapid degradation and biodiversity loss compared to other ecosystems (MEA 2005). Human-induced greenhouse gas emissions have exacerbated the natural greenhouse effect, causing unprecedented changes in the global climate system (Intergovernmental Panel on Climate Change 2021). In areas that are experiencing drying because of climate change, the high water table level required for peatlands is lowered, enabling oxygen to permeate the peatlands, increasing peat degradation and consequently rapidly releasing stored carbon into the atmosphere, contributing to greenhouse gas emissions (Joosten & Clarke 2002, Harenda *et al.* 2018, Minasny *et al.* 2019, Food and Agriculture Organization of the United Nations 2020). Such changes have a direct impact on the local and indigenous biota (Smith & Steenkamp 1990, Smith *et al.* 2001, Smith 2002). To better understand and address these ongoing changes, it is essential to track and assess the distribution and rates of loss of wetlands across landscapes.

The Prince Edward Islands (PEIs) are remote sub-Antarctic islands that have a stable climate with regular rainfall, high humidity and strong winds (Smith 2002, Pakhomov & Chown 2003, Smith & Mucina 2006, le Roux & McGeoch 2007), which promote the presence of water bodies and peat formation, resulting in the occurrence of mires in the terrestrial vegetation (Gremmen 1981, Dartnall & Smith 2012; Essl *et al.* 2012). However, similarly to other sub-Antarctic islands, the PEIs have experienced significant climate changes (Pendlebury & Barnes-Keoghan 2007, le Roux 2008). Since the 1960s steady increases in the mean diurnal and annual temperatures and a decrease in precipitation have been observed in the PEIs, resulting in a drier and warmer climate (le Roux 2008). The mean annual temperature increased from 5.4°C in the 1950s to 6.4°C in the 1990s, with average increases of 0.28°C and 0.24°C to daily maximum and minimum daily temperatures per decade, respectively, resulting in an increase from a maximum daily temperature of 7.6°C in the 1950s to 8.6°C in the 1990s and an increase from a minimum daily temperature of 2.8°C in the 1950s to 3.7°C in the 2000s (le Roux & McGeoch 2007). The islands have also experienced declining annual rainfall and increasing numbers of days without rainfall, along with rising wind speeds and potential evapotranspiration (le Roux & McGeoch 2007). Additionally, there is anecdotal evidence that water bodies on Marion Island are shrinking, resulting in drier conditions, including in mires, where peat moisture content is decreasing (Hedding & Greve 2018). This latter observation aligns with the consistent decrease in mire peat moisture content since 1966 (Chown & Smith 1993). Selkirk (2007) reported similar trends in mires on sub-Antarctic islands due to decreased precipitation and increasing wind speed in some parts of the region.

Since peatland areas have distinct hydrologic regimes, climates, chemistries, landforms, substrates and flora (Bourgeau-Chavez *et al.* 2018, Minasny *et al.* 2019), it may be possible to characterize and predict their occurrence using species distribution models (SDMs), which were developed to evaluate the relationship between known species occurrences and environmental factors thought to affect their occurrence. SDMs are often used in research into the distribution of species, ecological repercussions of climate change, as well as attempts to conserve species or biodiversity as a whole (Guisan & Zimmermann 2000, McPherson *et al.* 2004, Franklin 2009), and these predictive models have also been used successfully at both local and regional levels to map and detect wetlands (Hunter *et al.* 2012, Hiestermann & Rivers-Moore 2015, Rebelo *et al.* 2017). They have also been used in the sub-Antarctic context to determine the distributions of plant communities in sub-Antarctic vegetation (Fitzgerald *et al.* 2022) and to map sub-Antarctic cushion plants using satellite imagery and terrain attributes (Bricher *et al.* 2013). Könönen *et al.* (2023) recently used predictive models to model the suitable environments for palsa mires and peat plateaus across the Northern Hemisphere permafrost region.

The goal of this research is to investigate how well SDMs can predict the distribution of mires on the PEIs and the underlying drivers of their occurrence. However, preparing the data necessary to train these models in Geographic Information Systems (GISs) can be time-consuming (as noted by Brown 2014). To overcome this challenge, the data used in this study were pre-processed and visualized in *QGIS* and *ArcGIS Pro*, with remote sensing techniques utilized to create and prepare additional data as required. Therefore, this study employs a combination of SDMs, GIS and remote sensing to simulate the distribution of mires across the landscapes of the PEIs.

Materials and methods

Study area

The study area consists of the PEIs, which comprise two islands: Marion Island (46°54′ S, 37°45′ E) and Prince Edward Island (46°38′ S, 37°57′ E), located in the sub-Antarctic Ocean. Marion Island is larger and has a low, approximately oval shape, covering an area of 290 km^2 and rising to ~1230 m above sea level (a.s.l.; Smith & Mucina 2006). Prince Edward Island is smaller, covering an area of 46 km^2 and rising to ~672 m a.s.l. It has a distinctive asymmetric form and extensive vertical relief, with cliffs up to 400 m high on the western side and up to 500 m high to the north and south of the central block (see Fig. 1; Gremmen 1981, Rudolph *et al.* 2020).

The PEIs have an oceanic climate that is characterized by low temperatures with small seasonal variations, heavy rain, snow, strong prevailing westerly winds (50 km per hour or greater), high humidity and frequent cloud cover (Smith 2002, Pakhomov & Chown 2003, Smith & Mucina 2006, le Roux & McGeoch 2007, le Roux 2008). The climate on Marion Island varies across the landscape due to variations in aspect, altitude and recording height (le Roux 2008). The permanent meteorological station on Marion Island has recorded mostly uninterrupted weather observations since 1948 (le Roux 2008). Although Prince Edward Island has no meteorological records, its climate is assumed to be similar to that of Marion Island due to its proximity, with a slightly lower diurnal temperature variation (le Roux 2008). Peat formation is common on the PEIs (Gremmen 1981), where the water table is close to the surface for most of the year due to the wet and cool oceanic climate (Rydin *et al.* 1999, Raeymaekers *et al.* 2000). This results in the formation of waterlogged mires, mostly in lowland areas, which can range from a depth of a few centimetres to more than 4 m where drainage is impeded (Gremmen 1981).

