Investigating ecological drivers and impacts of vegetation change in sub-Antarctic tundra

by

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Declaration

I, Stephni van der Merwe, declare that the thesis/dissertation, which I hereby submit for the degree PhD Biological Sciences at the University of Cape Town, is my own work and has not previously been submitted by me for a degree at this or any other tertiary institution. This thesis has been submitted to plagiarism checking software and I confirm that my supervisor has seen the report, with all concerns resolved together with my supervisor.

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Abstract

Understanding the impact of environmental change on vegetation dynamics requires considering the individualistic responses of plant species, which are influenced by their specific habitat requirements and biotic interactions. For instance, habitat generalist species often have broad environmental tolerance, and may be able to adapt to and often dominate in dynamic or disturbed environments, compared to specialists that are adapted to specific environmental conditions and thus have more restricted tolerance to change. This study explores the potential for the combination of topographic, climatic, edaphic and biotic factors to influence different vascular plant species distributional and cover changes in response to the key drivers of change in the sub-Antarctic, focusing on Marion Island (MI). Given the recent origin and relative species poverty of the sub-Antarctic flora, changes in vegetation are expected to result from individual responses rather than collective trends across the entire flora or its communities.

To evaluate the appropriate scale for vegetation assessment in species-poor environments, the classification of vegetation on MI was revisited. Various modern classification techniques were used to classify vascular plant species data, and the resulting classifications were compared with previous units. Due to the limited development of strong plant assemblages with discrete boundaries in the sub-Antarctic islands, community-level classification may not be suitable in such species-poor environments. Consequently, this study proposes a species-level approach aligned with continuum theory rather than community theory for more accurate vegetation monitoring in species-poor environments.

Since the 1950s, MI has experienced changes in temperature, precipitation, wind conditions, and biotic interactions, with plant species thus experiencing altered environmental conditions. To investigate the vegetation cover changes across different habitats, repeat photography between 1965 and 2020 was used. Results showed an overall increase in vegetation cover in most habitats over the past five decades, accompanied by rapid drying, rising mean air temperature, changing wind direction, increased invasive plant species cover, and higher invasive house mouse abundance. Climate change and invasive species were identified as the primary interactive drivers of vegetation change. The increase in cover was primarily driven by more responsive species, such as habitat generalists, while habitat specialists either showed minimal changes or a decrease in cover.

Since edaphic properties are an often overlooked component of habitat suitability or changes therein, the edaphic properties were modelled for the first time on MI to determine the spatial variation of key soil properties across MI using boosted regression trees. The impact of temperature change on plant species distribution was then examined through species distribution models incorporating edaphic properties along with climatic, topographic and biotic factors. By considering a combination of climatic (changing), biotic, and non-climatic (fixed) predictors, the study aimed to determine the direction and constraints of species distributional changes under past and future temperature scenarios. Although the habitat requirements of vascular plant species on MI were species-specific, with species distributions predicted by differential variables, the responses of most generalist plant species to warming were similar, whereas responses of specialist species were similar. With continued warming, the habitat suitability of generalist plant species were predicted to increase on MI, within the physical constraints imposed by the environment, and toward the west, whereas the habitat suitability of most specialist species was not predicted to increase with warming.

The results support the overarching hypothesis of this study that vegetation change on MI occurred as a consequence of the interaction of factors, key among them being climate change and invasive species. This research emphasises the individualistic responses of vascular plant species to environmental change in species-poor and/or young environments. Most habitat generalists have increased in cover and expanded their ranges, and these trends are projected to continue with warming, within the physical limitations of the environment. In contrast, the habitat suitability of specialist species show limited change, with no significant changes in cover observed or changes in range predicted with warming. Consequently, a comprehensive assessment of habitat suitability for different plant species requires considering a combination of topographic, climatic, edaphic, and biotic factors. This study highlights the importance of studying individualistic responses and understanding the specific habitat requirements of individual vascular plant species, which may be overlooked when focusing solely on species assemblages.

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Chapter 1

General Introduction

Documenting and understanding the extent of vegetation change over space and time is essential for the ongoing conservation of biodiversity. Vegetation change is one of the leading causes of biodiversity loss and involves the alteration of composition, structure and/or distribution of plant species or communities (Nolan et al. 2018). While vegetation change is natural, for instance succession after a disturbance such as fire or drought, human activities have accelerated vegetation change at unprecedented rates in recent decades, exceeding early predictions of rates of change in many parts of the world (Overpeck & Breshears 2021). Investigating vegetation change is thus critical in understanding drivers, consequences and patterns of change, to develop effective strategies to mitigate their negative impacts and inform proactive adaptive actions (Nunez et al. 2019).

Understanding why vegetation patterns exist has challenged ecologists for decades (Oepik et al. 2014). Changes in vegetation patterns can alter the biophysical properties of the Earth's surface (Duveiller et al. 2021), the abundance and distribution of plant and animal species (Nolan et al. 2018), and ultimately ecosystem services such as soil stabilisation and water filtration (Diaz et al. 2006). Studying vegetation change involves identifying vegetation patterns and their underlying processes, and then recognising which patterns may change following alterations in the processes that led to their development. For instance, shrub expansion and resultant Arctic greening due to warming in the Arctic tundra (Piao et al. 2020) can affect the soil moisture, nutrient cycling, fire regimes and reduce plant species richness through the loss of shade-intolerant species (Myers-Smith et al. 2011). Therefore, understanding the mechanisms which drive vegetation change and predicting the consequences thereof is essential for addressing global environmental challenges. This has become particularly important as novel climates and ecosystems emerge (Oepik et al. 2014).

1.1. Vegetation patterns and underlying processes

Vegetation patterns are determined by a combination of evolutionary and ecological processes that dictate the species composition and community structure, as encapsulated by community assembly theory (HilleRisLambers et al. 2012). Firstly, dispersal determines the ability of species to reach and establish in a particular area. Once dispersed to a new site, plant species face many challenges due to environmental filtering (Chase & Myers 2011). This is the selective influence of the environmental conditions in a given habitat on the presence and survival of a plant species (Kraft et al. 2015). These environmental filters include abiotic factors such as climate, edaphic properties, topography, disturbance regimes and water availability that determine which species can establish and thrive in an environment (Kraft et al. 2015). Biotically, species interactions further shape communities, because it influences the coexistence and distribution of plant species (Weiher et al. 2011), for example through competitive exclusion or faunal disturbance. Stochastic or neutral processes, which are those that influence species composition that occur by chance or due to random events, may then also help shape communities, along with the historical factors that may have influenced any site (Chase & Myers 2011). Lastly, vegetation patterns are influenced by anthropogenic factors, such as land use change or non-native species introductions. Therefore, there are multiple abiotic and biotic factors to consider when analysing the underlying processes responsible for vegetation patterns and changes therein (Weiher et al. 2011).

Plant species have different environmental requirements that determine habitat suitability (Austin & Van Niel 2011). These requirements can be viewed as a continuum of habitat specialisation, with species with wider ecological niches, i.e., “generalist” species, on the one end and those with narrower ecological niches, i.e., “specialist” species, on the other end (Pandit et al. 2009). While habitat generalists are often also called “widespread” species, some widespread species may occupy a broadly distributed habitat type, but still have a narrow niche (Bossuyt et al. 2004). Therefore, to differentiate between specialists and generalists, species with limited habitat preferences and thus narrow niches (Ainsworth & Drake 2020), such as species limited to high salinity soils, are considered specialist species. On the other hand, habitat generalists may occupy multiple habitat types, because of their broader niche preferences (Denelle et al. 2020). Generalists may respond more to regional or spatial processes, while specialists may respond more to local processes (Pandit et al. 2009). Generalist species are considered to be more resilient to environmental change than specialist species, as they are able to adapt to changing conditions by altering their physiology or distributing to more suitable conditions (Brouat et al. 2004). Contrastingly, specialist species may not be able to survive or adapt if environmental change alters the conditions they depend on (Cramer et al. 2022), and may risk extinction (Ainsworth & Drake 2020). For example, halophytes in the sub-Antarctic grow in soil with high salt content, where competition is limited because most species cannot tolerate high salt concentrations, and thus they only occur in areas that receive high saltspray (Smith et al. 2001). If climate change, for instance changing wind patterns, alters the distribution of saltspray, halophytes may need to distribute accordingly or be excluded where other plant species can outcompete them.

The first step in quantifying vegetation change is to describe the spatial and temporal vegetation variation, i.e., classifying the vegetation and determining the appropriate change detection unit (De Cáceres et al. 2015). It is fundamental that the spatial scale and monitoring unit chosen are able to detect and describe the prevalent changes. For instance, at the species-level, change can occur as species range shifts, expansions and retractions (Nolan et al. 2018). At the community-level, vegetation change can result from species reorganisation that may lead to communities switching to alternate states or to no-analog states, also termed "novel", communities (compositionally unlike those found previously; Scheffer et al. 2001; Williams & Jackson 2007). The view of vegetation patterns and processes will determine the vegetation classification approach which may vary depending on the research question and scale. While there are various approaches to classify vegetation, hierarchical phytosociological classification, originally proposed by Weaver & Clements (1929) has been the most widely used. Hierarchical classification entails classifying vegetation plots into increasingly similar groups based on species composition or cover until communities are identified (Austin 2005). Mapping and species inventories are used to describe the distribution of vegetation (Mucina et al. 2016). Under this "Clementian" view, vegetation is seen as deterministic, composed of distinct and discrete units with "climax" states, perhaps interspersed by transitional vegetation (Weaver & Clements 1929). The alternative interpretation of vegetation views it as dynamic and continuous with no distinct boundaries. This idea was originally proposed by Gleason (1917; 1926) and conceptualized by Curtis & McIntosh (1951), and suggests that species respond individualistically to environmental and biotic conditions, and thus "communities" are constantly evolving (Palmer & White 1994). The "Clementian" view was criticised for underestimating the real diversity of vegetation under the assumption of improbable homogeneity (Gleason 1926). Therefore, it was advocated that vegetation be described as completely dependent on the individual species responses to their environment (Gleason 1917; Gleason 1927). The "Gleasonian" view was not well received at the time, and thus "Clementian" ecology largely persisted, although the individualistic view gained importance with time (Cushman et al. 2010). Each approach has its strengths and limitations, but no consensus has been reached to provide guidelines for when to use the different approaches to classify vegetation (Austin 2005). The choice of approach may be especially important in tracking shifts in the distribution of vegetation in response to environmental change, as it will influence the unit chosen to monitor vegetation change and ultimately the interpretation thereof. For example, distributional shifts of "communities" to higher elevations may be attributed to the expansion of only a few responsive species, rather than an entire assemblage of species in a community (see eg. le Roux & McGeoch 2008b), which may go unnoticed if only community-level responses are considered. Therefore, it is important to investigate under which circumstances each approach may be more appropriate.

Vegetation classification approaches have mainly been implemented on large scales in environments with high species richness, which are often older environments with an abundance of indicator species, frequently used to differentiate plant communities (Dufrene & Legendre 1997; De Cáceres & Legendre

2009; Mucina et al. 2016). Consequently, environments with low vascular plant species richness, such as deserts or tundra, have received much less attention (van der Merwe et al. 2023). Implementing approaches developed in species-rich environments may not be appropriate for species-poor environments. Low diversity may also be associated with lower stability under disturbance (Tilman et al. 2006), as few species are available to fill the niche gaps potentially created by a disturbance. Therefore, species-poor environments may be particularly vulnerable to change. For example, the loss of a plant species in an environment may provide the opportunity for an alien species to establish (Nolan et al. 2018). Indeed, climate change (Sala et al. 2000) and invasive species (Bennett et al. 2015) have disproportionately impacted higher latitudes, where species richness is lower than mid latitudes (Kreft & Jetz 2007). The Arctic, for instance, is warming and melting faster than previously expected (Overpeck & Breshears 2021). However, most change studies in species-poor environments have been conducted in the northern high latitudes (Hinzman et al. 2005; Myers-Smith et al. 2011; Overpeck & Breshears 2021), with the southern high latitudes often not included in global studies (Sala et al. 2000).

1.2. The sub-Antarctic region

The sub-Antarctic is an ecologically significant region due to its importance in global circulation systems (Ansorge et al. 2017), its geographic isolation (Selkirk 2007), variety of endemic plant and animal species, and the accelerated climate change experienced (Bergstrom & Chown 1999; Smith 2002). The sub-Antarctic falls in the convergence between ocean currents providing nutrient-rich water for a variety of marine mammals and seabirds (Allan et al. 2013), many of which breed on the islands and several are threatened or near-threatened (Whitehead et al. 2019). The only terrestrial land masses in the sub-Antarctic are scattered volcanic islands, comprising six island groups (the Prince Edward Islands, Crozet, Kerguelen, Heard & McDonald, Macquarie and South Georgia), most of which have a relatively recent origin (Rudolph et al. 2020) . The islands share similarities in terms of climate, vegetation, native mammals and seabirds. For example, they share many plant sister taxa, are all visited by large marine mammals and seabirds, and being far removed from continental lands, plant dispersal to the islands is limited to wind, animal and human transport. Therefore, the terrestrial environments have low species richness, and relatively simple trophic structures, providing the opportunity to study ecological and evolutionary processes (Chown et al. 1998).The similarities between the island groups also allow inference on the mechanisms that underpin vegetation change (Bazzichetto et al. 2021).

The taxonomically and functionally depauperate terrestrial systems, also make them vulnerable to invasions by alien species and rapid climatic changes (Frenot et al. 2005), due to the lack of biodiversity and thus presumably low ecosystem resilience. Consequently, the sub-Antarctic islands have been recognised as "sentinels of change" (Ansorge et al. 2017). However, each island group also has a unique topography and historical context that have impacted the vegetation differentially. For instance, while mammals were introduced to the islands at some point, each mammal have had their own unique impact on each island. For example, rabbits were introduced to and had detrimental impacts on Kerguelen and Macquarie Islands (Frenot et al. 2001), whereas mice are the key invasive mammal with negative impacts on Marion Island (McClelland et al. 2018). On the other hand, one exception amongst the island groups is Heard Island that has no known non-native species. However, the key threats of climate change and/or invasive species are shared by all islands in the sub-Antarctic (Bergstrom & Chown 1999; Bazzichetto et al. 2021), and thus the study of their interactive impact on vegetation is generalizable across the region. The islands are thus particularly suited to address questions concerned with vegetation change in relation to climate change and invasive species.

1.3. Drivers of vegetation change in sub-Antarctic tundra

A potentially important driver of vegetation change in the sub-Antarctic is climate change (Smith 2002; Lebouvier et al. 2011). Biodiversity in the sub-Antarctic is threatened by rapid climatic change, as the native biota are adapted to a cool (mean temperature mostly above freezing), thermally stable (little annual fluctuation) and humid (precipitation exceeds evaporation) climate (Chown et al. 2013). A rapid change in air temperature and rainfall has been documented on several sub-Antarctic islands (le Roux & McGeoch 2008a; Lebouvier et al. 2011), and the range-restricted plant species on the islands have been predicted to be particularly negatively impacted by climate change (Rogers et al. 2020). On the Prince Edward Islands (PEIs), South Africa's southernmost territory in the sub-Antarctic, the sea and air temperatures have increased at twice the mean global rate between the 1950's and early 2000's (le Roux & McGeoch 2008a; Ansorge et al. 2017). Along with warming, decreased precipitation and subsequent drying of the islands has been documented at the PEIs during the same period (le Roux & McGeoch 2008a; Hedding & Greve 2018). The impact of warming and drying on vegetation at the PEIs has not been well documented, but several species have extended their ranges upslope, with subsequent plant community reorganisation (le Roux & McGeoch 2008b). Rising global CO_2 may also have implications for sub-Antarctic tundra vegetation, especially in terms of enhanced growth with increased availability of carbon (Chen et al. 2011). Although plant growth is limited by low temperatures and nutrient availability in the sub-Antarctic (Smith & Steenkamp 1990; Molau et al. 2005), the combination of warmer temperatures and increased atmospheric CO_2 levels may stimulate biomass increase, within the constraints of nutrient limitations. Researchers have warned that significant plant community changes (Smith & Steenkamp

1990; Smith et al. 2001) and further species range shifts (le Roux & McGeoch 2008b) are probable. Likely consequences are that the suitability of current habitats to species that are adapted to a cooler and wetter environment may change, causing species to shift their distributions to track climate change. Poleward distribution of plant species to track changes in climate is limited due to the long distance between land masses in the sub-Antarctic. Distributing to habitats within a species' climatic envelope, such as dispersing upslope, may thus be one of the only options for plant species on the islands to track the rapid climatic changes. However, upslope movement may be limited by the elevational severity gradient at the PEIs, where environmental severity increases with elevation, including decreasing temperatures, increasing wind speeds and fewer biotic interactions as elevation increases (le Roux & McGeoch 2008c). Edaphic properties also change with elevation, likely further constraining species distributional shifts (Cramer et al. 2022), although this has not been tested.