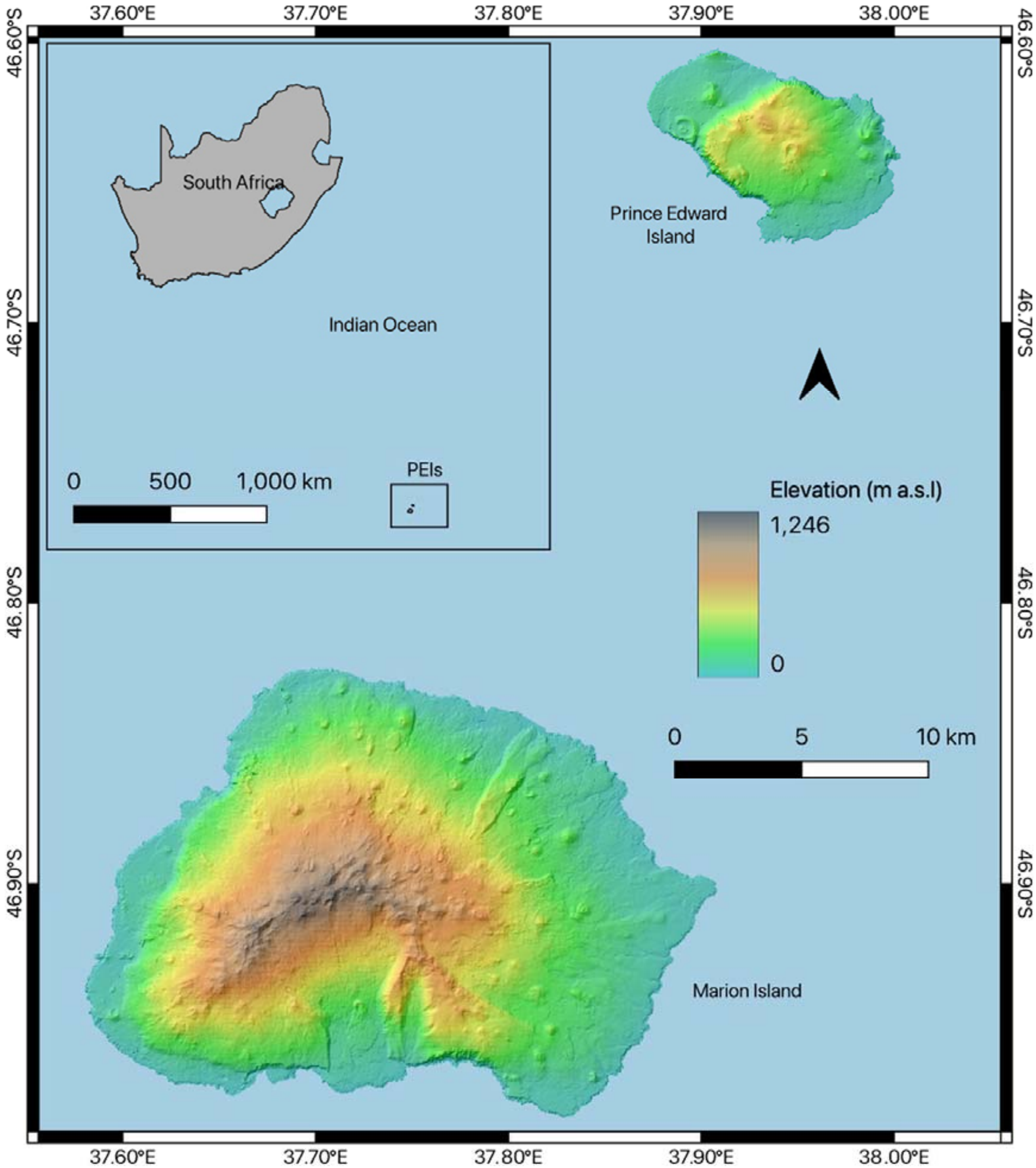

Figure 1. The Prince Edward Islands (PEIs) in relation to South Africa. a.s.l. = above sea level.

Occurrence data

The occurrence data used in this study were obtained from a vegetation field survey conducted on Marion Island from 2018 to 2020, which covered all of the main vegetation complexes proposed by Gremmen & Smith (2008). Two methods were used to collect data: 1) plots were laid out in a stratified random design based on geology and 2) rapid transects were walked, with vegetation scored at random points along the transects. The vegetation complex at each plot and point on the transects was visually estimated according to Gremmen & Smith (2008) using plant species abundances and topographical characteristics. One of the vegetation complexes recorded was mires, which are areas that are waterlogged. A total of 1415 points were recorded, of which 255 indicated the presence of mires and 1160 indicated other vegetation complexes (Fig. 2). For this study, points that supported the mire complex were used to indicate the presence of mires, while the other vegetation complexes were classified as mire absences.

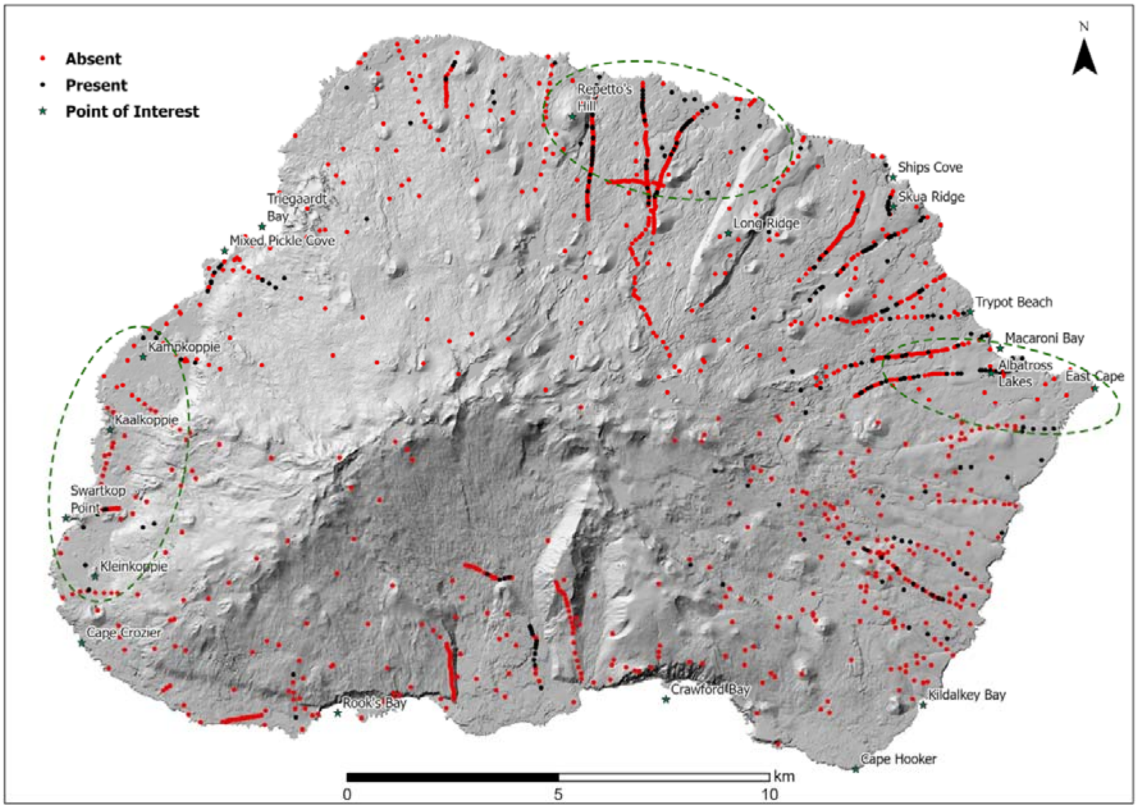

Figure 2. Survey points on Marion Island showing mire presence and absence. The locations of the largest wetlands, as identified by Smith & Mucina (2006), are circled in dashed green lines.