Another key driver of vegetation change in the sub-Antarctic is non-native species, often exacerbating the impacts of climate change (Frenot et al. 2005; Bergstrom et al. 2015; Greve et al. 2017; Dickson et al. 2021). While the residence time of each established invasive species needs to be considered when assessing species distributions, the range expansion of invasive species in the sub-Antarctic has been suggested to be partly driven by warming temperatures (le Roux et al. 2013; Chown et al. 2013). Sub-Antarctic islands are isolated and considerably less disturbed than continental systems yet are prone to invasion by non-native species (Shaw 2013; Greve et al. 2017). This may be because there are unoccupied niches for alien species to fill in species-poor environments as a result of the impoverished flora (Mathakutha et al. 2019) or that alien species outcompete native species (Ripley et al. 2020), particularly after disturbance (Haussmann et al. 2013), which may lead to native species range shifts or localised extinctions (Oduor 2013). As a result of the extreme isolation, low propagule pressure and absence of other anthropogenic confounding factors such as land clearing, the sub-Antarctic islands provide a unique opportunity to study invasive species and their impact on native species.

In the past, cats (*Felis catus*; introduced in 1949 and eradicated by 1991) were the dominant invasive species on Marion Island (MI) (Greve et al. 2020), the larger of the two PEIs. Cats had a detrimental impact on seabirds, especially burrow-nesting birds, eating up to 635 000 burrowing petrels and prions per year in the mid-1970s (Bester et al. 2002). Burrowing birds are an important source of allochthonous nutrients on the islands, with cats indirectly reducing nutrient-inputs by substantial amounts per year (Smith 1978) and likely reducing the habitat suitability for coprophilous species (le Roux & McGeoch 2008b). Reduction in guano enrichment of soils around burrows is the most likely cause of the reduction in the grass *Poa* *cookii* (Smith 1978), a coprophilous species, on slope systems where burrowing birds used to nest (Smith et al. 2001; Smith & Mucina 2006). After the cat eradication, burrow-nesting birds have not recovered as expected (Dilley et al. 2017). This is likely due to continued predation on hatchlings by the introduced house mouse (*Mus musculus*) that have had to find other sources of protein after depleting invertebrate biomass (Dilley et al. 2017). Therefore, nutrient-input from the ocean through burrow-nesting birds have likely not increased to past concentrations on MI.

By far the most detrimental extant invasive species at the PEIs, is the house mouse, accidentally introduced by sealers in the 1800s, that only occurs on MI (Greve et al. 2020). While mice have occurred on MI since the 1800s, they have become more abundant recently since cats were eradicated, with their population density increasing considerably in recent decades, accelerated by climate change (McClelland et al. 2018). Mice impact invertebrates, plants and seabirds, and ultimately affect ecosystem functioning (Greve et al. 2020). Mice have decreased macroinvertebrate abundance and size substantially, impacting litter decomposition rates, and thus nutrient cycling on the island (Smith 2008). The reduction in macroinvertebrates, previously their primary source of protein, has led to their predation on seabirds, causing declines in seabird populations (Dilley et al. 2018). Their impact on vegetation is less documented, although plant material, including seeds of the sedge *Carex dikei*, and seeds and leaves of grasses (*P. cookii, Poa annua* and *Polypogon magellanicus*), the Kergeulen cabbage (*Pringlea antiscorbutica*), a fern (*Austroblechnum penna-marina*) and a dwarf shrub (*Acaena magellanica*) have been found in their stomach content (Smith et al. 2002). Mice have likely reduced the reproductive output of *C. dikei* by removing up to 75% of seed heads (Chown & Smith 1993). Mouse burrowing and tunnelling also cause damage to plant species on MI, especially the slow growing, keystone cushion plant *Azorella selago* (Avenant & Smith 2003), where dieback has been documented due to mouse damage (Phiri et al. 2009).

Seventeen non-native plant species are currently established on MI. They were likely introduced by the importation of building material during construction of the research stations and through fodder for chickens and sheep between the 1940s and 1970s (Gremmen & Smith 1999; Greve et al. 2020). Eight plant species have become established and are considered invasive (Greve et al. 2017). Some of the more localised alien species that occur on MI are widespread across the sub-Antarctic islands (Shaw 2013), where many have established and spread successfully. Thus, they may be in the lag phase in the invasion process and may spread in the future (Greve et al. 2020). Little is known about the impact of the invasive plant species on the native flora at the PEIs (Greve et al. 2017), although the limited evidence suggests that their impacts may be more severe than previously thought, based on their rapid rate of expansion (le

Roux et al. 2013). For example, the invasive grass *Agrostis stolonifera* has reached dominance in several undisturbed sites, displacing native flora (Gremmen et al. 1998). An understanding of the impacts of invasive species on the native vegetation is an important research gap at the PEIs, and a significant component to consider in studying vegetation change.

The direct impact of humans at the PEIs is limited to the research stations and footpaths to the monitoring sites and field huts. Therefore, human impacts are localised, but trampling by humans have been shown to significantly impact the vegetation immediately surrounding the disturbed sites (Gremmen et al. 2003). For instance, the abundance of species was lower in trampled sites in mires and fellfield, but higher on slopes compared to control sites (Gremmen et al. 2003). The spread of invasive plant species may also have been assisted by human traffic (le Roux et al. 2013). However, the impact of direct human influence on the vegetation at the island-scale is likely not substantial, given the limited infrastructure and the physical constraints imposed by the harsh environment which restricts movement.

1.4. Vegetation characteristics on Marion Island

As a result of the harsh environment, abiotically, the distribution of species on MI is strongly linked to temperature, moisture, saltspray and wind exposure and biotically, and more localised, also by manuring and trampling of seals and seabirds (Smith et al. 2001). Environmental filtering thus plays a critical role in determining species composition in the sub-Antarctic. There are 21 native vascular plant species on MI (Table 1; Chau et al. 2020). Habitat specialist species are considered to be those restricted to particular habitats. These include coprophilous species (*P. cookii, Montia fontana, Callitriche antarctica*) requiring nutrient-enriched soils, hygrophilous species (C*. dikei, Juncus scheuchzerioides, Limosella australis*) restricted to high moisture habitats and halophilous species (*Crassula moschata, Leptinella plumosa*) requiring wind-blown saltspray input (Table 1; Huntley 1971; le Roux & McGeoch 2008b). All other vascular plant species are considered habitat generalists (n = 13), as they occupy various habitats, and thus presumably may tolerate broader environmental conditions. Five species dominate the aerial cover: the cushion plant *A. selago*, fern *A. penna-marina,* grasses *P. magellanicus* and *P. cookii* and dwarf shrub *A. magellanica* (Smith et al. 2001).

Table 1. Native vascular plant species of Marion Island. Adapted from Chau et al. (2020) and Huntley (1971).

Species	Family	Specialisation
Acaena magellanica (Lam.) Vahl	Rosaceae	Generalist
Austroblechnum penna-marina (Poir.) Gasper & V.A.O.Dittrich	Blechnaceae	Generalist
Azorella selago Hook. f.	Apiaceae	Generalist
Callitriche antarctica Engelm. ex Hegelm	Plantaginaceae	Coprophilous
Carex dikei (Nelmes) K.L.Wilson	Cyperaceae	Hygrophilous
Colobanthus kerguelensis Hook.f	Caryophyllaceae	Generalist
Crassula moschata G.Forst.	Crassulaceae	Halophilous
Elaphoglossum randii Alston & Schelpe	Dryopteridaceae	Generalist
Hymenophyllum peltatum (Poir.) Desv	Hymenophyllaceae	Generalist
Juncus scheuchzerioides Gaudich	Juncaceae	Hygrophilous
Leptinella plumosa Hook.f.	Asteraceae	Halophilous
Limosella australis R.Br	Scrophulariaceae	Hygrophilous
Lycopodium magellanicum (P.Beauv.) Sw	Lycopodiaceae	Generalist
Montia fontana L.	Montiaceae	Coprophilous
Notogrammitis crassior (Kirk) Parris	Polypodiaceae	Generalist
Phlegmariurus saururus (Lam.) B.Øllg	Lycopodiaceae	Generalist
Poa cookii (Hook.f.) Hook.f	Poaceae	Coprophilous
Polypogon magellanicus (Lam.) Finot	Poaceae	Generalist
Polystichum marionense Alston & Schelpe	Dryopteridaceae	Generalist
Pringlea antiscorbutica R.Br. ex Hook.f.	Brassicaceae	Generalist
Ranunculus biternatus Sm.	Ranunculaceae	Generalist

Since temperature, precipitation and wind conditions on MI have changed between the 1950s and early 2000s (le Roux & McGeoch 2008a), and presumably have continued to change, and biotically, invasive species have increased rapidly (le Roux et al. 2013; McClelland et al. 2018), plant species have been exposed to altered environmental conditions. A temperature change of between 1°C and 2°C is considered to result in strong biologically-relevant impacts on plant species, such as reduction in species richness (Nunez et al. 2019), with the probability of large compositional and structural change increasing with temperature increase (Nolan et al. 2018). On MI, mean annual temperature has already warmed by 1°C between the 1950s and 1990s (le Roux & McGeoch 2008b). Therefore, such rapid climate change can be expected to significantly alter species distributions and/or composition. Habitat generalists are predicted to expand along their cooler distributional boundaries to track such changes, whereas specialist species may be constrained by their adaptation to particular environmental conditions (Smith & Steenkamp 1990; le Roux & McGeoch 2008b; Cramer et al. 2022). However, distributional changes are complex and determined by which environmental conditions are altered, the individual plant species dependence on particular conditions, dispersal ability, biotic interactions and geographic boundaries (Austin 2002; Austin & Van Niel 2011). Therefore, all environmental conditions and biotic interactions that may impact a species' distribution at a study site need consideration when assessing distributional shifts.

1.5. Thesis outline

The overarching hypothesis of this study was that vegetation changes that have occurred on MI are a consequence of the interaction between factors, key among them being climate change and invasive species. Given that the species assemblage is of recent origin and relatively species-poor, I also hypothesised that the changes in vegetation are the consequence of individualistic responses of species to the environmental changes rather than a generalised response of the entire flora or of communities within the flora. This is based on the understanding that each species is constrained by different environmental conditions (Momberg et al. 2021; Cramer et al. 2022) and also potentially by biotic interactions (le Roux & McGeoch 2008b; Raath-Krüger et al. 2019). Therefore, a range of abiotic conditions and biotic interactions may impact distributional shifts in different species. Habitat specialists, defined as those species highly adapted to a particular environment, may not be able to shift their ranges in response to impacts of climate change and invasive species, unless the dominant environmental or biotic factor which determines their distribution shifts accordingly. In this thesis, I investigate the potential for the combination of topographic, climatic, edaphic and biotic factors to influence species distributional shifts in response to the key drivers of change on MI.

In Chapter 2, the vegetation classification for MI is revisited to determine whether the vegetation should be evaluated at the community- or species-level in species-poor environments. Particular attention is paid to the different plant community approaches and perspectives and their limitations in species-poor environments.

In Chapter 3, the current (2020) vegetation is compared to the past (1965) using a repeat photography approach to assess the change in species cover that has occurred on MI. The climate and key invasive species' abundance are also compared during the same period to investigate causes of vegetation change. Repeat photography often compliments modelling approaches when investigating vegetation change. It can be used to compare the vegetation at the same location at different times, along with the potential factors that have impacted the vegetation.

Chapter 4 investigates the spatial variability of edaphic properties to create the first soil maps of MI to include as potential predictors in plant species distribution models, since edaphic properties may limit distributional shifts in plant species. In general, soil properties are not included when studying vegetation change, often due to data limitations, and is thus a key research gap in change studies. The soil properties between the vegetation units found in Chapter 2 are compared to further investigate differences in vegetation units.

Plant species distributions are then modelled in Chapter 5, including for the first time the edaphic properties developed in Chapter 4, along with newly released spatial data, to determine key species-environmental relationships and the impact of predicted changes in environmental conditions. Species distribution models are used to investigate the most important underlying factors that influence the habitat suitability for plant species. Once the most important environmental factors are determined, retrodicting past species distributions and predicting future distributions is possible.

Lastly, the results are synthesised in Chapter 6 where I examine the consequences of vegetation change on MI and the broader relevance of this research for future studies. I also assess the key drivers of vegetation change and address the hypothesis that changes in the vegetation results from individual responses to the environment and not from shifts in entire plant communities.

References

Ainsworth, A., & Drake, D.R. 2020. Classifying Hawaiian plant species along a habitat generalist-specialist continuum: Implications for species conservation under climate change. *PLOS ONE* 15: e0228573.

Allan, E.L., Froneman, P.W., Durgadoo, J. V, McQuaid, C.D., Ansorge, I.J., & Richoux, N.B. 2013. Critical indirect effects of climate change on sub-Antarctic ecosystem functioning. *Ecology and Evolution* 3: 2994–3004.

Ansorge, I.J., Skelton, P., Bekker, A., de Bruyn, P.J.N., Butterworth, D., Cilliers, P., Cooper, J., Cowan, D.A., Dorrington, R., Fawcett, S., Fietz, S., Findlay, K.P., Froneman, P.W., Grantham, G.H., Greve, M., Hedding, D., Hofmeyr, G.J.G., Kosch, M., le Roux, P.C., Lucas, M., MacHutchon, K., Meiklejohn, I., Nel, W., Pistorius, P., Ryan, P.G., Stander, J., Swart, S., Treasure, A., Vichi, M., & van Vuuren, B.J. 2017. Exploring South Africa's southern frontier: A 20-year vision for polar research through the South African National Antarctic Programme. *South African Journal of Science* 113: 11–17.

Austin, M.P. 2002. Spatial prediction of species distribution: an interface between ecological theory and statistical modelling. *Ecological Modelling* 157: 101–118.

Austin, M.P. 2005. Vegetation and environment: discontinuities and continuities. In van der Maarel, E. (Ed.), *Vegetation Ecology*, Blackwell Publishing, Oxford, UK.

Austin, M.P., & Van Niel, K.P. 2011. Improving species distribution models for climate change studies: variable selection and scale. *Journal of Biogeography* 38: 1–8.

Avenant, N.L., & Smith, V.R. 2003. The microenvironment of house mice on Marion Island (sub-Antarctic). *Polar Biology* 26: 129–141.

Bazzichetto, M., Massol, F., Carboni, M., Lenoir, J., Lembrechts, J.J., Joly, R., Renault, D. 2021. Once upon a time in the far south: Influence of local drivers and functional traits on plant invasion in the harsh sub-Antarctic islands. *Journal of Vegetation Science* 32, e13057.

Bennett, J.R., Shaw, J.D., Terauds, A., Smol, J.P., Aerts, R., Bergstrom, D.M., Blais, J.M., Cheung, W.W.L., Chown, S.L., Lea, M.-A., Nielsen, U.N., Pauly, D., Reimer, K.J., Riddle, M.J., Snape, I., Stark, J.S., Tulloch, V.J., & Possingham, H.P. 2015. Polar lessons learned: long-term management based on shared threats in Arctic and Antarctic environments. *Frontiers in Ecology and The Environment* 13: 316–324.

Bergstrom, D.M., Bricher, P.K., Raymond, B., Terauds, A., Doley, D., McGeoch, M.A., Whinam, J., Glen, M., Yuan, Z., Kiefer, K., Shaw, J.D., Bramely-Alves, J., Rudman, T., Mohammed, C., Lucieer, A., Visoiu, M., van Vuuren, B.J., & Ball, M.C. 2015. Rapid collapse of a sub-Antarctic alpine ecosystem: the role of climate and pathogens. *Journal of Applied Ecology* 52: 774–783.

Bergstrom, D.M., & Chown, S.L. 1999. Life at the front: history, ecology and change on southern ocean islands. *Trends in Ecology & Evolution* 14: 472–477.

Bester, M.N., Bloomer, J.P., Van Aarde, R.J., Erasmus, B.H., Van Rensburg, P.J.J., Skinner, J.D., Howell, P.G., & Naude, T.W. 2002. A review of the successful eradication of feral cats from sub-Antarctic Marion Island, Southern Indian Ocean. *South African Journal of Wildlife Research* 32: 65-73.

Bossuyt, B., Honnay, O., & Hermy, M. 2004. Scale-dependent frequency distributions of plant species in dune slacks: Dispersal and niche limitation. *Journal of Vegetation Science* 15: 323–330.

Brouat, C., Chevallier, H., Meusnier, S., Noblecourt, T., & Rasplus, J.Y. 2004. Specialization and habitat: spatial and environmental effects on abundance and genetic diversity of forest generalist and specialist *Carabus* species. *Molecular Ecology* 13: 1815–1826.