Environmental variables

To model the distribution of mires on the PEIs, the authors selected SDM predictor variables that are believed to influence peatland distribution. Peatlands develop in areas with distinct hydrologic regimes, climates, chemistries, landforms, substrates and flora (Bourgeau-Chavez *et al.* 2018, Minasny *et al.* 2019). Three climate variables were chosen for this study, including annual precipitation (Bio12), which was extracted from WorldClim at a spatial resolution of 30 arc-seconds (~1 km; Fick & Hijmans 2017). Despite known high prediction errors in remote Southern Ocean islands, such as the PEIs, due to the scarcity of ground observations, the annual precipitation data from WorldClim2 were used because of its high spatial resolution (~1 km). This resolution was significantly finer than other available sources, especially given the small size of the islands, helping to avoid having only a few pixels of precipitation data (Fick & Hijmans 2017, Leihy *et al.* 2018). Additionally, two temperature variables - daytime mean monthly temperature and night-time mean monthly temperature - were obtained at a spatial resolution of 1 km (Leihy *et al.* 2018). Leihy *et al.* (2018) provided high-resolution (1 km) Moderate Resolution Imaging Spectroradiometer (MODIS) land surface temperature observations using a modified spatiotemporal gap-filling method, covering a monthly time series from 2001 to 2015. Unlike WorldClim2, this dataset was validated using fine-scale microclimate data and demonstrated a better ability to describe the thermal heterogeneity of the region, particularly for sub-Antarctic islands with steep elevational gradients and strong prevailing winds.

A digital elevation model (DEM) with a spatial resolution of 1 m was obtained from South Africa's National Geo-Spatial Information (NGI). To prepare the DEM for hydrologic modelling, a depressionless DEM was generated using the default parameters of the ‘Fill Sinks’ tool in *SAGA GIS* (Wang & Liu 2006). DEMs often contain artefact depressions that interrupt flow paths and alter drainage directions; therefore, removing artefact depressions from DEMs is essential for accurate flow routing, ensuring realistic surface water flow representation and reliable geomorphic and hydrologic modelling outcomes (Lindsay & Creed 2005). The Topographic Wetness Index (TWI) was extracted from the DEM using the ‘ArcPy’ script developed by Wolf & Fricker (2013), which is based on the TWI algorithm of Beven & Kirkby (1979). Distinct landform classes were extracted from the DEM using a Topographic Position Index (TPI) approach, which involved using two neighbourhood sizes to create an annulus neighbourhood (Radius 1 = 50 m, Radius 2 = 200 m; Weiss 2001). Slope (in degrees) and distance from the coast were also derived from the DEM. The geology and soil layers were created by Rudolph *et al.* (2020) and Lubbe (2010), respectively.

The study utilized remote sensing data in the form of Sentinel-2 imagery to extract two indices: Normalized Difference Vegetation Index (NDVI) and Normalized Difference Wetness Index (NDWI) as proxies for local vegetation productivity and surface wetness, respectively. These indices were extracted from geometrically and radiometrically corrected images. Due to persistent cloud cover, a mosaic of three images from 5 October 2020 and one from 10 October 2020 was created for Marion Island, while a cloud-free image from 10 November 2017 was used for Prince Edward Island. The NDVI was used to assess vegetation productivity using near-infrared and red bands, while the NDWI was used as an indicator of surface wetness or the presence of surface water using near-infrared and green bands. The Semi-Automatic Classification Plugin (*QGIS*) (Congedo 2021) was used to download Sentinel data, mask the clouds and create the mosaic. Seasonality was not a significant consideration in the study, as the mean monthly total rainfall and mean temperature on Marion Island vary only slightly throughout the year, with Marion Island experiencing a difference of 4.1°C between the coldest and warmest months, while the diurnal temperature varies by only 1.9°C, and the difference in precipitation between the wettest and driest months is 600 mm (ranging from 150 to 2100 mm; Smith 2002, Smith & Mucina 2006, Sadiki 2019).

All of the variables used in the study were resampled to a uniform spatial resolution of 10 m using the WGS 84 UTM Zone 37S projection and the same extent (Table I). The DEM was resampled to a 10 m spatial resolution to match the resolution of the Sentinel-2 imagery using a bilinear resampling method.

Table I. Predictor variables ($n = 12$) used in the study; variables are grouped into four variables scenarios.

Variable type	Predictor variable	Source
Topographic	Distance from coast (m)	Derived from DEM from NGI
	Elevation (metres above sea level)	Derived from DEM from NGI
	Slope (°)	Derived from DEM from NGI
	Topographic Position Index (TPI)	Derived from DEM from NGI
	Topographic Wetness Index (TWI)	Derived from DEM from NGI
Geology and soils	Geology	Rudolph *et al.* (2020)
	Soils	Lubbe (2010)
Satellite imagery	Normalized Difference Vegetation Index (NDVI)	Copernicus Sentinel data (2017, 2020)
	Normalized Difference Water Index (NDWI)	Copernicus Sentinel data (2017, 2020)
Climatic	Daytime mean monthly temperature	Leihy *et al.* (2018)
	Night-time mean monthly temperature	Leihy *et al.* (2018)
	Bio12: Annual Precipitation	Fick & Hijmans (2017)

DEM = digital elevation model; NGI = National Geo-Spatial Information.

Species distribution modelling

The distribution of mires on the PEIs was modelled using six commonly used presence-absence SDM algorithms (Table II) with default settings available within the 'sdm' package in *R* (Naimi & Araújo 2016, R Core Team 2024). Validation of the models utilized the 10-fold cross-validation with five replications (Naimi & Araújo 2016).

Table II. Regression-based and machine learning species distribution modelling used in the study.

Model	Description	Reference
BRT	Boosted regression trees	Elith *et al.* (2008)
CART	Classification and regression trees	Breiman *et al.* (1984)
GAM	Generalized additive models	Guisan *et al.* (2002)
GLM	Generalized linear models	McCullagh & Nelder (1989)
MARS	Multivariate adaptive regression splines	Friedman (1991)
RF	Random forests	Breiman (2001)

Models were created using six variable scenarios, namely:

1) Climate variables

2) Topographic, geology, soil and satellite imagery variables

3) Wetland classification proxy variables, including:

   a) The Ramsar Convention classification system

   b) The Hydrogeomorphic (HGM) classification system

c) The International Union for Conservation of Nature (IUCN) Global Ecosystem Typology 2.0

4) All predictor variables

For each variable scenario, collinearity between predictor variables was assessed using the variance inflation factor (VIF) stepwise technique analysis (Naimi & Araújo 2016). If VIF values were larger than 10, one of the collinear variables was removed prior to modelling. The VIF values were recalculated as a stepwise process until all values were below the threshold. A summary of all predictor variables, after accounting for multicollinearity, is presented for each scenario in Table III.

Table III. Predictor variables for each scenario with collinearity accounted for by removing highly collinear variables (variance inflation factor > 10). Final variable selection is shown. (See main text for details regarding the variable scenarios.)

	Variable scenario					
Predictor variable	Climate	Topo-geo-sat	Ramsar	HGM	IUCN	All
Annual Precipitation (Bio12)	X				X	X
Daytime mean monthly temperature	X				X	X
Night-time mean monthly temperature	X				X	X
Distance from coast		X				X
Elevation		X				
Slope		X				X
Topographic Wetness Index (TWI)		X	X	X		X
Topographic Position Index (TPI)		X		X		X
Normalized Difference Vegetation Index (NDVI)			X		X	
Normalized Difference Water Index (NDWI)		X		X		X
Geology		X				X
Soils		X	X			X

Scenario 1: Climate variables

This variable scenario only includes the climatic variables (Table III). None of the three variables were removed based on VIF.