De Cáceres, M., Chytrý, M., Agrillo, E., Attorre, F., Botta-Dukát, Z., Capelo, J., Czúcz, B., Dengler, J., Ewald, J., Faber-Langendoen, D., Feoli, E., Franklin, S.B., Gavilán, R., Gillet, F., Jansen, F., Jiménez-Alfaro, B., Krestov, P., Landucci, F., Lengyel, A., Loidi, J., Mucina, L., Peet, R.K., Roberts, D.W., Roleček, J., Schaminée, J.H.J., Schmidtlein, S., Theurillat, J.P., Tichý, L., Walker, D.A., Wildi, O., Willner, W., & Wiser, S.K. 2015. A comparative framework for broad-scale plot-based vegetation classification. *Applied Vegetation Science* 18: 543–560.

De Cáceres, M., & Legendre, P. 2009. Associations between species and groups of sites: indices and statistical inference. *Ecology* 90: 3566–3574.

Chase, J.M. & Myers, J.A. 2011. Disentangling the importance of ecological niches from stochastic processes across scales. *Philosophical Transactions of the Royal Society B: Biological Sciences* 366, 2351–2363.

Chau, J.H., Mtsi, N.I.S., Munbergova, Z., Greve, M., le Roux, P.C., Mairal, M., Le Roux, J.J., Dorrington, R.A., & van Vuuren, B. 2020. An update on the indigenous vascular flora of sub-Antarctic Marion Island: taxonomic changes, sequences for DNA barcode loci, and genome size data. *Polar Biology* 43: 1817–1828.

Chen, I.-C., Hill, J.K., Ohlemueller, R., Roy, D.B., & Thomas, C.D. 2011. Rapid range shifts of species associated with high levels of climate warming. *Science* 333: 1024–1026.

Chown, S.L., Gremmen, N.J.M., & Gaston, K.J. 1998. Ecological biogeography of southern ocean islands: Species-area relationships, human impacts, and conservation. *American Naturalist* 152: 562–575.

Chown, S.L., le Roux, P.C., Ramaswiela, T., Kalwij, J.M., Shaw, J.D., & McGeoch, M.A. 2013. Climate change and elevational diversity capacity: do weedy species take up the slack? *Biology Letters* 9: 0120806.

Chown, S.L., & Smith, V.R. 1993. Climate change and the short-term impact of feral house mice at the sub-Antarctic Prince Edward Islands. *Oecologia* 96: 508-516.

Cramer, M.D., Hedding, D., Greve, M., Midgley, G.F., & Ripley, B.S. 2022. Plant specialisation may limit climate-induced vegetation change to within topographic and edaphic niches on a sub-Antarctic island. *Functional Ecology* 36, 2636–2648.

Curtis, J., & McIntosh, R. 1951. An upland forest continuum in the prairie-forest border region of wisconsin. *Ecology* 31: 476–796.

Cushman, S., Evans, J., McGarigal, K., & Kiesecker, J. 2010. *Toward Gleasonian landscape ecology: From communities to species*. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, USA.

Denelle, P., Violle, C., Munoz, F., & Consortium, D. 2020. Generalist plants are more competitive and more functionally similar to each other than specialist plants: insights from network analyses. *Journal of Biogeography* 47: 1922–1933.

Diaz, S., Fargione, J., Chapin III, F.S., & Tilman, D. 2006. Biodiversity loss threatens human well-being. *PLOS BIOLOGY* 4: 1300–1305.

Dickson, C.R., Baker, D.J., Bergstrom, D.M., Brookes, R.H., Whinam, J., & McGeoch, M.A. 2021. Widespread dieback in a foundation species on a sub-Antarctic World Heritage Island: Fine-scale patterns and likely drivers. *Austral Ecology* 46: 52–64.

Dilley, B.J., Schoombie, S., Stevens, K., Davies, D., Perold, V., Osborne, A., Schoombie, J., Brink, C.W., Carpenter-Kling, T., & Ryan, P.G. 2018. Mouse predation affects breeding success of burrow-nesting petrels at sub-Antarctic Marion Island. *Antarctic Science* 30: 93–104.

Dilley, B.J., Schramm, M., & Ryan, P.G. 2017. Modest increases in densities of burrow-nesting petrels following the removal of cats (*Felis catus*) from Marion Island. *Polar Biology* 40: 625–637.

Dufrene, M., & Legendre, P. 1997. Species assemblages and indicator species: The need for a flexible asymmetrical approach. *Ecological Monographs* 67: 345–366.

Duveiller, G., Hooker, J., & Cescatti, A. 2021. A dataset mapping the potential biophysical effects of vegetation cover change. *Scientific Data* 8: 180014.

Frenot, Y., Gloaguen, J.C., Massé, L., Lebouvier, M. 2001. Human activities, ecosystem disturbance and plant invasions in subantarctic Crozet, Kerguelen and Amsterdam Islands. *Biological Conservation* 101: 33–50.

Frenot, Y., Chown, S.L., Whinam, J., Selkirk, P.M., Convey, P., Skotnicki, M., & Bergstrom, D.M. 2005. Biological invasions in the Antarctic: extent, impacts and implications. *Biological Reviews* 80: 45–72.

Gleason, H.A. 1917. The structure and development of the plant association. *Bulletin of the Torrey Botanical Club* 43: 463–481.

Gleason, H.A. 1927. The individualistic concept of the plant association. *Bulletin of the Torrey Botanical Club* 53: 7–26.

Gremmen, N.J.M., Chown, S.L., & Marshall, D.J. 1998. Impact of the introduced grass Agrostis stolonifera on vegetation and soil fauna communities at Marion Island, sub-Antarctic. *Biological Conservation* 85: 223-231.

Gremmen, N.J.M., & Smith, V.R. 1999. New records of alien vascular plants from Marion and Prince Edward Islands, sub-Antarctic. *Polar Biology* 21: 401-409.

Gremmen, N.J.M., Smith, V.R., & Tongeren, O.F.R. van. 2003. Impact of trampling on the vegetation of Subantarctic Marion Island. *Arctic, Antarctic, and Alpine Research* 35: 442-446.

Greve, M., Mathakutha, R., Steyn, C., & Chown, S.L. 2017. Terrestrial invasions on sub-Antarctic Marion and Prince Edward Islands. *Bothalia* 47: a2143.

Greve, M., von Der Meden, C.E.O., & Janion-Scheepers, C. 2020. Biological invasions in South Africa's offshore sub-antarctic territories. In van Wilgen, B., Measey, J., Richardson, D., Wilson, J., & Zengeya, T. (Eds.), *Biological invasions in South Africa*, pp. 207–227. Springer.

Haussmann, N.S., Rudolph, E.M., Kalwij, J.M., & McIntyre, T. 2013. Fur seal populations facilitate establishment of exotic vascular plants. *Biological Conservation* 162: 33–40.

Hedding, D. & Greve, M. 2018. Decreases in precipitation on sub-Antarctic Marion Island: implications for ecological and geomorphological processes. *Weather* 6: 203.

HilleRisLambers, J., Adler, P.B., Harpole, W.S., Levine, J.M., Mayfield, M.M. 2012. Rethinking Community Assembly through the Lens of Coexistence Theory, in: Futuyma, D.J. (Ed.). *Annual Review Of Ecology, Evolution and Systematics* 43. *Annual Reviews*, Palo Alto, pp. 227–248.

Hinzman, L.D., Bettez, N.D., Bolton, W.R., Chapin, F.S., Dyurgerov, M.B., Fastie, C.L., Griffith, B., Hollister, R.D., Hope, A., Huntington, H.P., Jensen, A.M., Jia, G.J., Jorgenson, T., Kane, D.L., Klein, D.R., Kofinas, G., Lynch, A.H., Lloyd, A.H., McGuire, A.D., Nelson, F.E., Oechel, W.C., Osterkamp, T.E., Racine, C.H., Romanovsky, V.E., Stone, R.S., Stow, D.A., Sturm, M., Tweedie, C.E., Vourlitis, G.L., Walker, M.D., Walker, D.A., Webber, P.J., Welker, J.M., Winker, K., & Yoshikawa, K. 2005. Evidence and implications of recent climate change in northern Alaska and other arctic regions. *Climatic Change* 72: 251–298.

Huntley, B. 1971. Vegetation. In E. M. Van Zinderen Bakker (Ed.), *Marion and Prince Edward Islands,* pp. 98-160, A.A. Balkema, Cape Town, South Africa.

Kraft, N.J.B., Adler, P.B., Godoy, O., James, E.C., Fuller, S. & Levine, J.M. 2015. Community assembly, coexistence and the environmental filtering metaphor. *Functional Ecology* 29: 592-599.

Kreft, H., & Jetz, W. 2007. Global patterns and determinants of vascular plant diversity. *Proceedings of The National Academy of Sciences of The United States of America* 104: 5925–5930.

Lebouvier, M., Laparie, M., Hulle, M., Marais, A., Cozic, Y., Lalouette, L., Vernon, P., Candresse, T., Frenot, Y., & Renault, D. 2011. The significance of the sub-Antarctic Kerguelen Islands for the assessment of the vulnerability of native communities to climate change, alien insect invasions and plant viruses. *Biological Invasions* 13: 1195–1208.

Mathakutha, R., Steyn, C., le Roux, P.C., Blom, I.J., Chown, S.L., Daru, B.H., Ripley, B.S., Louw, A., & Greve, M. 2019. Invasive species differ in key functional traits from native and non-invasive alien plant species. *Journal of Vegetation Science* 30: 994–1006.

McClelland, G.T.W., Altwegg, R., Van Aarde, R.J., Ferreira, S., Burger, A.E., & Chown, S.L. 2018. Climate change leads to increasing population density and impacts of a key island invader.*Ecological Applications* 28: 212–224.

van der Merwe, S., Greve, M., Skowno, A.L., Hoffman, M.T., & Cramer, M.D. 2023. Can vegetation be discretely classified in species-poor environments? Testing plant community concepts for vegetation monitoring on sub-Antarctic Marion Island. *Ecology And Evolution* 13: e9681.

Molau, U., Nordenhall, U., & Eriksen, B. 2005. Onset of flowering and climate variability in an alpine landscape: A 10-year study from Swedish Lapland. *American Journal of Botany* 92: 422–431.

Momberg, M., Hedding, D.W., Luoto, M., & le Roux, P.C. 2021. Species differ in their responses to wind: the underexplored link between species fine-scale occurrences and variation in wind stress. *Journal of Vegetation Science* 32:.

Mucina, L., Bueltmann, H., Dierssen, K., Theurillat, J.-P., Raus, T., Čarni, A., Śumberová, K., Willner, W., Dengler, J., Garcia, R.G., Chytrý, M., Hajek, M., Di Pietro, R., Iakushenko, D., Pallas, J., Daniels, F.J.A., Bergmeier, E., Santos Guerra, A., Ermakov, N., Valachovic, M., Schaminee, J.H.J., Lysenko, T., Didukh, Y.P., Pignatti, S., Rodwell, J.S., Capelo, J., Weber, H.E., Solomeshch, A., Dimopoulos, P., Aguiar, C., Hennekens, S.M., & Tichy, L. 2016. Vegetation of Europe: hierarchical floristic classification system of vascular plant, bryophyte, lichen, and algal communities. *Applied Vegetation Science* 19: 3–264.

Myers-Smith, I.H., Forbes, B.C., Wilmking, M., Hallinger, M., Lantz, T., Blok, D., Tape, K.D., Macias-Fauria, M., Sass-Klaassen, U., Levesque, E., Boudreau, S., Ropars, P., Hermanutz, L., Trant, A., Collier, L.S., Weijers, S., Rozema, J., Rayback, S.A., Schmidt, N.M., Schaepman-Strub, G., Wipf, S., Rixen, C., Menard, C.B., Venn, S., Goetz, S., Andreu-Hayles, L., Elmendorf, S., Ravolainen, V., Welker, J., Grogan, P., Epstein, H.E., & Hik, D.S. 2011. Shrub expansion in tundra ecosystems: dynamics, impacts and research priorities. *Environmental Research Letters* 6: 045509.

Nolan, C., Overpeck, J.T., Allen, J.R.M., Anderson, P.M., Betancourt, J.L., Binney, H.A., Brewer, S., Bush, M.B., Chase, B.M., Cheddadi, R., Djamali, M., Dodson, J., Edwards, M.E., Gosling, W.D., Haberle, S., Hotchkiss, S.C., Huntley, B., Ivory, S.J., Kershaw, A.P., Kim, S.-H., Latorre, C., Leydet, M., Lezine, A.-M., Liu, K.-B., Liu, Y., Lozhkin, A. V, McGlone, M.S., Marchant, R.A., Momohara, A., Moreno, P.I., Mueller, S., Otto-Bliesner, B.L., Shen, C., Stevenson, J., Takahara, H., Tarasov, P.E., Tipton, J., Vincens, A., Weng, C., Xu, Q., Zheng, Z., & Jackson, S.T. 2018. Past and future global transformation of terrestrial ecosystems under climate change. *Science* 361: 920–923.

Nunez, S., Arets, E., Alkemade, R., Verwer, C., & Leemans, R. 2019. Assessing the impacts of climate change on biodiversity: is below 2 degrees C enough? *Climatic Change* 154: 351–365.

Oduor, A.M.O. 2013. Evolutionary responses of native plant species to invasive plants: a review. *New Phytologist* 200: 986–992.

Oepik, M., de Bello, F., Price, J.N., & Fraser, L.H. 2014. New insights into vegetation patterns and processes. *New Phytologist* 201: 383–387.

Overpeck, J.T., & Breshears, D.D. 2021. The growing challenge of vegetation change. *Science* 372: 786–787.

Palmer, M.W., & White, P.S. 1994. On the existence of ecological communities. *Journal of Vegetation Science* 5: 279–282.

Pandit, S.N., Kolasa, J., & Cottenie, K. 2009. Contrasts between habitat generalists and specialists: an empirical extension to the basic metacommunity framework. *Ecology* 90: 2253–2262.

Phiri, E.E., Mcgeoch, M.A., & Chown, S.L. 2009. Spatial variation in structural damage to a keystone plant species in the sub-Antarctic: interactions between *Azorella selago* and invasive house mice. *Antarctic Science* 21: 189–196.

Piao, S., Wang, X., Park, T., Chen, C., Lian, X., He, Y., Bjerke, J.W., Chen, A., Ciais, P., Tommervik, H., Nemani, R.R., & Myneni, R.B. 2020. Characteristics, drivers and feedbacks of global greening. *Nature Reviews Earth & Environment* 1: 14–27.

Raath-Krüger, M.J., McGeoch, M.A., Schöb, C., Greve, M., & le Roux, P.C. 2019. Positive plant-plant interactions expand the upper distributional limits of some vascular plant species. *Ecosphere* 10: e02820.

Ripley, B.S., Edwardes, A., Rossouw, M.W., Smith, V.R., & Midgley, G.F. 2020. Invasive grasses of sub-Antarctic Marion Island respond to increasing temperatures at the expense of chilling tolerance. *Annals of Botany* 125: 765–773.

Rogers, A.D., Frinault, B.A. V, Barnes, D.K.A., Bindoff, N.L., Downie, R., Ducklow, H.W., Friedlaender, A.S., Hart, T., Hill, S.L., Hofmann, E.E., Linse, K., McMahon, C.R., Murphy, E.J., Pakhomov, E.A., Reygondeau, G., Staniland, I.J., Wolf-Gladrow, D.A., & Wright, R.M. 2020. *Antarctic futures: an assessment of climate-driven changes in ecosystem structure, function, and service provisioning in the Southern Ocean*. In Carlson, C.A. & Giovannoni, S.J. (Eds.), Annual Review of Marine Science. Annual Reviews, Palo Alto, CA, USA.

le Roux, P.C., & McGeoch, M.A. (2008a). Changes in climate extremes, variability and signature on sub-Antarctic Marion Island. *Climatic Change* 86: 309–329.

le Roux, P.C., & McGeoch, M.A. (2008b). Rapid range expansion and community reorganization in response to warming. *Global Change Biology* 14: 2950-2962.

le Roux, P.C., & McGeoch, M.A. (2008c). Spatial variation in plant interactions across a severity gradient in the sub-Antarctic. *Oecologia* 155: 831–844.

le Roux, P.C., Ramaswiela, T., Kalwij, J.M., Shaw, J.D., Ryan, P.G., Treasure, A.M., McClelland, G.T.W., McGeoch, M.A., & Chown, S.L. 2013. Human activities, propagule pressure and alien plants in the sub-Antarctic: Tests of generalities and evidence in support of management. *Biological Conservation* 161: 18–27.

Rudolph, E.M., Hedding, D.W., Fabel, D., Hodgson, D.A., Gheorghiu, D.M., Shanks, R., & Nel, W. 2020. Early glacial maximum and deglaciation at sub-Antarctic Marion Island from cosmogenic Cl-36 exposure dating. *Quaternary Science Reviews* 231:.

Sala, O.E., Chapin, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D.M., Mooney, H.A., Oesterheld, M., Poff, N.L., Sykes, M.T., Walker, B.H., Walker, M., & Wall, D.H. 2000. Biodiversity - Global biodiversity scenarios for the year 2100. *Science* 287: 1770–1774.