Scenario 2: Topographic, geology, soil and satellite imagery variables

This scenario includes all of the predictor variables with the exclusion of climatic variables (Table III). Due to a strong correlation between NDVI and NDWI, the former was removed, leaving eight variables under this variable scenario (Table III). This variable scenario is hereafter referred to as ‘topo-geo-sat variables'.

Scenario 3: Wetland classification proxy variables

Scenario 3 consisted of three sub-versions, each based on a common wetland classification method, namely: 1) the Ramsar Convention classification (Finlayson 2018), 2) the HGM classification system (Brinson 1993) and 3) IUCN's typology for wetland ecosystem types (Keith *et al.* 2020b).

The Ramsar Convention classification system

The Ramsar Convention classification system (Scenario 3a) categorizes wetlands into marine and coastal, inland and human-made, with subcategories based on location, water permanence, soils, substrates and flora (Finlayson 2018). As such, TWI was selected as a proxy for water permanence and NDVI for vegetation. Additionally, we included soil variables in this scenario. None of the variables were removed due to collinearity. This variable scenario is hereafter referred to as 'Ramsar proxy variables'.

The HGM classification system

The HGM classification system (Scenario 3b) is based on the premise that water flows from higher to lower places and water collects in areas of gentler slopes, hence hydrology and landforms are the most evident factors that can be used to characterize wetlands (Semeniuk & Semeniuk 1995, Ollis *et al.* 2013). The system categorizes wetlands into classes based on geomorphic, water supply and hydrodynamic properties (Ollis *et al.* 2013). Therefore, landforms (modelled using the TPI), surface wetness (modelled using the NDWI) and TWI were selected as proxy predictor variables for the occurrence of mires. None of the three variables were removed based on VIF. This variable scenario is hereafter referred to as 'HGM proxy variables'.

The IUCN Global Ecosystem Typology 2.0

The IUCN Global Ecosystem Typology 2.0 (Scenario 3c) describes the profiles of biomes and ecosystem functional groups (EFGs), providing key ecological traits of functionally different ecosystems and their drivers (Keith *et al.* 2020a). Marion Island is structurally and functionally characteristic of the most climatically harsh variety of tundra, with some evidence of high Arctic polar deserts (Smith 2008). Smith & Mucina (2006) identified sub-Antarctic tundra in the lowland areas and sub-Antarctic polar desert limited to higher elevations as the two major biomes on the PEIs. Thus, the PEIs can be classified within the polar-alpine biome of the IUCN Global Ecosystem Typology 2.0, which encompasses the extensive Arctic and Antarctic regions (Keith *et al.* 2020a). Within this functional biome, the polar tundra and deserts EFG is the most applicable to the PEIs, considering the two major biomes identified by Smith & Mucina (2006). This functional group is characterized by extreme cold temperatures and short growing seasons that exclude trees and a continuous to sparse cover of cold-tolerant mosses, liverworts, lichens, grasses, low shrubs and other flowering plants, while permafrost substrates accumulate peat due to slow decomposition rates. However, despite its global recognition and wide application, the IUCN Global Ecosystem Typology 2.0 has faced criticism for its inconsistencies and potential unreliability, particularly regarding the classification of biomes and EFGs (Mucina 2023). Mucina (2023) offers an alternative perspective by categorizing all sub-Antarctic islands, including the PEIs, under two global biomes: Antarctic Tundra and Southern Polar Desert, both part of the Antarctic Zone zonobiome. Despite these critiques, the IUCN Global Ecosystem Typology 2.0 remains a widely acknowledged classification system, which justifies its use in this context. Given the ecological drivers of polar tundra and desert regions in the IUCN Global Ecosystem Typology 2.0, the vegetation density proxy (NDVI), temperature and precipitation were chosen as proxies for peatland occurrence. NDVI effectively captures the health and distribution of vegetation, which are crucial where plant cover directly reflects wetland conditions. Temperature data are vital for understanding permafrost dynamics (these are absent from the PEIs; Boelhouwers *et al.* 2008) and seasonal thawing, which influence peat accumulation and stability. Precipitation data are critical for assessing water availability and the overall hydrological balance, which affect both soil moisture and the development of peatlands. None of the variables were removed based on VIF. This variable scenario is hereafter referred to as 'IUCN proxy variables'.

Scenario 4: All predictor variables

All 12 predictor variables (Table I) were considered under this variable scenario. The VIF revealed a correlation between NDVI and NDWI, as well as between Annual Precipitation and Elevation. Therefore, NDVI and Elevation were removed due to multicollinearity issues, resulting in total of 10 variables under this variable scenario. This variable scenario is hereafter referred to as 'all variables'.

Model comparison

The area under the curve (AUC) of a receiver operating characteristic plot and the true skill statistic (TSS) are commonly used to assess SDM predictive performance (Fielding & Bell 1997, Allouche *et al.* 2006), allowing for comparison across models, and thus they were used in this study. AUC values vary from 0 to 1, with an AUC score between 0.9 and 1.0 indicating an excellent model, between 0.8 and 0.9 indicating a good model, between 0.7 and 0.8 indicating a fair model, between 0.6 and 0.7 indicating a poor model and between 0.5 and 0.6 indicating a failed model (Swets 1988, González-Ferreras *et al.* 2016). As such, an AUC of at least 0.7 is required for a model to be considered sufficient for modelling species distributions (Swets 1988). Although it is widely accepted as the standard technique for assessing SDM correctness, others (see Mainali *et al.* 2015, Leroy *et al.* 2018, Shambani *et al.* 2018) do not advocate using this metric as a comparison measure of model accuracy (Termansen 2006, Austin 2007, Lobo 2008, Peterson 2008, Jiménez-Valverde 2012). As a result, the AUC is frequently employed in combination with another metric when utilized as a measure of accuracy (Mainali *et al.* 2015, Leroy *et al.* 2018).

As an alternative, Allouche *et al.* (2006) suggest using the TSS as a measure of SDM success. The metric compares the proportion of correct predictions to the proportion of hypothetical predictions, disregarding any predictions that may be due to random guesses (Allouche *et al.* 2006). The TSS is not affected by species prevalence and the size of the validation dataset (Allouche *et al.* 2006). Unlike the AUC, the TSS requires that the resulting continuous model predictions be transformed into binary predictions based on a threshold (Fielding & Bell 1997). The threshold was selected as the value that maximized the sum of sensitivity and specificity, which is one of the better threshold selection methods for presence-absence data (Liu *et al.* 2005). TSS values less than 0.2 are considered failed or null models, values between 0.2 and 0.4 are considered poor, values between 0.4 and 0.6 are considered fair and values greater than 0.6 are considered good to excellent models (González-Ferreras *et al.* 2016).

Results

Model comparison

The AUC and TSS for all 36 models in this study indicated poor to fair model performance (AUC mean = 0.68, TSS mean = 0.34; Table IV). The best models were developed on variables from Scenarios 2 (topographic, geology, soil, and satellite imaging variables) and 4 (all variables; Fig. 3), while the modelling techniques with the highest AUC and TSS scores were boosted regression trees and random forest (RF) models (Fig. 4). The RF model based on

Scenario 4 variables performed the best overall, outperforming all other models for both measures, with an AUC value of 0.74 and a TSS of 0.42 (Table IV). Therefore, the model was selected as the best model to predict the distribution of mires on the PEIs.

Table IV. The mean area under the Curve (AUC) and true skill statistic (TSS) values and their standard deviations (SDs), associated with 10-fold cross-validation (five replications) of models (see Table II for model definitions) run using six variable scenarios (see Table III for variable scenarios and main text for details regarding the variable scenarios). Fair-performing models according to the AUC and TSS values are indicated in bold alone and bold and italics, respectively.

		Variable scenario											
		Climate		Topo-geo-sat		Ramsar		HGM		IUCN		All	
Model	Metric	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
BRT	AUC	0.65	0.06	**0.72**	**0.07**	0.67	0.06	0.70	0.06	0.68	0.05	**0.73**	**0.06**
	TSS	0.30	0.10	***0.40***	***0.12***	0.36	0.09	0.37	0.10	0.35	0.07	***0.41***	***0.08***
CART	AUC	0.60	0.03	0.68	0.06	0.66	0.06	0.64	0.06	0.68	0.04	**0.71**	**0.07**
	TSS	0.18	0.07	0.29	0.10	0.30	0.10	0.26	0.10	0.30	0.07	0.35	0.11
GAM	AUC	0.63	0.04	**0.72**	**0.06**	0.68	0.07	0.70	0.06	0.65	0.04	**0.73**	**0.05**
	TSS	0.27	0.08	0.39	0.11	0.35	0.11	0.37	0.09	0.32	0.07	***0.42***	***0.09***
GLM	AUC	0.62	0.04	**0.71**	**0.04**	0.66	0.03	0.70	0.04	0.66	0.04	**0.71**	**0.04**
	TSS	0.27	0.08	0.38	0.06	0.32	0.06	0.37	0.07	0.33	0.07	0.39	0.07
MARS	AUC	0.61	0.05	0.69	0.05	0.66	0.05	0.69	0.05	0.65	0.05	0.70	0.04
	TSS	0.26	0.08	0.36	0.08	0.34	0.11	0.37	0.09	0.31	0.07	0.36	0.08
RF	AUC	0.69	0.06	**0.72**	**0.06**	0.65	0.04	0.67	0.06	**0.71**	**0.04**	**0.74**	**0.06**
	TSS	0.34	0.08	0.39	0.09	0.30	0.08	0.32	0.10	0.37	0.06	***0.42***	***0.09***

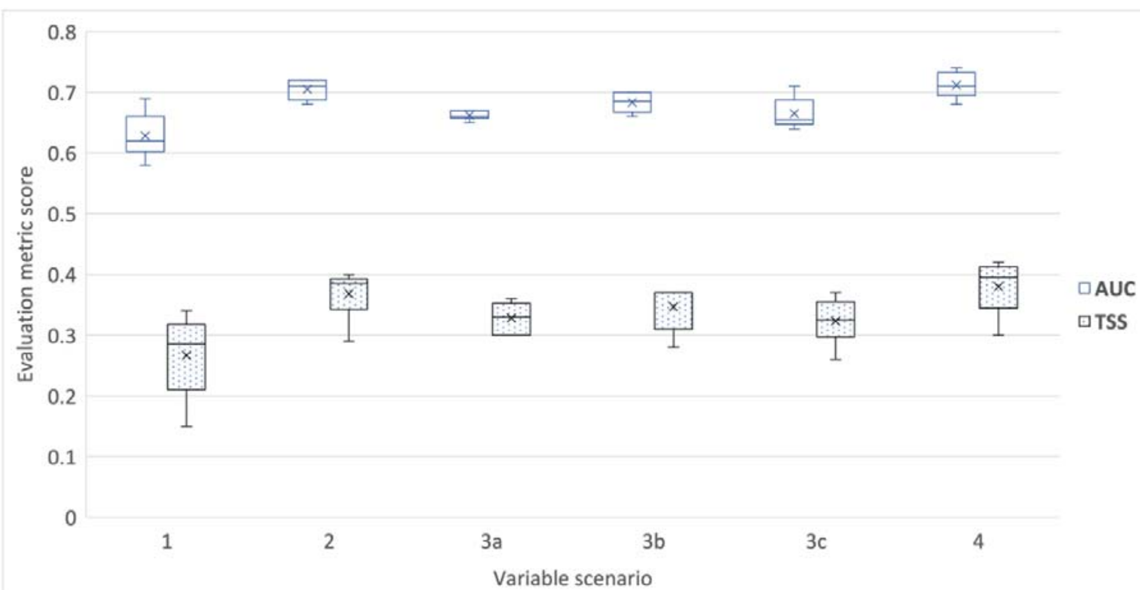

Figure 3. Box plots showing the distribution of area under the curve (AUC) and true skill statistic (TSS) values for each variable scenario for all species distribution models.

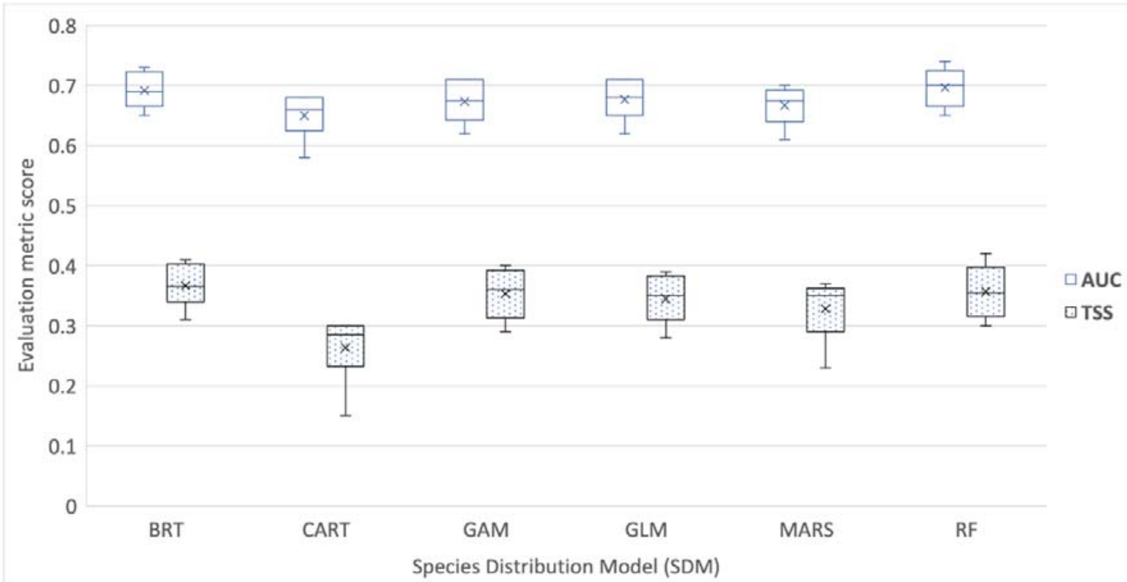

Figure 4. Box plots showing the distribution of area under the curve (AUC) and true skill statistic (TSS) values for each model type across all variable scenarios (see Table II for model definitions).