Scheffer, M., Carpenter, S., Foley, J.A., Folke, C., & Walker, B. 2001. Catastrophic shifts in ecosystems.

Nature 413: 591–596.

Selkirk, P.M. 2007. The nature and importance of the sub-Antarctic. *Papers and Proceedings of the Royal Society of Tasmania* 141: 1-6.

Shaw, J.D. 2013. Southern Ocean Islands Invaded: Conserving Biodiversity in the World's Last Wilderness. In Foxcroft, L., Pyšek, P., Richardson, D., & Genovesi, P. (Eds.), *Plant Invasions in Protected Areas. Invading Nature - Springer Series in Invasion Ecology, vol 7*, Springer, Dordrecht.

Smith, V.R. 1978. Animal-plant-soil nutrient relationships on Marion Island (Subantarctic). *Oecologia* 32: 239–253.

Smith, V.R. 2002. Climate change in the sub-Antarctic: An illustration from Marion Island. *Climatic Change* 52: 345-357.

Smith, V.R. 2008. Energy flow and nutrient cycling in the Marion Island terrestrial ecosystem: 30 years on. *Polar Record* 44: 211–226.

Smith, V.R., Avenant, N., & Chown, S.L. 2002. The diet and impact of house mice on a sub-Antarctic island. *Polar Biology* 25: 703–715.

Smith, V.R., & Mucina, L. 2006. Vegetation of sub-Antarctic Marion and Prince Edward Islands. In Mucina, L., Rutherford, M.C., & Powrie, L.W. (Eds.), *Vegetation of South Africa, Lesotho and Swaziland*, pp. 699–723. South African National Biodiversity Institute, Pretoria, South Africa.

Smith, V.R., & Steenkamp, M. 1990. Climatic change and its ecological implications at a subantarctic island. *Oecologia* 85, 14–24.

Smith, V.R., Steenkamp, M., & Gremmen, N.J.M. 2001. Terrestrial habitats on sub-Antarctic Marion Island: Their vegetation, edaphic attributes, distribution and response to climate change. *South African Journal of Botany* 67: 641–654.

Tilman, D., Reich, P.B., & Knops, J.M.H. 2006. Biodiversity and ecosystem stability in a decade-long grassland experiment. *Nature* 441: 629–632.

Weaver, J., & Clements, F. 1929. *Plant Ecology*. McGraw-Hill Book Company, New York.

Weiher, E., Freund, D., Bunton, T., Stefanski, A., Lee, T., Bentivenga, S. 2011. Advances, challenges and a developing synthesis of ecological community assembly theory. *Philosophical Transactions of the Royal Society B-Biological Sciences* 366: 2403–2413.

Whitehead, T.O., von der Meden, C., Skowno, A.L., Sink, K.J., van der Merwe, S., Adams, R., & Holness, S. 2019. *South African National Biodiversity Assessment 2018 Technical Report Volume 6: sub-Antarctic Territory.* South African National Biodiversity Institute, Pretoria, South Africa.

Williams, J.W., & Jackson, S.T. 2007. Novel climates, no-analog communities, and ecological surprises. *Frontiers in Ecology and The Environment* 5: 475–482.

Chapter 2

Can vegetation be discretely classified in species-poor environments? Testing plant community concepts for vegetation monitoring on sub-Antarctic Marion Island*

The coastal plains on the west coast of Marion Island, where lakes are surrounded by mire vegetation and interspersed by slope vegetation in the midground. In the background, the topography rapidly slopes toward the mountainous interior of the island, where predominantly fellfield vegetation occurs. At the bottom of the photograph, biotic vegetation around a macaroni penguin colony is visible (bright green).

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"…I went off through gusts and rain to East Cape, examining the plant communities en route. One thing is clear about Marion's vegetation: plant succession, ecologically, is very hard to detect, due to the small number of plants and nearly all with a very wide range of tolerance – so different from the forests of Natal (South Africa), or even less complex communities, which, with increased number of species and increased competition and selection, are easily definable into seral stages from floristic composition alone."

> from Huntley,B.J. 1965. *Exploring a sub-Antarctic Wilderness*, pp. 54. Antarctic Legacy of South Africa, Stellenbosch, South Africa.

Abstract

The updating and rethinking of vegetation classifications is important for ecosystem monitoring in a rapidly changing world, where the distribution of vegetation is changing. The general assumption that discrete and persistent plant communities exist that can be monitored efficiently, is rarely tested before undertaking a classification. Marion Island is comprised of species-poor vegetation undergoing rapid environmental change. It presents a unique opportunity to test the ability to discretely classify species-poor vegetation with recently developed objective classification techniques and relate it to previous classifications. We classified vascular species data of 476 plots sampled across Marion Island, using Ward hierarchical clustering, divisive analysis clustering, non-hierarchical kmeans and partitioning around medoids. Internal cluster validation was performed using silhouette widths, Dunn index, connectivity of clusters and gap statistic. Indicator species analyses were also conducted on the best performing clustering methods. We evaluated the outputs against previously classified units. Ward clustering performed the best, with the highest average silhouette width and Dunn index, as well as the lowest connectivity. The number of clusters differed amongst the clustering methods, but most validation measures, including for Ward clustering, indicated that two and three clusters are the best fit for the data. However, all classification methods produced weakly separated, highly connected clusters with low compactness and low fidelity and specificity to clusters. There was no particularly robust and effective classification outcome that could group plots into previously suggested vegetation units based on species composition alone. The relatively recent age (*c.* 450 000 years B.P.), glaciation history (last glacial maximum 34 500 years B.P.) and isolation of the sub-Antarctic islands may have hindered the development of strong vascular plant species assemblages with discrete boundaries. Discrete classification at the community-level using species composition may not be suitable in such species-poor environments. Species-level, rather than community-level, monitoring may thus be more appropriate in species-poor environments, aligning with continuum theory rather than community theory.

Introduction

Plant ecologists identify, describe and map vegetation variation that represents underlying ecological processes in an effort to understand the complex spatial and temporal interactions between taxa and the environments in which they occur (De Cáceres et al. 2015). While vegetation variation is complicated and arguably varies along a continuum in space and time, humans tend to think categorically. This requires simplification through classification to create useful, logical and manageable units for theoretical and practical purposes (Wiser & De Cáceres 2013; De Cáceres et al. 2015). The aim of vegetation classification is to delineate and describe environments using the characteristics of the standing vegetation (De Cáceres et al. 2015) to provide a surrogate for ecosystem delineation (Brown et al. 2013). A vegetation classification serves as baseline data for ecosystem research, land-use planning, environmental assessments and scientifically based decisions in biodiversity management (Brown & Bredenkamp 2018). Policy-making, conservation and research therefore depend on accurate and up to date description and delineation of vegetation units.

Plant ecology concepts have evolved over time, and have recently enjoyed renewed interest, especially in terms of updating and advancing previous classifications (De Cáceres et al. 2015; Mucina et al. 2016; van Staden et al. 2021). Early approaches to vegetation variation viewed vegetation as either hierarchical, compositionally distinct units ("communities") that vary as an entire unit in space and time (i.e., discrete community concept or "Clementian" view; Weaver & Clements 1929) or entities made up of a continuum of a temporary co-occurrence of species that fluctuate in composition, space or time (i.e., the continuum concept or "Gleasonian" view; Gleason 1927; Curtis & Macintosh 1951). The continuum concept proposes that vegetation does not consist of homogeneous persistent units, but is the outcome of individual species' responses to their environment and to each other (Gleason 1927; Palmer & White 1994). This Gleasonian view is related to the niche concept which proposes that each species partitions a resource along a gradient (Austin 2013). The two extremes in approaches viewed vegetation as either a super-organism of co-evolved groups of species (i.e., community) or as species that assemble entirely individualistically (Austin 2013). No consensus has been reached on which perspective is most appropriate for classifying particular environments (Weaver & Clements 1929; Curtis & McIntosh 1951; Austin & Smith 1989; Scott 1995; Lortie et al. 2004; Austin 2013). However, the categorical, compositionally discontinuous, discrete model of plant communities, the "Clementian" view initially proposed by Weaver & Clements (1929), persists mainly due to historical legacy and its utility in creating vegetation maps for ecological management (Feilhauer et al. 2020). While the two approaches are not necessarily incompatible, most ecologists interested in vegetation description continue to define vegetation as an assemblage of distinct hierarchical plant communities (Gremmen 1981; Mucina et al. 2016; De Cáceres et al. 2018; Tsakalos et al. 2018; van Staden et al. 2021).

The general assumption of the community concept, that discrete and persistent vegetation units exist, is rarely tested before undertaking a classification, with the exception of more recent research (Lortie et al. 2004; Pavão et al. 2019; Feilhauer et al. 2020). This raises concerns about the widespread use of the traditional community concept and the application of methods developed that have underlying assumptions rooted in the existence of homogenous discrete spatial entities. Assuming, *a priori*, that specific floristically distinct communities exist may disregard the unique vegetation patterns often found in environments with few vascular plant species such as in aquatic (Landucci et al. 2015) or tundra (Yang et al. 2021) vegetation. In recent decades, a variety of new tools have been developed for vegetation scientists (see e.g. Aho et al. 2008 or Lötter et al. 2013). While these approaches may encourage new perspectives on the complex nature of vegetation patterns, they bring new challenges, for example, in the selection of appropriate clustering methods (Maechler et al. 2019; Oksanen et al. 2020). Lötter et al. (2013) referred to this as "the classification conundrum". The amount of research available which advocates particular methods, ideologies and approaches to classify vegetation (Lortie et al. 2004; Lötter et al. 2013; Feilhauer et al. 2020; Lengyel et al. 2021; Pakgohar et al. 2021), reflects the impracticality of the use of one universal approach in all environments. Nevertheless, there is general agreement that expert opinion is needed to select vegetation units at some stage in the classification process (Mucina 1997; Brown et al. 2013; Lötter et al. 2013) even if this adds subjectivity to the classification, possibly resulting in bias (Wolda 1981; Lötter et al. 2013), often with little objective validation of clustering results. However, recent classification methods, especially those used in data science (Flynt & Dean 2016), have made it possible to formally test the effectiveness of classifications, thereby reducing the number of subjective choices (Lötter et al. 2013; Pakgohar et al. 2021). The existence of discrete groups in the data can thus be tested objectively, before expert interpretation is needed.

Updating and rethinking vegetation classification is especially important in tracking shifts in the distribution of species in response to changes in climate and other anthropogenic drivers. In the sub-Antarctic, the regional climate has changed at an accelerated pace compared to lower latitudes (le Roux & McGeoch 2008a). For example, between 1949 and 2003, Marion Island (MI) which occurs in the sub-Antarctic, has experienced an increase in mean annual temperature from 5.4°C to 6.4°C, which is double the mean global rate of increase (le Roux & McGeoch 2008a). Mean annual rainfall has also decreased from *c.* 3000 mm to *c.* 2000 mm during the same period (le Roux & McGeoch 2008b). The vegetation is closely coupled with abiotic conditions and consists of 21 native vascular plant species and ranges from near continuous short-statured plant cover in sub-Antarctic tundra to barren polar desert (Smith & Mucina 2006). The island is remote, has a relatively recent origin – only emerging above sea level for the first time *c.* 450 000 years B.P. (McDougall et al. 2001) – and has been glaciated with the greatest extent of ice occurring most recently *c.* 34 500 years ago during the last glacial maximum (Rudolph et al. 2020). Recent rapid climatic change has presumably altered the distribution and relationships between plant species and perhaps redistributed some species which were used to previously classify communities on MI (le Roux & McGeoch 2008b). In addition, a more temperate climate coupled with anthropogenic disturbances and low diversity has created new opportunities for the establishment and spread of non-native species (Greve et al. 2017). Three alien plant species have become particularly widespread on MI (*Poa annua*, *Sagina procumbens, Cerastium fontanum*), especially in areas influenced by animals near the coast (le Roux et al. 2013). The most widespread invasive species on MI is the house mouse (*Mus musculus*) which has rapidly increased in density, abundance and distribution since feral cats (*Felis catus*), originally introduced to control mice, were eradicated in 1991 (McClelland et al. 2018). The mice impact most aspects of the biodiversity of MI including causing damage to and mortality in plant species (Phiri et al. 2009), decreasing invertebrate abundance (Smith et al. 2002), increasing seabird deaths (Dilley et al. 2016) and reducing indigenous seed caches (Smith et al. 2002). Due to both invasive species and climate change impacts, the vegetation has likely been changing on MI and is expected to change significantly in the near-future with the planned mouse eradication (Preston et al. 2019), with monitoring becoming a key conservation objective for the island.

To effectively study and monitor the impact of climate change and invasive species on the vegetation, an ecologically meaningful vegetation classification and monitoring unit is needed that can be objectively and repeatedly defined, mapped and monitored at a fine scale. Since using remote sensing data for image classification of vegetation in the near permanent cloud cover experienced on most islands in the sub-Antarctic is challenging (Fitzgerald et al. 2021), a floristic approach to classification using plot data may show intrinsic vegetation patterns and thus act as a proxy for underlying environmental variation and patterns that form the standing vegetation. Using a floristic classification may uncouple the vegetation distribution from previous assumptions of environmental drivers and allow modelling of change in abiotic conditions with resultant groups acting as the units of change.

Here, we tested whether vegetation forms compositionally discrete units in a species-poor environment, which are generally neglected environments in classification research. Marion Island presents an opportunity to test plant community concepts and to elucidate appropriate classification approaches in species-poor environments that are closely coupled with abiotic conditions. The first objective was to identify and differentiate vegetation units using both hierarchical and non-hierarchical classification algorithms. The second objective was to compare and validate clustering methods. The third objective was to describe the vegetation units using indicator species analysis. The best performing clustering method was related to earlier classifications that used phytosociological relevè table sorting based on vascular and bryophyte species (Gremmen 1981) and a cluster analysis using scores from an ordination based largely on soil chemistry and plant guilds (Smith et al. 2001) to classify vegetation. Since previous research suggested viewing the vegetation as discontinuous, we expected compositionally well separated vegetation groups where the variation between groups can be related to abiotic and biotic influences.

Methods

Study site

Marion Island (46°54' S, 37°45' E) is a volcanic, remote, sub-Antarctic island covering an area of *c*. 290 km^2 (Fig. 1). The South African-governed island has a cool, thermally-stable, oceanic climate with mean annual precipitation of *c.* 2000 mm (le Roux & McGeoch 2008a). The islands' geology consists of smoothed pre-glacial grey lava and rough post-glacial black lava with *c.* 130 more recent red scoriaceous cinder/scoria cones scattered around the island (Rudolph et al. 2020; Fig. 1). The vegetation changes along an elevational severity gradient (le Roux & McGeoch 2008c), from the coast to the highest elevation of 1230 m, and generally occurs in two layers at lower elevations. These are a prostrate vascular plant layer, rarely exceeding 50 cm in height and a low ground cover of bryophytes (Gremmen 1981). The flora comprises 21 native (Chau et al. 2020) and 17 alien vascular plant species (Greve et al. 2017), along with 134 bryophyte and 100 lichen species (Øvstedal & Gremmen 2001). Many alien vascular plant species have been controlled and only occur in isolated locations (Greve et al. 2017).

Five vegetation units have been mapped previously based on field research, photographs and field observations, and informed by expert opinion (Smith & Mucina 2006; Fig. 1). Smith & Mucina (2006) recognised that mapping at the scale of plant community identified in previous studies (Gremmen 1981; Smith & Steenkamp 2001), in vegetation that changes within a few meters, would not be possible, and thus mapped five units (Fig. 1) at a broader scale. Polar desert was indicated by the absence of vascular plant species and by the presence of bryophytes (Smith & Steenkamp 2001). Cinder cones, conspicuous red volcanic ash deposits, were largely associated with bryophytes, although Gremmen (1981) included cinder cones under fellfield vegetation. Fellfield is dominated by *Azorella selago* cushion plants and epiphytic *Polypogon magellanicus* grasses, with several vascular plant species co-occurring at lower altitudes (Smith & Steenkamp 2001). The mire-slope unit is made up of the mire and slope communities combined, as mapping at the fine scale needed to differentiate mires and slopes was not possible (Smith & Mucina 2006). Slope communities are either dominated by the fern *Austroblechnum penna-marina* or shrub *Acaena magellanica* (on slopes with impeded drainage). Mires occur on flat or slightly sloping areas, dominated by graminoids *P. magellanicus, Juncus scheuchzerioides* and *Carex dikei* and various bryophytes. Lastly, coastal vegetation is either largely dominated by *Crassula moschata* (exposed to high saltspray) or by *Leptinella plumosa*, *Callitriche antarctica* or *Poa cookii* (in areas influenced by faunal activity; Smith & Steenkamp 2001).

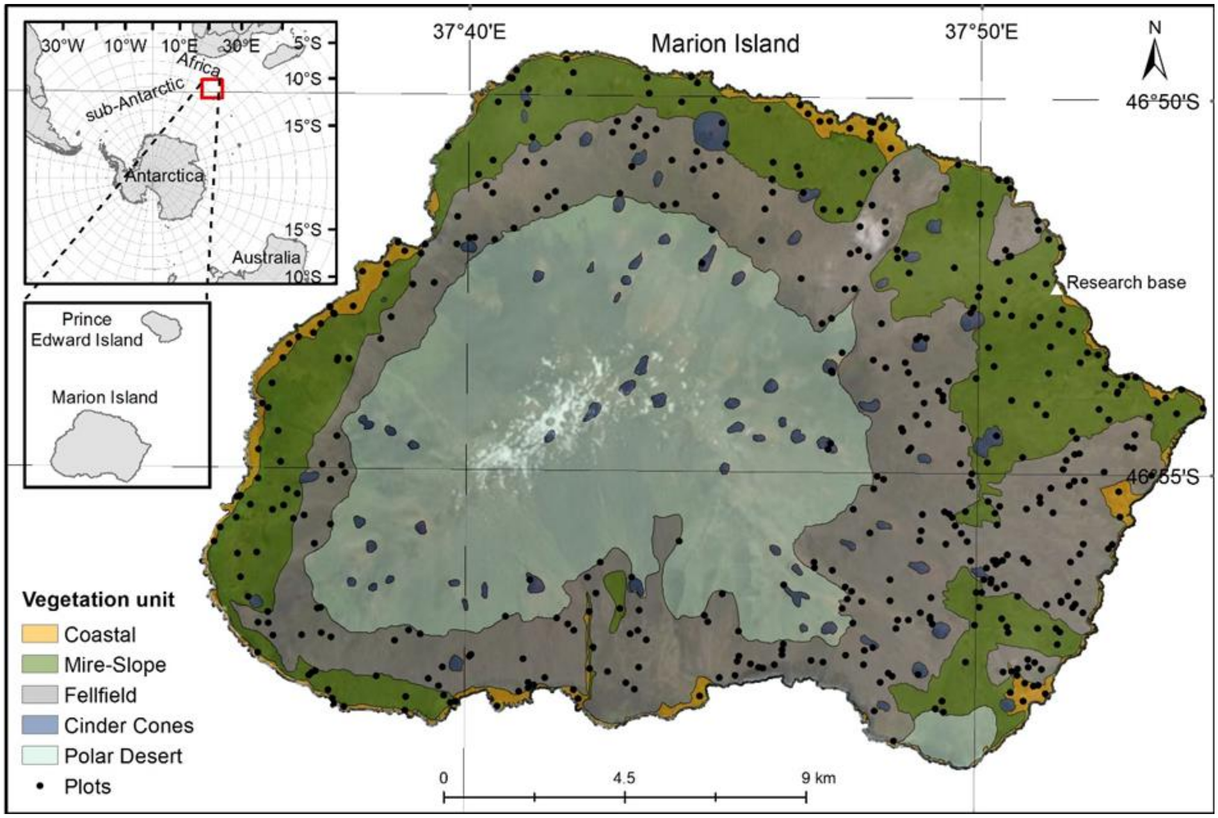


Figure 1. Vegetation map of Marion Island showing the five units (in colour) delineated by Smith & Mucina (2006). Black points indicate the location of plots sampled in this study.

Vegetation sampling

Vegetation data consisted of 476 vegetation plots that were sampled on MI using systematic randomised sampling in 2018 and 2019. Plot locations thus included a wide range of environmental conditions (Fig. 1). In each 3x3 m plot, the percentage ocular canopy cover of all vascular plant species was estimated by trained observers following Daubenmire (1959). The percentage cover of two non-vegetated cover classes were also estimated: bare rock or soil and open water. A description of the vegetation was produced for each plot in the field to assist the classification. Two bryophytes were identified to genus level, namely *Breutelia* and *Brachythesium,* and three to species-level namely *Marchantia polymorpha, Marchantia berteroana* and *Racomitrium lanuginosum.* These bryophytes were easily identified in field and were indicator species for plant communities in previous classifications (Gremmen 1981). All other bryophytes were estimated collectively as "bryophytes". Lichens were also given a collective cover estimate. To reduce noise, species with two or less observations in the matrix were removed and thus rare species were not considered (see e.g. Addicott et al. 2018). Five alien species were recorded in the data, with only *P. annua*, *S. procumbens* and *C.*

fontanum retained in analyses after rare species were removed. All analyses were initially conducted on two subsets of the data: including *vs.* excluding the three alien species. However, the optimality of clustering did not improve with their exclusion, and these alien species were thus included in the analyses. Indeed, Smith et al. (2001) suggested that alien species should be included in classifications in future due to the increasingly important role of invasive species on community function, structure, and dynamics.

Cluster analysis

To select the most robust classification procedure for our study site, the best practice was to test a variety of procedures to determine if the vegetation data do indeed form clusters that can be interpreted ecologically (Aho et al. 2008; Lötter et al. 2013). The classifications were undertaken in three steps: (1) pre-processing involved the selection of a distance measure and normalisation of the data; (2) cluster analysis involved the selection and application of the clustering algorithm and its various parameters; (3) cluster validation involved the selection and application of appropriate internal validation techniques to evaluate the quality of the classification. Four clustering algorithms and four validation measures were explored based on demonstrated performance in recent literature (Handl et al. 2005; Aho et al. 2008; Lengyel et al. 2021; Pakgohar et al. 2021). We defined a vegetation classification as being comprised of a cluster of plots organised into units with discrete boundaries between them. The aim was to identify clusters of plots containing small within-cluster variance (i.e., compact clusters) and sufficiently large between-cluster variance (i.e., spatially well-separated). All analyses were conducted in R statistical software (R Core Team 2020).

One divisive and three agglomerative clustering algorithms prominent in the literature were tested using the raw data. Divisive analysis clustering (DIANA; Maechler et al. 2019) was chosen as the divisive hierarchical clustering method; it starts with all plot data in one cluster and successively divides plots based on a “distance” metric, selected by the researcher, into clusters. Conversely, agglomerative hierarchical clustering starts with each plot as an individual cluster locating pairs of plots with the smallest distance, fusing the two plots into a cluster. The approach then re-iteratively calculates the distance from fused plots to all remaining plots until all sites are grouped into one cluster. For agglomerative clustering, the hierarchical “Ward” clustering method was chosen after comparison to single, average and complete linkage clustering (linkage refers to the way the distance measure is implemented to form clusters; see Aho et al. 2008 for a summary of the linkage methods). This was done by calculating the agglomerative coefficient and divisive coefficient for DIANA in the “cluster” package in R (Maechler et al. 2019). The Ward method aims to minimise the within-cluster variance and searches for clusters in multivariate "Euclidean" space (Murtagh & Legendre 2014). The Ward method, which showed the strongest clustering, implements squared Euclidian distances based on sum of squares (Murtagh & Legendre 2014), but is not appropriate for non-metric distance (e.g. "Bray-Curtis"), thus Euclidean distance was chosen as the dissimilarity metric, calculated using the "vegan" package (Oksanen et al. 2020). To include non-hierarchical classification, kmeans and partitioning around medoids (PAM) clustering were chosen as centroid-based algorithms that identify *k* centroids, allocating each data point to the nearest centroid. Kmeans aims to minimise the sum of squared distances of data points to their cluster centroid, whereas PAM minimises dissimilarity between data points in a cluster and its cluster centre (medoids). Initial investigations showed that all dissimilarity measures explored (i.e., "Hellinger", "Manhattan" and Bray-Curtis distances) with single, average and complete linkage, where possible, produced similar results (see also Aho et al. 2008).

Number of clusters

There is no consensus on an ideal measure to estimate the optimum number of clusters or most appropriate clustering method (Aho et al. 2008; Lötter et al. 2013). To choose the optimum number of clusters for each clustering method, we used (1) silhouette widths, (2) "Dunn" index and the (3) gap statistic in the "NbClust" package (Charrad et al. 2014). Silhouette width is widely used to simultaneously determine the optimum number of clusters and quality of the entire classification (Handle et al. 2005). Silhouette width estimates the average distance between clusters, i.e., how close data points in a cluster are to data points in neighbouring clusters (Rousseeuw 1987). The Dunn index calculates the ratio between maximum intra-cluster distance and minimum inter-cluster distance (Dunn 1974). The gap statistic compares within-cluster distance to a uniformly distributed null reference distribution with bootstrapping (Tibshirani et al. 2001). The optimum cluster number is indicated where the gap curve reaches an inflection point and changes to a higher value. Previous classifications of the vegetation on MI defined between five and 41 vegetation units (Huntley 1971; Gremmen 1981; Smith et al. 2001; Smith & Mucina 2006), so there was no *a priori* reason to choose any particular number of clusters. However, we explored five clusters along with the optimal number of clusters indicated by the validation measures, to compare to the suggested five vegetation units mapped previously (Smith & Mucina 2006).

Cluster validation

Since various R packages have been created for internal cluster validation, multiple packages and validation measures were explored. We evaluated optimality as maximising intra-cluster homogeneity and inter-cluster distance, and minimising the degree to which a cluster groups data points together with the nearest neighbours (Handl et al. 2005). To determine the optimal clustering method based on compactness, separation and connectivity (the three most important clustering criteria) of each clustering algorithm, the (1) silhouette widths, (2) Dunn index and (3) connectivity of clusters were calculated for two to 20 clusters with the "clValid" package (Brock et al. 2008). Individual silhouette plots were drawn for each clustering method with the "cluster" package (Maechler et al. 2019) using the optimal number of clusters per method. These plots show the silhouette widths estimated for each plot within a cluster and calculates the average silhouette width for each cluster. Both the Dunn index and silhouette width compute a final score that combines two clustering criteria: compactness and separation (Handle et al. 2005). Connectivity indicates the degree to which clusters are connected to the nearest neighbours to determine to what extent data items are placed in the same cluster as their nearest neighbour (Saha & Bandyopadhyay 2012). While most of these are heuristic methods, well-separated and compact clusters are indicated by large silhouette widths and Dunn index values. Ideally, connectivity should be minimised so that plots nearby are more related than plots further away. Furthermore, dendrograms and centroids assisted to visually determine groupings in the data.

Indicator species analysis

Indicator species analysis (ISA) was conducted with the "indicspecies" package (De Cáceres & Legendre 2009), to determine the association of diagnostic species with each cluster and to compare with previously classified groups which were indicated by particular species (Gremmen 1981). The analysis was run for the optimal number of clusters in the best performing clustering method and also for five clusters, to compare to the five groups that were previously proposed in the vegetation map (Smith & Mucina 2006). The ISA is based on an Indicator Value (Dufrêne & Legendre 1997) that calculates a plant species' relative abundance and frequency of occurrence to estimate the strength of species associations with the predetermined groups (Dufrêne & Legendre 1997). The statistical significance of the association is then tested with a permutation test (De Cáceres & Legendre 2009). This analysis thus indicates species fidelity (the probability of finding the species in plots that belong to the cluster) and specificity (the probability that a plot belongs to the cluster given that the species is present in the plot). Fidelity is fundamental to interpreting the association of species with a vegetation group under the “Braun-Blanquet” approach. These two components combined gives an association statistic to a group.

A vegetation map was created with the output of the classification using ArcGIS Desktop (Environmental Systems Research Institute, CA, USA) and Google Earth Pro (Google, CA, USA). We used Google Earth satellite imagery, the previous vegetation map (Smith & Mucina 2006), plot data from 2018-2020 and a digital surface model of the island to inform the map.

Results

Cluster analysis

Ward hierarchical clustering consistently performed better than kmeans, DIANA and PAM clustering in all validation measures (Fig. 2). Ward clustering also had the highest agglomerative coefficient (0.98), compared to single (0.80), complete (0.89) and average (0.86) linkage, and the divisive coefficient for DIANA (0.87). Ward clustering had the highest ASW (0.39, Table 1) and Dunn index (0.47, Table 1). It also had the lowest connectivity for any number of clusters (Fig. 2).

Number of clusters

In all methods, clustering performance decreased with increasing cluster number (Fig. 2). Most validation measures indicated that two clusters are the best fit for the data (Table 2). The ASW indicated that the data were clustered most strongly when the Ward method was clustered in two (0.34) or three (0.34) groups (Fig. 3). DIANA had the highest ASW for three (0.37) and seven clusters (0.36), followed by kmeans with the highest ASW for two (0.36) and three (0.35) clusters (Table 2). PAM clustering had the highest ASW for two (0.35) and three (0.33) clusters (see Fig. A1-A3 in Appendix A for detailed results). The Dunn index was the highest in the two-cluster solution for all clustering methods, decreasing with the number of clusters (Fig. 2). If the first inflection point of the gap curve is considered, two clusters are suggested for Ward, kmeans and PAM, and three clusters for DIANA (Fig. A4-A7). None of the validation methods indicated five groups as a good fit for the data (Fig. 4). The highest linkage distance of the Ward cluster dendrograms also visually indicate two or three clusters may be appropriate for the data (Fig. 5), as below three clusters (Height = 400), the linkage distance is short (i.e., the groups are not well separated; Fig. 5). The Ward method with two, three and five clusters was chosen for the indicator species analysis.

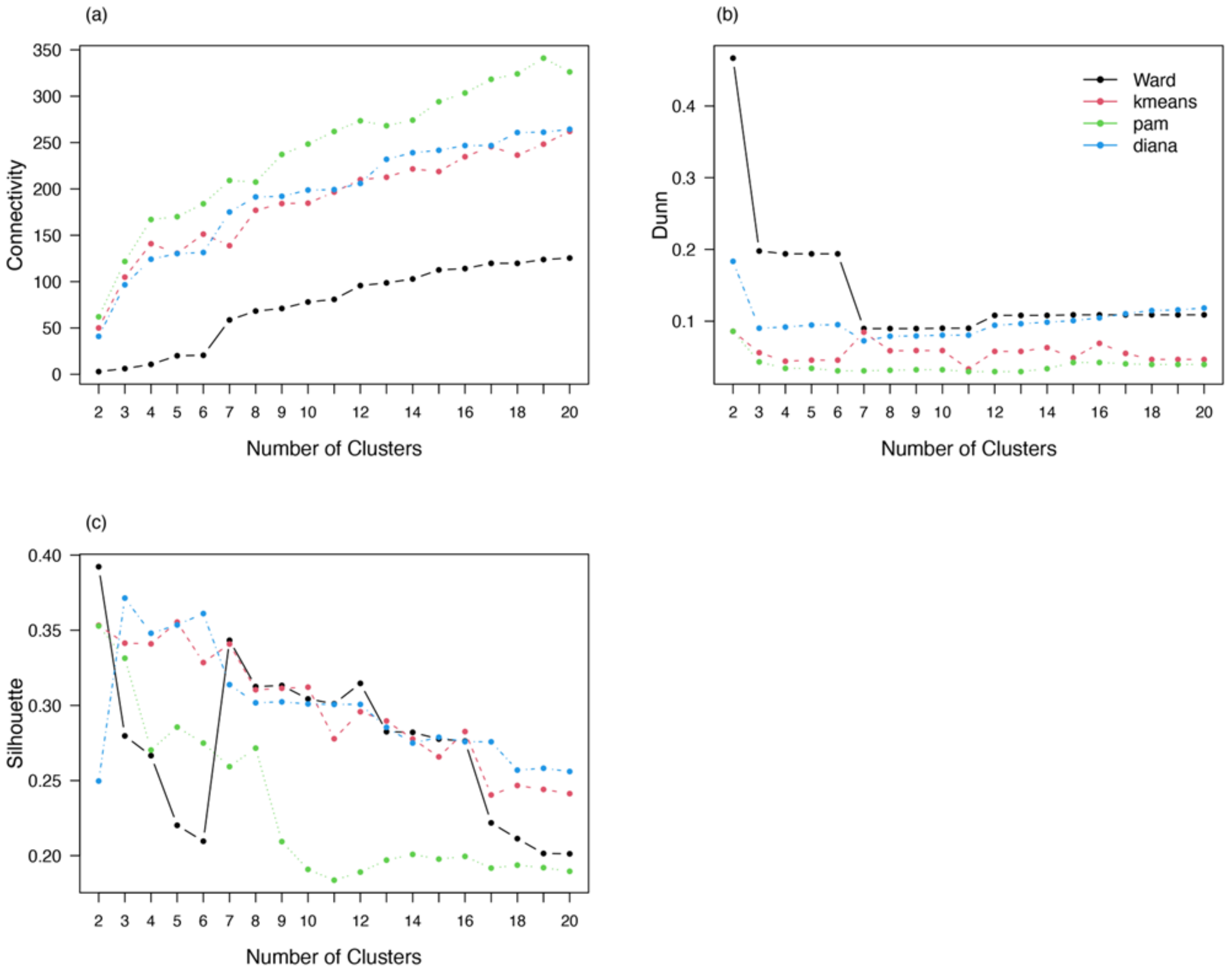


Figure 2. Cluster validation measures to determine the optimal clustering method between Ward, kmeans, PAM and DIANA clustering (indicated by the colours) using a) connectivity, b) Dunn index, and c) average silhouette width (ASW) for two to 20 clusters. The Dunn index calculates the ratio between maximum intra-cluster distance and minimum inter-cluster distance, and ASW estimates the average distance between clusters. Large Dunn index and silhouette width values thus indicate compact and well separated vegetation groups. Connectivity refers to the connectivity of clusters to nearest neighbours and should ideally be low so that plots nearby are more related than those further away.