A variable importance analysis was performed to determine the extent to which each predictor contributed to the prediction of mire occurrence (Fig. 5). The most important variables were NDWI with a 36% contribution to the model, followed by slope with a 29% contribution to the model and night-time mean monthly temperature with a 13% contribution to the model. Annual precipitation, distance from the coast, TPI and daytime mean monthly temperature also made considerable contributions to the model, with contributions ranging from 9% to 5%. Geology and soils had minimal importance, contributing only 2% and 3% to the model, respectively. As such, they were removed from the predictor variables used to train the RF model to predict the distribution of mires on the PEIs. This decision was also supported by the unavailability of a soil dataset for Prince Edward Island; such a dataset was only available for Marion Island. The removal of the two variables, as expected due to their low relative importance to the model, did not change model performance, with the performance measurement metrics remaining the same (AUC = 0.74, TSS = 0.42). Overall, the analysis indicated that environmental variables related to topography, hydrology and climate were the most important predictors of mire occurrence on the island.

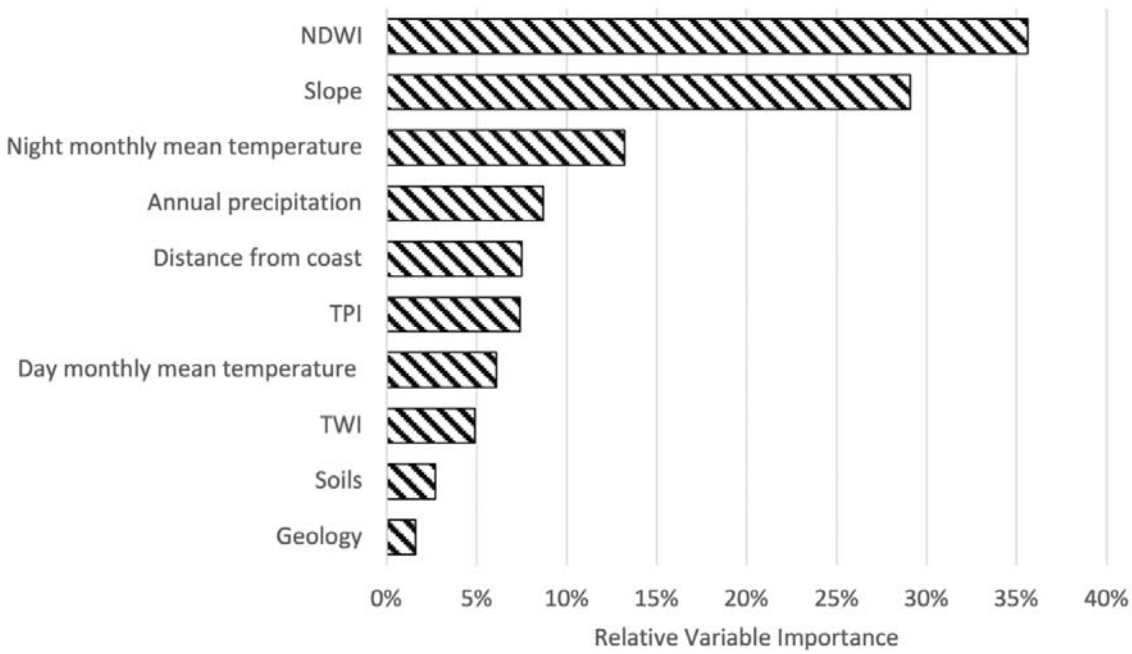

Figure 5. Relative variable importance of the variables used in the prediction of the distribution of mires on Marion Island of the best model (random forest model with all predictor variables). NDWI = Normalized Difference Water Index; TPI = Topographic Position Index; TWI = Topographic Wetness Index.

The response curve for NDWI (Fig. 6a) indicates a steep decline in the probability of mire occurrence as NDWI values increase. NDWI values represent the proportion of surface water, and as mires are known to occur where there is high soil moisture, this suggests that mires are unlikely to occur in areas where water is visible at the surface, such as open surface water. Based on the response curve for the slope (Fig. 6b), there is an increase in the probability of mire occurrence with increasing slope from ~30° to 62°. This suggests that mires are more likely to occur on steeper slopes rather than flatter ones. However, there is also some indication that mires may prefer slopes between 0° and 10°, although the probability of occurrence on such slopes is lower than for steeper slopes.