Table 1. Cluster validation results of the four cluster analyses. Only the highest values for ASW ("average silhouette width") and Dunn index, as well as lowest values for connectivity are shown. "Rank" indicates the best to worst performing clustering method based on all three validation measures.

Method	**ASW**	**Dunn**	**Connectivity**	**Rank**
Ward	0.39	0.47	2.93	1
DIANA	0.37	0.18	40.94	2
kmeans	0.36	0.09	50.02	3
PAM	0.35	0.09	62.05	4

Table 2. Summary of the suggested number of clusters for each validation method for the four cluster analysis methods. See Fig. A1-A7 in the Appendix for detailed results.

Method	**ASW**	**Dunn**	**Gap**
Ward	2	2	2
DIANA	3	2	3
kmeans	2	2	2
PAM	2	2	2

Cluster validation

The presence of clusters with below average silhouette scores, as well as the fluctuation in the thickness of silhouette width group sizes in the Ward two, three and five cluster solutions (Fig. 3), indicate suboptimal groupings for the data. Based on the overall silhouette width and Dunn index ranges of all clustering methods, which generally increase with cluster compactness and separation, most clustering methods produced weak separation, low compactness, and high connectivity (Fig. 2). None of the algorithms produced strong clusters, as even the highest ASW was still low (Table 1). Centroids for kmeans and PAM clustering are also visually not well separated for neither two nor five clusters (Fig. A8-A11). Therefore, overall, there is no strong clustering tendency in the data.

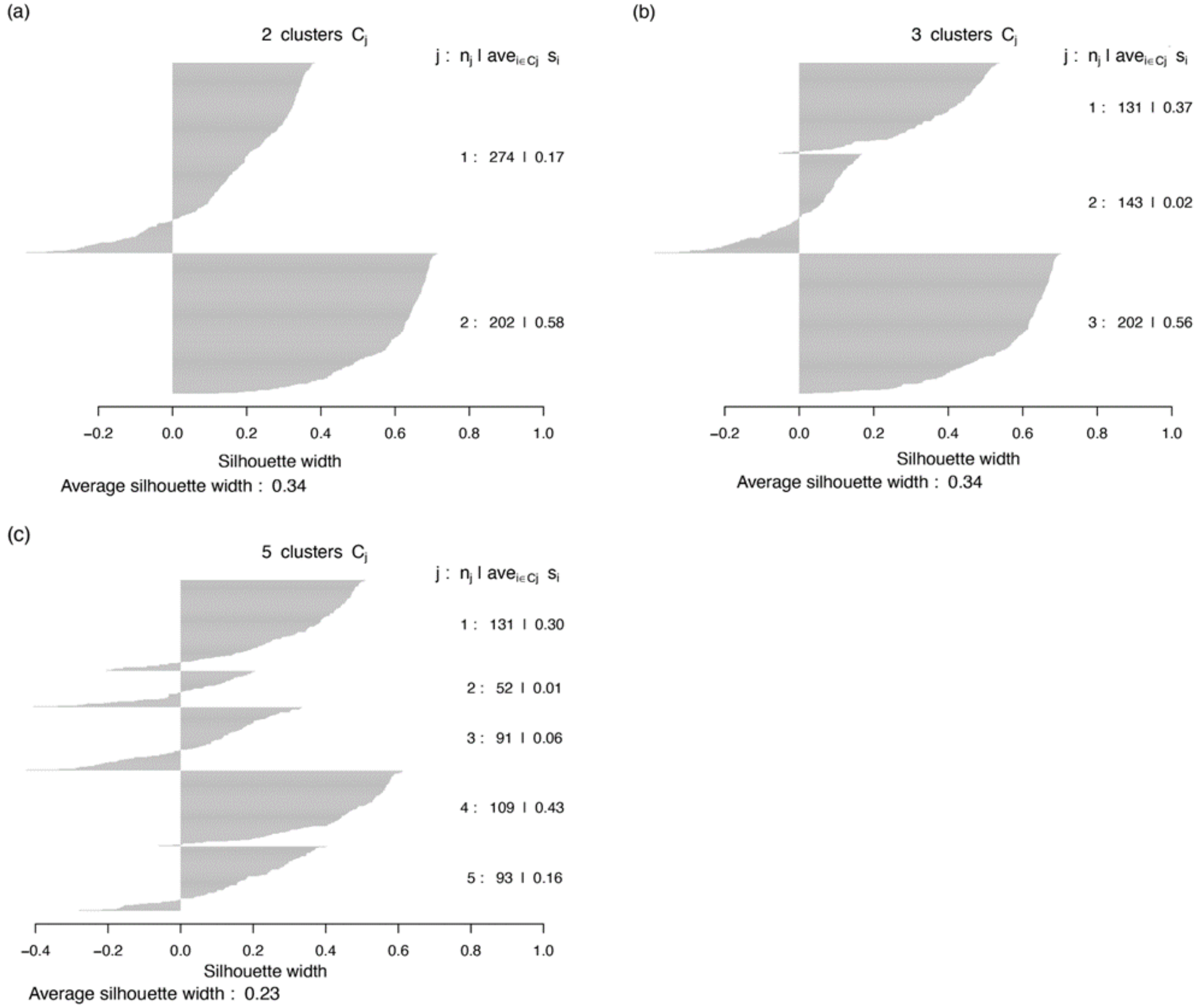


Figure 3. Silhouette plots of Ward hierarchical clustering for a) two, b) three and c) five clusters. The number of clusters (n = 2 and 3) were chosen based on the two clustering solutions with highest average silhouette width (ASW) and Dunn statistic. Five clusters were chosen based on the number of vegetation complexes suggested by Smith & Mucina (2006) for MI. Each grey horizontal line represents the silhouette width of a plot that was allocated to each cluster (j). The number of plots (n_j; n=476) allocated to each cluster and the ASW for each cluster ($\text{ave}_{i\in CiSi}$) is shown on the right, as well as the overall average of the entire classification (shown below the graph). Small within-cluster ASW values indicate that plots within a cluster are compositionally dissimilar. A small overall ASW for the entire classification indicates that clusters are not well separated and compact. Negative silhouette values indicate plots might have been placed in the incorrect cluster. Ideally, the plots clustered within a group would all have high and similar silhouette widths, i.e., the grey lines would be uniform within a cluster. The overall average would also ideally be high in a well separated and compact grouping of a data set.

The Ward clustering with five groups does not spatially match the previously mapped units (Fig. 4). The low overall ASW for the five-cluster solution also indicates poor clustering of groups (Fig. 3). The in-field descriptions of vegetation in plots confirmed that plots were not classified correctly, according to previously suggested units.

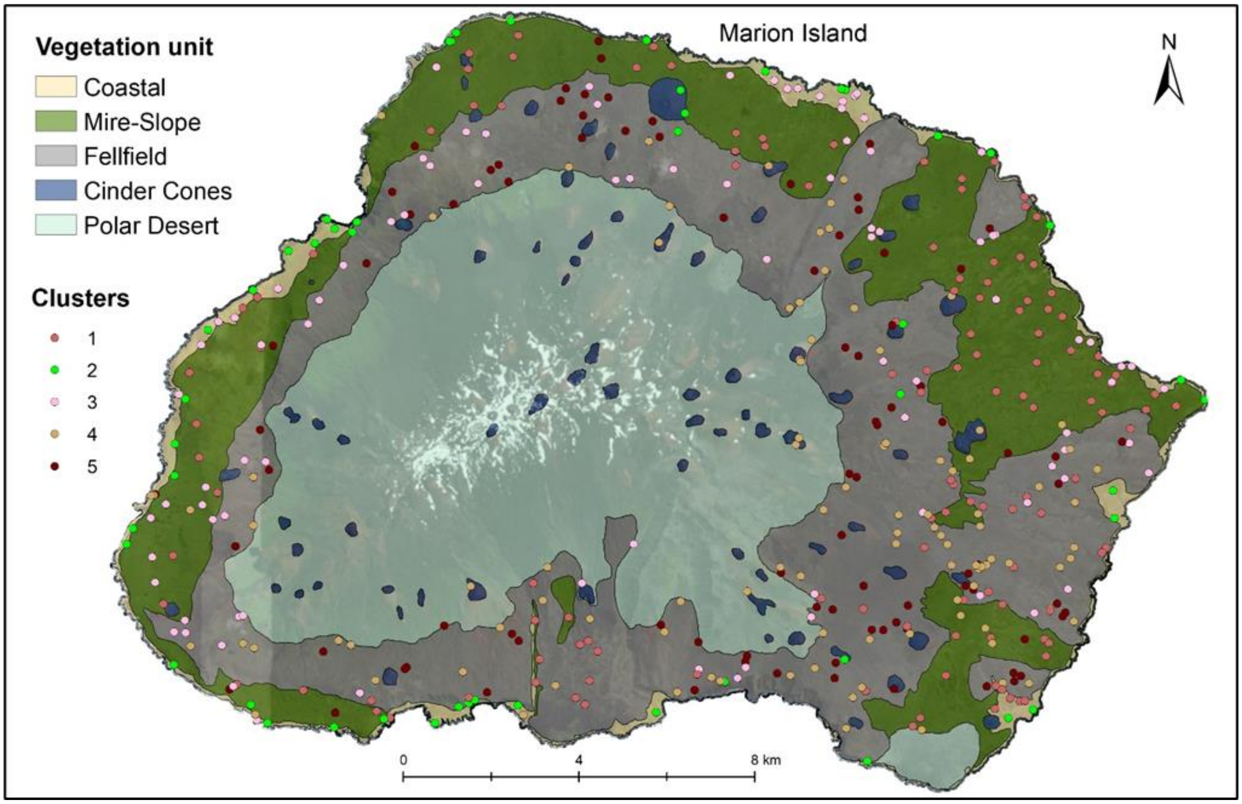


Figure 4. Smith & Mucina's (2006) vegetation map of Marion Island (same as in Figure 1) with the location of plots allocated to each cluster in this study indicated as five differently-coloured dots. The five clusters are the result of the Ward cluster analysis with five groups, chosen to compare to the five mapped vegetation units. The five clusters do not match well with the five vegetation units.

Indicator species analysis

If two clusters are selected (Table 3), *A. penna-marina*, *Brachythesium, P. cookii, L. plumosa, Juncus scheuchzerioides, M. polymorpha, P. annua* and *C. antarctica* are indicator species for cluster 1 (i.e., there is high specificity for these species). Furthermore, *A. magellanica, C.dikei* and *C. moschata* are significant ($p < 0.05$) indicators species for cluster 1 based on high specificity, but are not strongly associated to the cluster (Table 3). None of the species occur in all or most plots belonging to cluster 1 (i.e., there is low fidelity). Lichen and *Notogrammitis crassior* are indicator species for cluster 2 (Table 3).

Table 3. Indicator species analysis (ISA) results showing species that are associated with two vegetation groups. Only results for significant ($p < 0.05$) indicator species are shown. The ISA is based on a species' relative abundance and frequency of occurrence to estimate the strength of species associations within the predetermined groups. Specificity indicates the probability that the plots belong to the group given that the species has been found. Fidelity estimates the probability of finding the species in the plots belonging to the group. These two components combined give an association statistic. Strong indicator species would have fidelity and/or specificity values close to 1.

Species	**Cluster**	**Specificity**	**Fidelity**	**Association statistic**	**P value**
Austroblechnum penna-marina	1	0.93	0.69	0.80	< 0.05
Acaena magellanica	1	0.89	0.52	0.68	< 0.05
Carex dikei	1	0.83	0.34	0.53	< 0.05
Brachythesium spp.	1	0.97	0.19	0.43	< 0.05
Poa cookii	1	0.97	0.30	0.53	< 0.05
Leptinella plumosa	1	0.98	0.13	0.35	< 0.05
Juncus scheuchzerioides	1	0.94	0.11	0.32	< 0.05
Marchantia polymorpha	1	1.0	0.10	0.30	< 0.05
Poa annua	1	1.0	0.06	0.24	< 0.05
Crassula moschata	1	0.84	0.06	0.21	0.05
Callitriche antarctica	1	0.98	0.04	0.19	0.02
Lichen	2	0.87	0.69	0.78	< 0.05
Notogrammitis crassior	2	0.90	0.10	0.30	< 0.05

If three clusters are selected (Fig. 5; Table 4), *A. penna-marina* is a good indicator for cluster 1; it occurs in almost all plots belonging to this cluster (i.e., high fidelity), and is largely restricted to cluster 1 (Table 4). *Leptinella plumosa, M. polymorpha, Montia fontana, P. annua, C. antarctica, C. moschata,* open water and *Collobanthus kergeulensis* are good indicators for cluster 2 (Table 4), with almost all plots containing these species belonging to cluster 2 (i.e., high specificity), although they do not occur in all plots belonging to the cluster. Furthermore, most plots that contain *P. cookii* and *S. procumbens* also belong to this cluster (Table 4). No species occurs in all plots that belong to cluster 2 (Table 4). Lichen appears in many plots belonging to cluster 3 and is mostly restricted to cluster 3. *Notogrammitis crassior* is also a good indicator species for cluster 3 with most plots containing this species belonging to cluster 3 (Table 4).

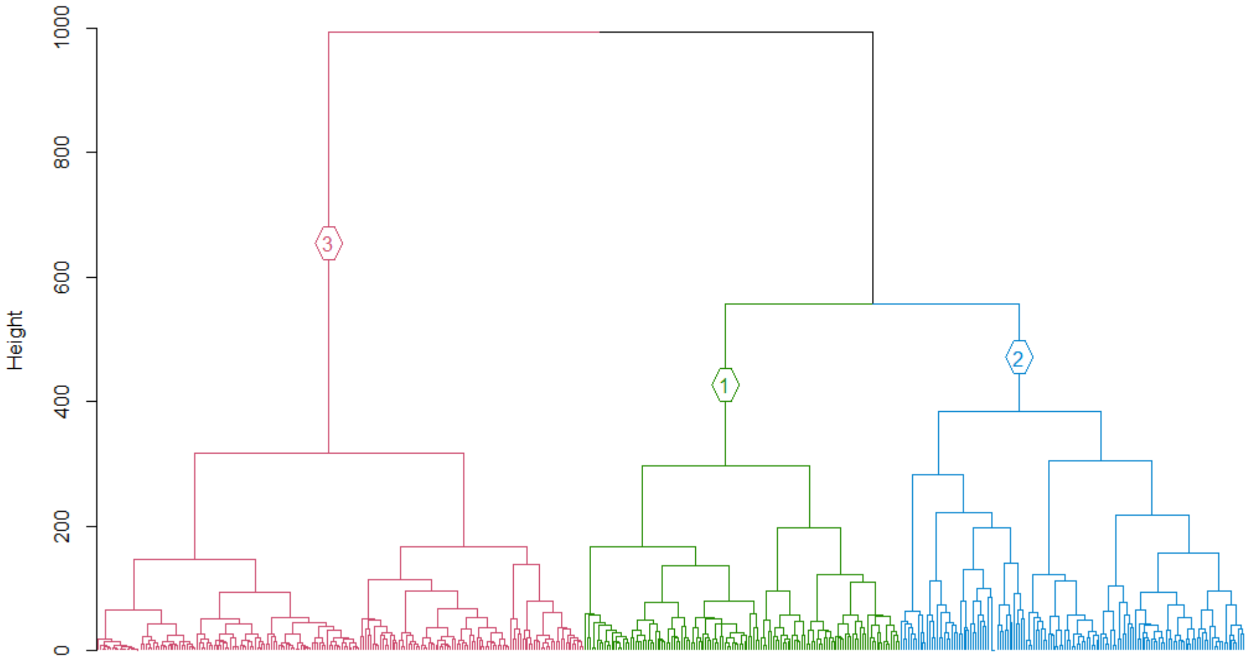


Figure 5. Ward hierarchical clustering dendrogram showing three clusters (coloured). Height indicates the Euclidian distance between clusters and the horizontal end points show the 476 plots. Short distances (i.e., small differences in height) between data points indicate similarity. Below Height = 400 or three clusters, branches split at relatively short distances, indicating low separation between clusters or high similarity. The height of the link that joins two clusters is the longest.

If five clusters are selected (Fig. 6), *A. penna-marina* is a good indicator for cluster 1, as it occurs in all plots belonging to this cluster (i.e., high fidelity), and it is mostly restricted to cluster 1 (Table 5). *Leptinella plumosa, M. fontana, P. annua, C. antarctica, C. kergeulensis, C. moschatta* were significant indicator species ($p < 0.05$) for cluster 2, and to a lesser extent also *P. cookii* and *M. polymorpha* (Table 5). They are good indicator species for this cluster because they mostly occur in sites belonging to this cluster only (i.e., high specificity). No species occurs in all plots in cluster 2. Cluster 5 is indicated by *N. crassior* as most plots that contain this species belong to cluster 5. Other species are indicators for a combination of vegetation clusters, but none are good indicators for only cluster 3 or cluster 4.

Table 4. Indicator species analysis (ISA) results showing significant indicator species for three vegetation clusters. The ISA is based on a plant species' relative abundance and frequency of occurrence to estimate the strength of species associations with the predetermined clusters (De Cáceres & Legendre 2009). Specificity indicates the probability that the plots belong to the cluster given that the species has been found. Fidelity estimates the probability of finding the species in the plots belonging to the cluster. These two components combined give an association statistic to a cluster. Strong indicator species would have fidelity and/or specificity values close to 1. Only results for significant ($p < 0.05$) indicator species are shown.

Species	**Cluster**	**Specificity**	**Fidelity**	**Association statistic**	**P value**
Austroblechnum penna-marina	1	0.87	0.99	0.93	< 0.05
Poa cookii	2	0.85	0.35	0.55	< 0.05
Water	2	0.94	0.06	0.23	< 0.05
Collobanthus kergeulensis	2	0.97	0.03	0.17	0.03
Leptinella plumosa	2	0.99	0.24	0.49	< 0.05
Marchantia polymorpha	2	0.99	0.15	0.39	< 0.05
Sagina procumbens	2	0.81	0.19	0.39	< 0.05
Poa annua	2	0.98	0.10	0.32	< 0.05
Crassula moschata	2	0.91	0.10	0.31	0.05
Callitriche antarctica	2	0.99	0.07	0.26	0.03
Montia fontana	2	0.98	0.13	0.35	< 0.05
Lichen	3	0.77	0.69	0.73	< 0.05
Notogrammitis crassior	3	0.82	0.10	0.29	< 0.05
Acaena magellanica	1+2	0.94	0.52	0.70	< 0.05
Carex dikei	1+2	0.91	0.34	0.56	< 0.05
Brachythecium spp.	1+2	0.99	0.19	0.43	< 0.05
Juncus scheuchzerioides	1+2	0.97	0.11	0.33	< 0.05
Racomitrium	1+3	0.90	0.62	0.75	< 0.05
Lycopodium magellanicum	1+3	0.98	0.08	0.28	0.02
Ranunculus biternatus	2+3	0.85	0.22	0.43	< 0.05

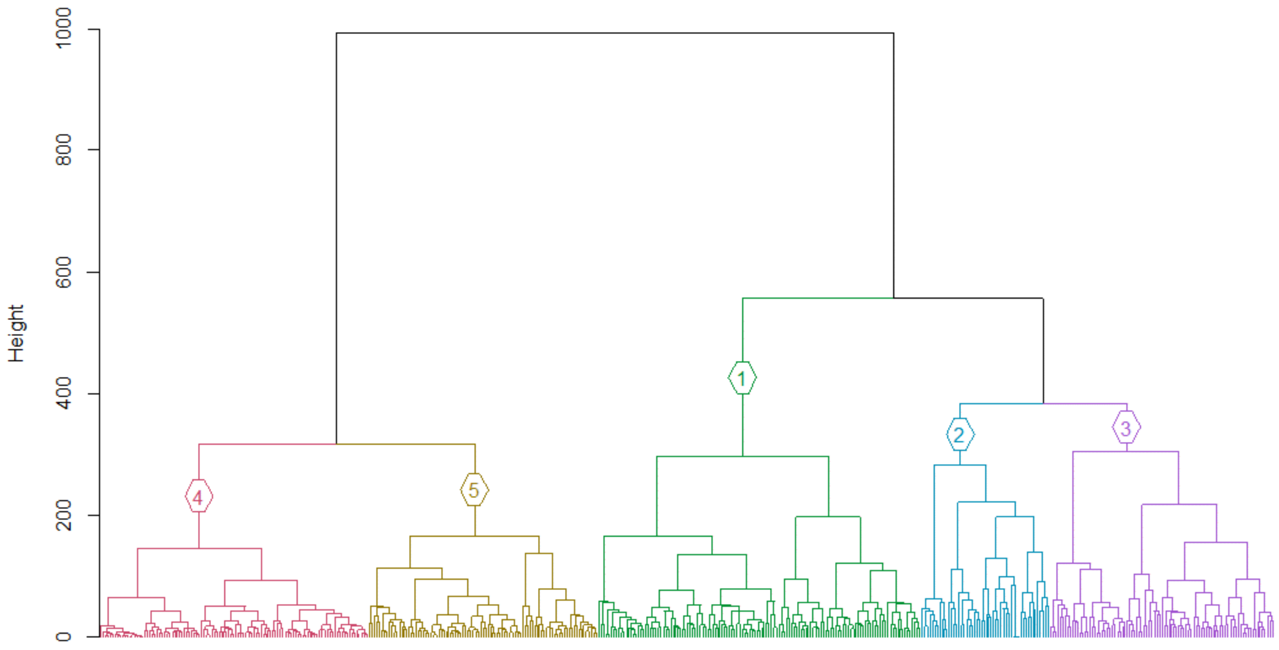


Figure 6. Ward hierarchical clustering dendrogram showing five clusters (coloured). Height indicates the Euclidian distance between clusters and the horizontal end points show the 476 plots. Short distances (i.e., small differences in height) between data points indicate similarity. Below Height = 400 or three clusters, branches split at relatively short distances, indicating low separation between clusters or high similarity. The height (*c.* 350) of the links that split the dendrogram into five clusters is at a low linkage distance, indicating a small difference between clusters.

Table 5. Indicator species analysis (ISA) results showing significant indicator species for five vegetation clusters, as suggested by previous research (Smith & Mucina 2006). The ISA is based on a plant species' relative abundance and frequency of occurrence to estimate the strength of species associations with the predetermined clusters (De Cáceres & Legendre 2009). Specificity indicates the probability that the plots belong to the cluster given that the species has been found. Fidelity estimates the probability of finding the species in the plots belonging to the cluster. These two components combined give an association statistic to a cluster. Strong indicator species would have fidelity and/or specificity values close to 1. Only results for significant ($p < 0.05$) indicator species are shown.

Species	**Cluster**	**Specificity**	**Fidelity**	**Association statistic**	**P value**
Austroblechnum penna-marina	1	0.78	0.99	0.88	< 0.05
Leptinella plumosa	2	0.97	0.52	0.71	< 0.05
Poa cookii	2	0.81	0.56	0.67	< 0.05
Poa annua	2	0.99	0.29	0.54	< 0.05
Crassula moschata	2	0.92	0.27	0.50	< 0.05
Marchantia polymorpha	2	0.86	0.25	0.46	< 0.05
Callitriche antarctica	2	0.91	0.15	0.37	< 0.05
Collobanthus kergeulensis	2	0.98	0.08	0.27	< 0.05
Notogrammitis crassior	5	0.79	0.14	0.33	< 0.05
Brachythecium spp.	1+2	0.94	0.25	0.48	< 0.05
Carex dikei	1+3	0.82	0.41	0.58	< 0.05
Montia fontana	2+3	0.98	0.13	0.35	< 0.05
Water	2+3	0.92	0.06	0.23	0.01
Lichen	4+5	0.84	0.69	0.76	< 0.05

Discussion

The low clustering tendency in all methods indicates that the vegetation of MI is not well differentiated by cover-abundance. Since all classification attempts failed to strongly cluster vegetation into stable units on MI, vascular plant species may not form compositionally discrete communities based on aerial cover. In all methods, the clusters that were generated were not well isolated and were also not ecologically meaningful based on the presence of particular species suggested by the ISA. Bricher (2012) similarly tested various clustering methods and found that clusters were not well isolated for the species-poor vegetation on the sub-Antarctic Macquarie Island, concluding that stable groupings could not be found in the floristic data and suggesting individual species distributions rather be used to differentiate vegetation. Macquarie Island has a similar climate, age, plant functional groups and species richness (45 vascular plant species) to MI (Bricher 2012). Therefore, this study suggests that a discrete community concept may not be appropriate for species-poor vegetation.

Our initial intention was to update previous vegetation classifications, but the plot data could not robustly be divided into the previously mapped five vegetation units (Smith & Mucina 2006) or into the plant communities suggested in earlier classifications (Huntley 1971; Gremmen 1981; Smith & Steenkamp 2001). Previous classifications used various methods to classify the vegetation on MI, although all applied the discrete Clementian concept of hierarchical plant communities (Huntley 1971; Gremmen 1981; Smith & Steenkamp 2001). The first two classifications of MI were floristic and largely qualitative (Huntley 1971; Gremmen 1981). Smith & Steenkamp (2001) then defined 21 habitats in seven habitat complexes based on the main drivers of variation, such as moisture and biotic influence, found with ordination, rather than species occurrence. These previous classifications informed the MI vegetation map that delineated five vegetation units (Smith & Mucina 2006). We expected to find similar groupings in our data despite using a different methodology since the previous classifications were consistent with each other. However, we found weak substantiation for a floristic community classification with all ISAs having low fidelity, which is a key metric under the Braun-Blanquet approach. Indeed, if ecologists require discrete communities for management on MI, incorporating the full range of abiotic factors to which species are known to respond, such as wind (Momberg et al. 2021a) or soil chemistry (Cramer et al. 2022), may need to be included in the classification.

Our inability to find previously identified communities in the current classification, may be because the previous research did not formally describe the cluster analysis choices in detail or validate the classification (Gremmen 1981; Smith & Steenkamp 2001). The justification for a discontinuous view of the vegetation was not described and, as was common in classification research at the time (Lötter et al. 2013), the classification was not methodologically or conceptually specified at the detail necessary to be reproduceable. Therefore, the previously described communities or habitats will likely not be suitable for tracking vegetation change, as they are not objectively reproducible. While expert opinion is invaluable in interpreting classifications, the formal testing of the effectiveness of classifications with various internal and external measures is an essential step that should be reported. Therefore, cluster validation is recommended to improve the quality of the results and increase confidence (Handle et al. 2005). Providing detailed justification for methodological choices in classification research may aid comparisons between classifications and help future researchers in their analytical decision-making.

A key limitation in the present study is that bryophyte species were not included, unlike Gremmen (1981) who identified all bryophyte species and Smith & Steenkamp (2001) who included some plant guilds of non-vascular plants. The taxonomic bias towards vascular plant species may have overlooked a substantial part of the vegetation. Nevertheless, regardless of bryophyte species exclusion, vascular plant species were still expected to indicate previously identified communities, as most communities had at least one diagnostic vascular plant species or guild (Gremmen 1981; Smith & Steenkamp 2001) and communities dominated by vascular plant species were predicted to become more important (at the expense of bryophytes) in the vegetation as a whole (Smith & Steenkamp 1990).

Another possible reason for the inability to classify discrete communities, is that the vegetation may have changed rapidly since the previous classifications were formulated, perhaps resulting in species reorganisation and novel associations due to climate change (le Roux & McGeoch 2008a; Raath-Krüger et al. 2019), as well as an increase in mouse populations due to the eradication of cats (Smith & Steenkamp 1990; Smith et al. 2001; Smith & Steenkamp 2001, McClelland et al. 2018). The previous classifications' fieldwork was conducted at times with much smaller mouse populations, as cats were still present (Huntley 1971; Gremmen 1981) and/or recently eradicated (Smith & Steenkamp 2001), which together with climate change has increased peak mouse densities by 430% from 1979-1980 to 2008-2011 (McClelland et al. 2018). While we cannot definitely establish whether these changes are a cause of the inability to classify discrete communities, sub-Antarctic vegetation has changed rapidly in recent decades, including changes in plant species distributions (Raath-Krüger et al. 2019), community reorganisation (le Roux & McGeoch 2008b), changes in phenology (March-Salas & Pertierra 2020) and the collapse of an entire ecosystem (Bergstrom et al. 2015). There is thus a possibility that the vegetation has reorganised or become transitional between previously described communities, as was predicted by the authors of previous classifications (Smith & Steenkamp 1990; Smith et al. 2001; Smith & Steenkamp 2001), leading to more continuous vegetation as species expanded their ranges across the island in response to the changes in climate (le Roux & McGeoch 2008b).

In this study, the strongest clustering was for two or three clusters. Here, we interpret the three clusters and attempt to relate them to earlier vegetation descriptions that applied a Clementian view of vegetation variation (Smith & Steenkamp 2001). From the ISA of three clusters, the first is indicated by the "specialist" species (see le Roux et al. 2013) on the coast (labelled "Coastal zone" in Fig. 7). In the coastal zone, either the biotic nutrient input by seals and seabirds, or saltspray created by rough seas on the high cliffs, increases the nutrient content of soils (Smith & Steenkamp 2001) and thus creates conditions for species with narrow ecological amplitude to occur. *Crassula moschata* for instance, only occurs where there is high saltspray and thrive in coastal areas where many generalist species cannot (le Roux & McGeoch 2008b). *Poa annua, L. plumosa, P. cookii, C. antartica* and *M. polymorpha* also occur in the coastal zone in areas with biotic nutrient input (Smith and Steenkamp 2001). The three most widespread alien plant species are also common here (le Roux et al. 2013). Similarly, in previous classifications, the coastal vegetation was very strongly distinguished as the cluster that differed from all other vegetation (Gremmen 1981; Smith & Steenkamp 2001). The next cluster (labelled "Inland vegetation" in Fig. 7), is only indicated here by the fern *A. penna-marina* which is widespread and abundant across the lowlands of the island and occurs occasionally at higher elevations. It is the dominant species on inland slopes and could be related to the "Slope" complex of previous classifications (Smith & Steenkamp 2001). The third cluster (labelled "Fellfield" in Fig. 7) includes sites with low vegetation cover (i.e., high rock cover), as the only indicators were lichens and *N. crassior* which is a small fern that grows between rock crevices. Despite this attempt to identify clusters, interpreting these as discrete units is misleading because there were no strong grounds for this based on floristic composition, because (a) the silhouette widths and Dunn index were low for any number of clusters, (b) fidelity and specificity to optimal clusters were low and (c) the in-field descriptions of vegetation did not match well with the three-cluster classification.

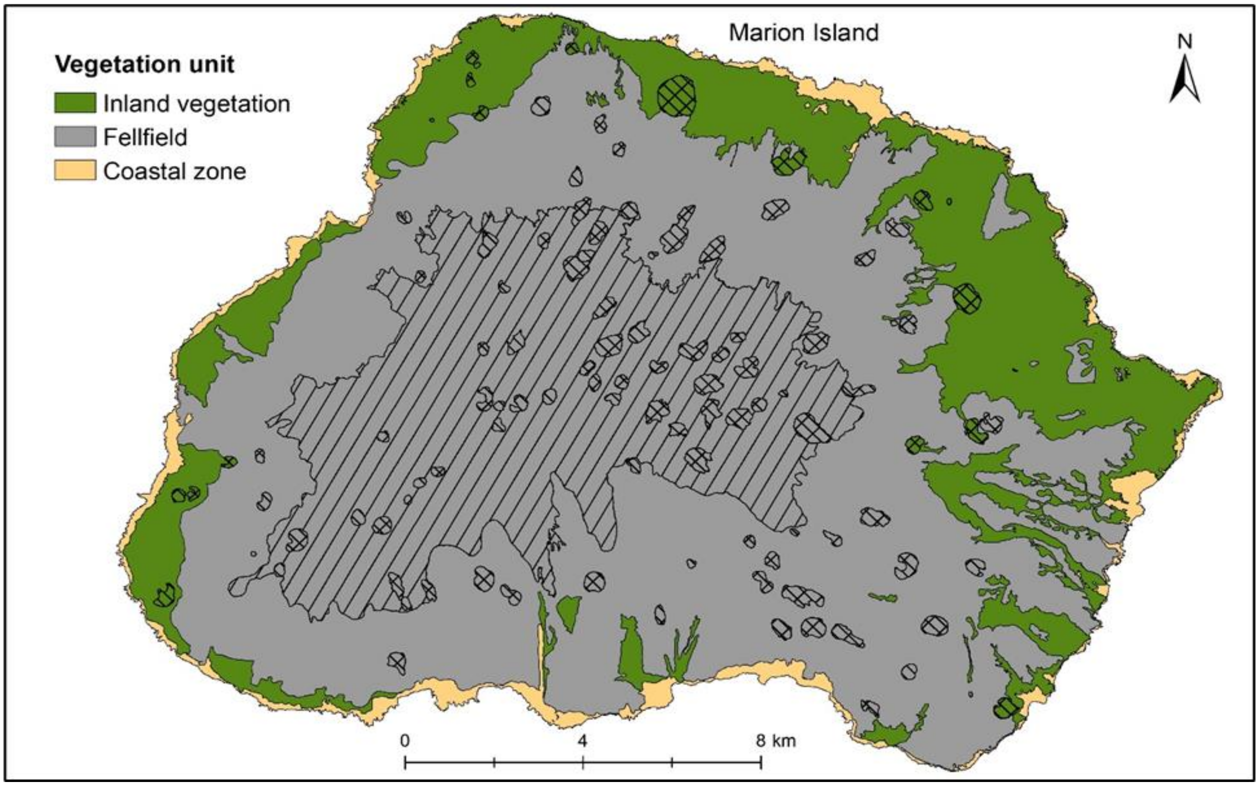


Figure 7. Updated vegetation map of Marion Island showing the three vegetation clusters from the classification in this study. Inland vegetation may correspond to previously mapped “Slope” and “Mire” complexes. Vegetation previously called “Polar Desert” and “Fellfield” were allocated to one cluster called “Fellfield” in the current classification due to lack of differentiation by indicator species. The area mapped in the centre of the map with diagonal lines is near 100% bare rock, which would indicate “Polar Desert”. The coastal zone was clearly separated in the classification by specialist species that only occur along the coast. Cinder cones did not form a vegetation unit but are conspicuous geological features in the landscape with little vegetation and are indicated by crossed lines. The updated map was created with the assumption that the original Smith & Mucina (2006) vegetation map was accurate for their classification.