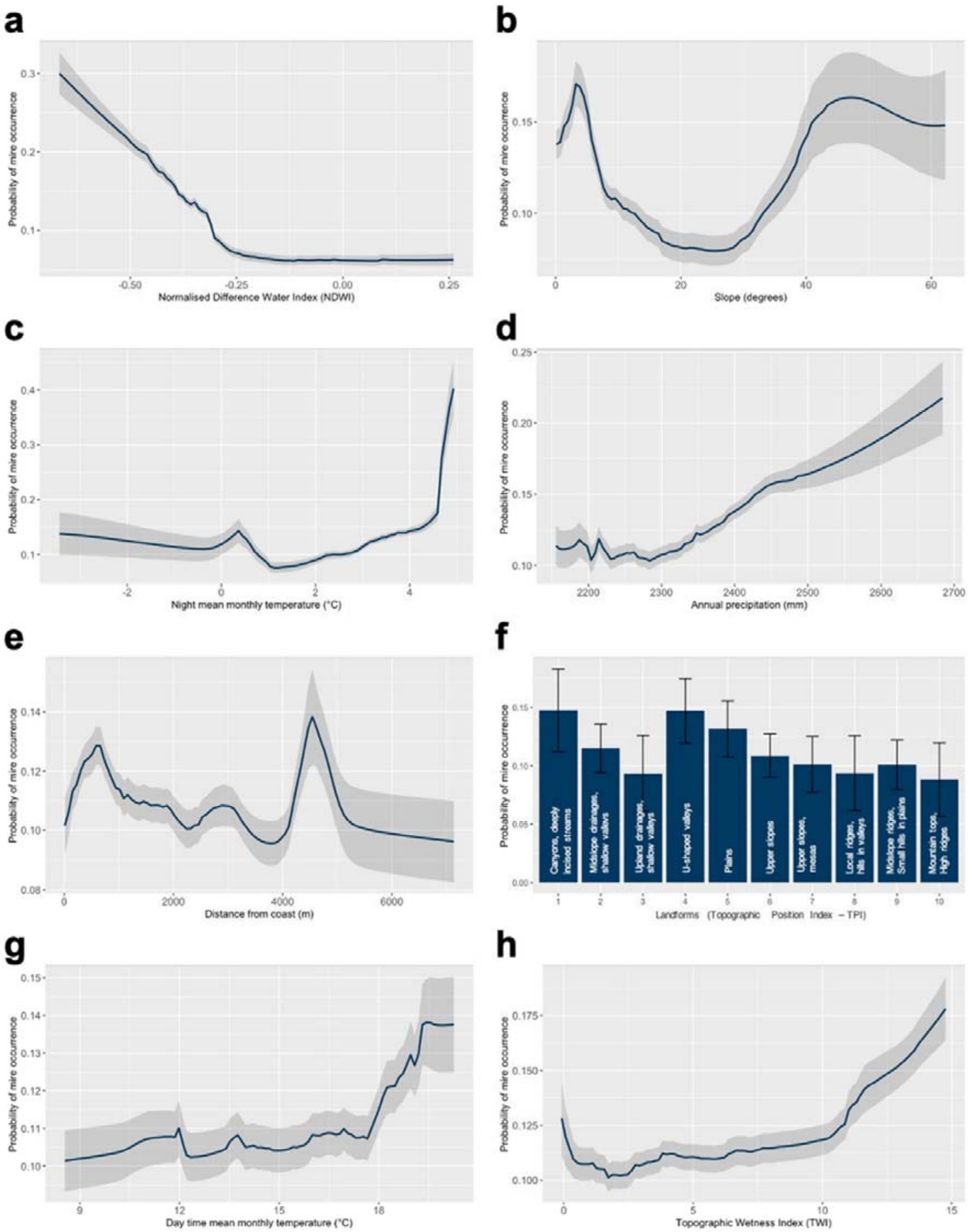

Figure 6. Response curves for each of the eight variables (except the categorical variables (soils and geology)), indicating the effect of a predictor variable on the probability of the response variable. Values closer to 1 on the *y*-axis indicate a high probability of occurrence at a range of predictor variable values on the *x*-axis. The curves include standard deviation values, highlighted by greyed areas for continuous variables and error bars for categorical variables, which show the variability in predicted probabilities across different ranges of each predictor variable. **a.** Normalized Difference Water Index (NDWI): shows the effect of water presence on the probability of occurrence. **b.** Slope (degrees): represents the impact of terrain slope on the probability of occurrence. **c.** Night-time mean monthly temperature (°C):

shows how the average night-time temperature affects the probability of occurrence. **d.** Annual precipitation: displays the effect of total yearly rainfall on the likelihood of the response variable. **e.** Distance from coast: Indicates how the proximity to the coast influences the probability of occurrence. **f.** Landforms (Topographic Position Index): illustrates the influence of terrain shape, such as valleys or ridges, on the probability of occurrence. **g.** Daytime mean monthly temperature: shows how average daytime temperatures affect the probability of occurrence. **h.** Topographic Wetness Index (TWI): represents the potential for water accumulation based on topography.

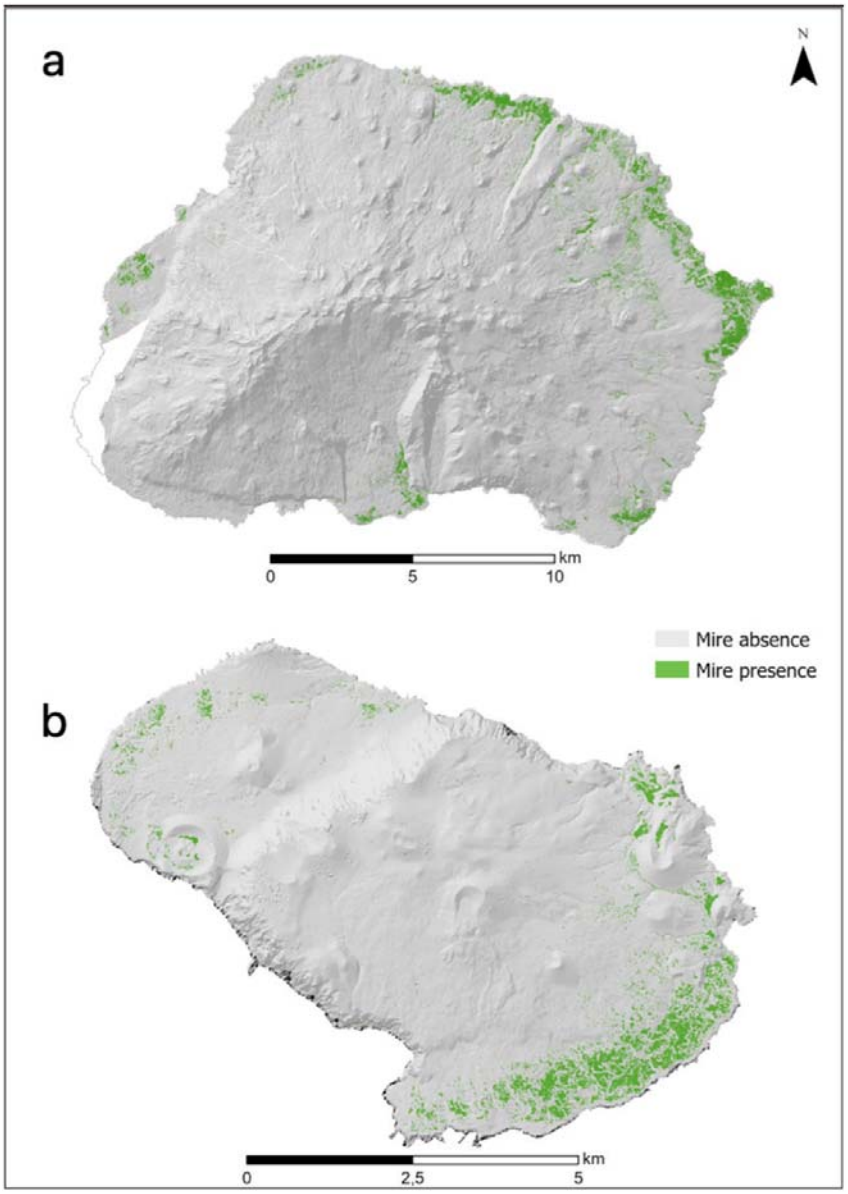

Figure 7. Predicted distributions of mires on **a.** Marion Island and **b.** Prince Edward Island. The white area on the western side of Marion Island indicates a region where mires could not be modelled due to the lack of available satellite data and therefore no surface wetness information being available.

The distribution of mires on the Prince Edward Islands

As no training data (mire presence-absence) exist for Prince Edward Island, the model trained on Marion Island was projected onto Prince Edward Island. The binary map indicates that mires on Prince Edward Island mostly occur on the eastern side of the island, while Prince Edward Island's mires are prevalent in the north-western and south-eastern parts of the island, where plains are the dominant landform (Fig. 7).

Discussion

The ability of multiple regression-based and machine learning species distribution modelling algorithms (Table II) to predict the distribution of mires on the PEIs using several combinations of predictor variables (Table III) was assessed in this study. The best model in this study performed only 'fairly' (i.e. moderately well; AUC = 0.74, TSS = 0.42). Therefore, the predictive power of this study's models was limited.

While the best model was able to identify general regions where mires were known to occur, it was not as accurate at predicting the occurrence of individual mires. One possible explanation for this could be that some mires on the PEIs were small and confined to a limited area, with an approximate size of 3 × 3 m. The input data used in the model had a coarser resolution than this. This mismatch in sampling and modelling resolution may have resulted in limited matching between the precise locations of mires and the predicted locations. Additionally, the distribution of mires on Marion Island is patchy in certain areas, with vegetation changing rapidly from mire to non-mire vegetation and back again over short distances; this variability has already noted by Momberg *et al.* (2021). Overall, the study suggests that further refinement of the models and more precise data collection may be necessary to improve the accuracy of mire distribution predictions on the PEIs.

The models that performed the best in this study utilized variables from Scenario 2 (topo-geo-sat variables) and Scenario 4 (all variables). The two most important predictor variables, slope and NDWI, were consistently included in the best models across Scenarios 2 and 4. Conversely, models relying solely on climatic variables (Scenario 1) performed the worst across all measures, as shown in Fig. 3. The input variables, although resampled to 10 m of the satellite imagery, have different spatial resolutions in their original format. Climate variables at 30 arc-seconds simply do not capture the spatial variations required for a fine-scale study. The same applies to the coarse-scale geology and soil layers that required removal before final modelling based mostly on poor spatial resolution. The original spatial resolution of the input variable is thus an important factor to consider for future modelling. In addition, some variables might have been excluded completely, as in many cases the required proxy data used to predict mire occurrence were not available. Regardless, a comparison of the performance of models based on climatic factors to those based on a combination of variables, including topography and satellite imagery-derived variables, indicates that the latter better determine the prevalence of mires across the terrain at the spatial scale examined in this study.

The response curves of the model variables (shown in Fig. 6) indicate that mires are more likely to occur in areas where NDWI values (which serve as proxies for surface water) fall between -0.75 and -0.25. This range of values indicates the lack of open surface water and is commonly associated with land-cover classifications such as vegetation, bare soil or rock. This implies that while mires are habitats that require high soil moisture, their water is typically not visible at the surface on the PEIs. As mires are characterized by a layer of peat at the surface covered by vegetation, this range of values is plausible. The finding that the model suggests mires on the PEIs prefer slopes between 30° and 62°, with some preferring gentler slopes between 0° and 10°, is somewhat surprising given that the largest mires on Marion Island are known to occur on undulating landscapes with gentle slopes. While this discrepancy may suggest that the model is flawed, it is important to consider the complexity of the landscape on Marion Island. Mires on Marion Island often have exposed ridges and plateaus around their edges (Yeloff *et al.* 2007), which may not have been captured at the scale of the study (10 m), potentially leading to a generalization of slopes, ridges and plateaus, influencing the modelling of mire occurrence. Moreover, the variability in vegetation cover, soil moisture and other factors across the island may also contribute to the inconsistency between the model's predictions and observations. These environmental factors can vary greatly over short distances, as demonstrated by Momberg *et al.* (2021) on Marion Island, where wind stress was linked to species richness, vegetation cover and community composition using fine-scale, field-collected data. As the model does not account for this fine-scale variation, it struggles to accurately predict mire occurrence and distribution. Therefore, it is necessary to conduct further investigation to explore the potential sources of bias in the model and refine it accordingly. Overall, the findings highlight the need for caution when interpreting the results of species distribution modelling, particularly in complex and heterogeneous landscapes where small-scale variations may have significant impacts on the occurrence and distribution of species.

The predicted distribution of mires on Marion Island and Prince Edward Island (Fig. 7) corresponds somewhat to the areas in which mires are described as common. Smith & Mucina (2006) state that 'mire vegetation is found in most lowland areas, being most extensive below 200 m, but found up to 400 m altitude. On Marion Island approximately 30% of the area below 100 m and approximately 3% of that between 100 and 300 m is occupied by mire vegetation; the largest mires on Marion Island are found on the coastal plain between Repetto's Hill and Long Ridge, inland of East Cape, Macaroni Bay and on the western coastal plain between Kleinkoppie and Kampkoppie.' However, it should be noted that mires on the western side of Marion Island are not as common as they are on the eastern side. Figure 2 offers a visual depiction of this description. Based on this description, the model was able to predict two of the large mires known to exist on the eastern coast of Marion Island, on the coastal plain between Repetto's Hill and Long Ridge, inland of East Cape, Macaroni Bay. Smith & Mucina (2006) indicated that a third mire exists on the western coastal plain between Kleinkoppie and Kampkoppie; however, the model predicted a minimal extent of mires in this area. In addition to the fact that prediction was impossible for a small section of the area, this underestimation could suggest the absence of critical environmental factors. Additionally, variations in environmental factors, such as climate, between the eastern and western sides of the island could also affect the model's predictive ability.

For Prince Edward Island, the model suggests mires are common in the north-western and south-eastern sections of the island, where plains represent the major landform and slopes are gentler. Whether the SDM trained on data from Marion Island can be used to accurately predict distributions of mires on Prince Edward Island remains to be determined. While the PEIs experience similar climates (le Roux 2008) and possess similar geologies and landforms, Marion Island has permanent human habitation and many more invasive species than Prince Edward Island (Greve *et al.* 2017, 2020). This is because, for conservation reasons, Prince Edward Island may only be accessed for short periods of time at intervals greater than 4 years, and visits sometimes happen even less frequently. Human activities and invasive species affect not only individual species, but also ecosystem processes (Smith 2002, Greve *et al.* 2017), which could potentially influence the position of mires. With both islands thought to be similar in environmental variables, this difference regarding human activity (and invasive species presence) is worth noting, as the prediction based on Marion Island data might not be suitable for mire prediction on Prince Edward Island. However, without the relevant datasets required for Prince Edward Island to perform such modelling, the results from Marion Islands provide the next best option for modelling mire occurrence on Prince Edward Island.

Conclusion

We showed some, but not very strong, support for the use of SDMs in predicting mire distributions on sub-Antarctic Marion Island. Our models identified most of the general areas in which mires occur and would thus be useful in predicting for potential mire presence over broader regions if the methods used here are applied to other sub-Antarctic islands. While the models were not very successful at identifying mires at finer grain, improved geospatial layers at finer resolution could improve prediction. Of note is that climate played almost no role in predicting the distribution of mires on Marion Island. This finding implies that, within the range of climatic variation considered in this study, non-climatic factors were more influential. Yet it is also important to note that the impact of climate change on mire distribution might not be immediately apparent unless there are significant shifts in climatic conditions. Regardless, there are some indications that mires on Marion Island are drying out due to ongoing climate change (Hedding & Greve 2018), and such changes can be attributed to macroclimatic changes that simultaneously affect the whole island. Considering the present climatic trajectory on the PEIs, the islands can be expected to become warmer and dryer, which will dry out mires and potentially reduce their distribution over the terrain.

Author contributions

MMS performed data quality assessment and preparation, analysis, interpretation and map/graph production. MG provided initial field data and was instrumental in concept design and interpretation of findings. CDH was instrumental in concept design, interpretation and discussion of findings, and she prepared and edited the manuscript for submission.

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Competing interests

The authors declare none.

Ethical standards

The authors declare that all ethical practices have been followed in relation to the development, writing and publication of the article. Ethical approval for working with primary and secondary data has also been obtained by the Faculty of Natural and Agricultural Sciences Ethical Committee of the University of Pretoria, with NAS219/2020.

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