The sub-Antarctic islands have a relatively recent origin (Rudolph et al. 2020). There have been three glaciations in the last 300 000 years on MI, with the last glaciation reaching a maximum extent around 34 500 years ago, and no evidence of glaciation during the Holocene (Rudolph et al. 2020). Biological refugia, which allowed species to persist, most likely occurred in low lying areas (Rudolph et al. 2020). Marion Island’s age and glaciation history, coupled with extreme isolation from continental species pools, has thus resulted in a taxonomically and functionally depauperate system (Smith & Mucina 2006). Environments with low species richness and turnover do not conform to a methodology that relies on diagnostic species. This is because the vegetation on MI has a high percentage of shared species across the island, and their occurrence does not differentiate between sites, except perhaps along the coast. In older environments (such as fynbos vegetation in South Africa) that have been stable for millennia and that have contained continental refugia during periods of glaciation (Verboom et al. 2009), community-level associations may be more apparent, and thus changes more easily monitored.

No comprehensive studies have been published that differentiate criteria for community *vs.* continuum approaches, or under which conditions either are appropriate (Austin 2013). However, our results align more with the continuum theory where vegetation is viewed as the outcome of individualistic species responses to their environment and to each other (Curtis & McIntosh 1951; Palmer & White 1994). Austin (2013) suggested that the continuum concept is preferred in vegetation-environment investigation. Since the vegetation on MI is closely coupled with the harsh abiotic conditions (le Roux & McGeoch 2008c; Cramer et al. 2022), a continuum view may better represent the vegetation variation. Indeed, species on MI do respond independently to abiotic conditions (Momberg et al. 2021b; Cramer et al. 2022), biotic interactions (Raath-Krüger et al. 2019) and disturbance (Phiri et al. 2009). The individual responses may vary along environmental gradients, such as the change in vegetation structure along an elevation gradient (le Roux & McGeoch 2008c). For example, *A. selago,* is a keystone generalist cushion plant species that occurs at low and high elevations, but at different densities (i.e., the structure differs; Phiri et al. 2009). At high elevations, in low densities, *A. selago* facilitates other generalist species that cannot necessarily survive without the protection of cushion plants (Raath-Krüger et al. 2019). Therefore, while species distributions may overlap at high and low elevations, each responds differently to abiotic conditions and biotic interactions (le Roux & McGeoch 2008b). The recent rapid change in climate on MI has also altered the distribution of (Raath-Krüger et al. 2019) and relationships between vascular species with some ranges expanding and others retracting (le Roux & McGeoch 2008b). This suggests that individual plant species may respond variably to climate change and biotic disturbance (Raath-Krüger et al. 2019; Cramer et al. 2022).

Despite the acknowledged difficulty in using species fidelity to classify vegetation into communities in cold-temperate (Huntley 1971; Gremmen 1981), species-poor environments (Landucci et al. 2015), the vegetation on MI continues to be discretely defined at the community-level, perhaps in order to adhere to the European standard (Braun-Blanquet 1932; Mucina et al. 2016). The discrete community concept was originally predominantly used to classify broad-scale representative stands in environments with sharp compositional boundaries that have high turnover and species fidelity to differentiate communities (Pavão et al. 2019). However, the unit for monitoring vegetation in species-poor environments should not rely on assemblages of species, but rather individual species, as shown to be more suitable on Macquarie Island (Bricher et al. 2013). Species distribution models (Elith & Leathwick

2009; Poggiato et al. 2021) could be more promising for differentiating and monitoring vegetation in environments with few vascular plant species that respond individualistically to abiotic conditions, as it predicts species distributions based on their environmental niches (Cramer et al. 2022).

Conclusion

Despite testing a range of clustering and validation methods for MI vegetation, there was no solution that could reliably separate clusters, suggesting that the traditional discrete community view of vegetation may not be appropriate in species-poor and/or young environments. The marine and terrestrial ecosystems of the sub-Antarctic have been identified as core areas to understand the rapid climate change that is occurring in the region (Ansorge et al. 2017). In this region, permanent plots to track individual changes in species occurrence and abundance, including bryophytes, across the structural vegetation gradient will likely be more effective to monitor and easily detect real world change than tracking hard to define plant “communities”. Future research should thus focus on the continuous variation in individual species distributions along key environmental gradients, rather than viewing vegetation as discontinuous communities.

References

Addicott, E., Laurance, S., Lyons, M., Butler, D., & Neldner, J. 2018. When rare species are not important: linking plot-based vegetation classifications and landscape-scale mapping in Australian savanna vegetation. *Community Ecology* 19: 67–76.

Aho, K., Roberts, D.W., & Weaver, T. 2008. Using geometric and non-geometric internal evaluators to compare eight vegetation classification methods. *Journal of Vegetation Science* 19: 549-U13.

Ansorge, I.J., Skelton, P., Bekker, A., de Bruyn, P.J.N., Butterworth, D., Cilliers, P. et al. 2017. Exploring South Africa's southern frontier: A 20-year vision for polar research through the South African National Antarctic Programme. *South African Journal of Science* 113: 11–17.

Austin, M.P. 2013. Vegetation and environment: discontinuities and continuities. In: van der Maarel, E. (Eds), pp. 52-84, Vegetation Ecology. Blackwell Publishing, Oxford, UK.

Austin, M.P., & Smith, T. 1989. A new model for the continuum concept. *Vegetatio* 83: 35–47.

Bergstrom, D.M., Bricher, P.K., Raymond, B., Terauds, A., Doley, D., McGeoch, M.A. et al. 2015. Rapid collapse of a sub-Antarctic alpine ecosystem: the role of climate and pathogens. *Journal of Applied Ecology* 52: 774–783.

Bergstrom, D.M., Bricher, P.K., Raymond, B., Terauds, A., Doley, D., McGeoch, M.A., Whinam, J., Glen, M., Yuan, Z., Kiefer, K., Shaw, J.D., Bramely-Alves, J., Rudman, T., Mohammed, C., Lucieer, A., Visoiu, M., van Vuuren, B.J., & Ball, M.C. 2015. Rapid collapse of a sub-Antarctic alpine ecosystem: the role of climate and pathogens. *Journal of Applied Ecology* 52: 774–783.

Bricher, P. 2012. Methods for mapping the tundra vegetation of sub-Antarctic Macquarie Island. PhD thesis, University of Tasmania, Tasmania.

Bricher PK, Lucieer A, Shaw J, Terauds A, Bergstrom DM. 2013. Mapping sub-Antarctic cushion plants using random forests to combine very high resolution satellite imagery and terrain modelling. *PLOS ONE* 8: e72093.

Braun-Blanquet, J. 1932. Plant sociology: the study of plant communities. McGraw-Hill, New York, USA.

Brock, G., Pihur, V., Susmita, D., & Somnath, D. 2008. clValid: An R Package for Cluster Validation. *Journal of Statistical Software* 25: 1–22.

Brown, L.R., & Bredenkamp, G.J. 2018. An overview of the vegetation classification approach in South Africa. *Phytocoenologia* 48: 163–170.

Brown, L.R., du Preez, P.J., Bezuidenhout, H., Bredenkamp, G.J., Mostert, T.H.C., & Collins, N.B. 2013. Guidelines for phytosociological classifications and descriptions of vegetation in southern Africa. *Koedoe* 55.

Charrad M., Ghazzali N., Boiteau V., Niknafs A. 2014. NbClust: an R package for determining the relevant number of clusters in a data set. *Journal of Statistical Software* 61: 1-36.

De Cáceres, M., Chytrý, M., Agrillo, E., Attorre, F., Botta-Dukát, Z., Capelo, J. et al. 2015. A comparative framework for broad-scale plot-based vegetation classification. *Applied Vegetation Science* 18: 543–560.

De Cáceres, M., Franklin, S.B., Hunter, J.T., Landucci, F., Dengler, J., & Roberts, D.W. 2018. Global overview of plot-based vegetation classification approaches. *Phytocoenologia* 48: 101–112.

De Cáceres, M., & Legendre, P. 2009. Associations between species and groups of sites: indices and statistical inference. *Ecology* 90: 3566–3574.

Dunn, J.C. 1974. Well-separated clusters and optimal fuzzy partitions. *Journal of Cybernetics* 4: 95-104.

Chau, J.H., Mtsi, N.I.S., Münbergova, Z., Greve, M., le Roux, P.C., Mairal, M., le Roux, J.J., Dorrington, R.A., & van Vuuren, B. 2020. An update on the indigenous vascular flora of sub-Antarctic Marion Island: taxonomic changes, sequences for DNA barcode loci, and genome size data. *Polar Biology* 43: 1817–1828.

Cramer, M.D., Hedding, D., Greve, M., Midgley, G.F., & Ripley, B.S. 2022. Plant specialisation may limit climate-induced vegetation change to within topographic and edaphic niches on a sub-Antarctic island. *Functional Ecology* 36: 2636–2648.

Curtis, J., & McIntosh, R. 1951. An upland forest continuum in the prairie-forest border region of wisconsin. *Ecology* 31: 476–796.

Daubenmire, R. F. 1959. Canopy coverage method of vegetation analysis. *Northwest Science* 33: 43–64.

Dilley, B.J., Schoombie, S., Schoombie, J., & Ryan, P.G. 2016. `Scalping' of albatross fledglings by introduced mice spreads rapidly at Marion Island. *Antarctic Science* 28: 73–80.

Dufrêne, M., & Legendre, P. 1997. Species assemblages and indicator species: The need for a flexible asymmetrical approach. *Ecological Monographs* 67: 345–366.

Elith, J., & Leathwick, J.R. 2009. Species distribution models: ecological explanation and prediction across space and time. *Annual Review of Ecology, Evolution and Systematics* 40: 677–697.

Feilhauer, H., Zlinszky, A., Kania, A., Foody, G.M., Doktor, D., Lausch, A., & Schmidtlein, S. 2020. Let your maps be fuzzy!-Class probabilities and floristic gradients as alternatives to crisp mapping for remote sensing of vegetation. *Remote Sensing in Ecology and Conservation* 7: 292–305.

Fitzgerald, N.B., Kirkpatrick, J.B., & Scott, J.J. 2021. Rephotography, permanent plots and remote sensing data provide varying insights on vegetation change on subantarctic Macquarie Island, 1980-2015. *Austral Ecology* 46: 762–775.

Flynt, A., & Dean, N. 2016. A survey of popular R packages for cluster analysis. *Journal of Educational* *and Behavioral Statistics* 41: 205–225.

Gleason, H.A. 1927. The individualistic concept of the plant association. *Bulletin of the Torrey Botanical Club* 53: 7–26.

Gremmen, N.J.M. 1981. The vegetation of the Subantarctic islands Marion and Prince Edward. Dr W. Junk Publishers, The Hague, Netherlands.

Greve, M., Mathakutha, R., Steyn, C., & Chown, S.L. 2017. Terrestrial invasions on sub-Antarctic Marion and Prince Edward Islands. *Bothalia* 47: a2143.

Handl, J., Knowles, J., & Kell, D.B. 2005. Computational cluster validation in post-genomic data analysis. *Bioinformatics* 21: 3201–3212.

Huntley, B. 1971. Vegetation. In E. M. Van Zinderen Bakker (Ed.), *Marion and Prince Edward Islands,* pp. 98-160, A.A. Balkema, Cape Town, South Africa.

Landucci, F., Tichý, L., Šumberová, K., & Chytrý, M. 2015. Formalized classification of species-poor vegetation: a proposal of a consistent protocol for aquatic vegetation. *Journal of Vegetation Science* 26: 791–803.

Lengyel, A., Roberts, D.W., & Botta-Dukát, Z. 2021. Comparison of silhouette-based reallocation methods for vegetation classification. *Journal of Vegetation Science* 32: e12984.

Lortie, C.J., Brooker, R.W., Choler, P., Kikvidze, Z., Michalet, R., Pugnaire, F.I., & Callaway, R.M. 2004. Rethinking plant community theory. *Oikos* 107: 433–438.

Lötter, M.., Mucina, L., & Witkowski, E.T.F. 2013. The classification conundrum: species fidelity as leading criterion in search of a rigorous method to classify a complex forest data set. *Community Ecology* 14: 121–132.

Maechler, M., Rousseeuw, P., Struyf, A., Hubert, M., & Hornik, K. 2019. cluster: Cluster Analysis Basics and Extensions. Available at https://cran.r-project.org/web/packages/cluster. [Accessed 17 July 2022].

March-Salas, M., & Pertierra, L.R. 2020. Warmer and less variable temperatures favour an accelerated plant phenology of two invasive weeds across sub-Antarctic Macquarie Island. *Austral Ecology* 45: 572–585.

McClelland, G.T.W., Altwegg, R., Van Aarde, R.J., Ferreira, S., Burger, A.E., & Chown, S.L. 2018. Climate change leads to increasing population density and impacts of a key island invader. *Ecological Applications* 28: 212–224.

McDougall, I., Verwoerd, W., & Chevallier, L. 2001. K-Ar geochronology of Marion Island, Southern Ocean. *Geological Magazine* 138: 1–17.

Momberg, M., Hedding, D.W., Luoto, M., & le Roux, P.C. 2021a. Exposing wind stress as a driver of fine-scale variation in plant communities. *Journal of Ecology* 109: 2121–2136.

Momberg, M., Hedding, D.W., Luoto, M., & le Roux, P.C. 2021b. Species differ in their responses to wind: the underexplored link between species fine-scale occurrences and variation in wind stress. *Journal of Vegetation Science* 32: e13093.

Mucina, L. 1997. Classification of vegetation: Past, present and future. *Journal of Vegetation Science* 8: 751–760.

Mucina, L., Bültmann, H., Dierßen, K., Theurillat, J.-P., Raus, T., Čarni, A. et al. 2016. Vegetation of Europe: hierarchical floristic classification system of vascular plant, bryophyte, lichen, and algal communities. *Applied Vegetation Science* 19: 3–264.

Murtagh, F., & Legendre, P. 2014. Ward's hierarchical agglomerative clustering method: which algorithms implement ward's criterion? *Journal of Classification* 31: 274–295.

Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D. et al. 2020. vegan: community ecology package. Available at https://CRAN-R.project.org/web/packages/vegan. [Accessed 17 July 2022].

Øvstedal, D.O., & Gremmen, N.J.M. 2001. The lichens of Marion and Prince Edward Islands. *South African Journal of Botany* 67: 552–572.

Pakgohar, N., Rad, J.E., Gholami, G., Alijanpour, A., & Roberts, D.W. 2021. A comparative study of hard clustering algorithms for vegetation data. *Journal of Vegetation Science* 32: 13042.

Palmer, M.W., & White, P.S. 1994. On the existence of ecological communities. *Journal of Vegetation Science* 5: 279–282.

Pavão, D.C., Elias, R.B., & Silva, L. 2019. Comparison of discrete and continuum community models: Insights from numerical ecology and Bayesian methods applied to Azorean plant communities. *Ecological modelling* 402: 93–106.

Phiri, E.E., Mcgeoch, M.A., & Chown, S.L. 2009. Spatial variation in structural damage to a keystone plant species in the sub-Antarctic: interactions between *Azorella selago* and invasive house mice. *Antarctic Science* 21: 189–196.

Poggiato, G., Münkemüller, T., Bystrova, D., Arbel, J., Clark, J.S., & Thuiller, W. 2021. On the interpretations of joint modelling in community ecology. *Trends in Ecology and Evolution* 36: 391–401.

Preston, G.R., Dilley, B.J., Cooper, J., Beaumont, J., Chauke, L.F., Chown, S.L., Devanunthan, N., Dopolo, M., Fikizolo, L., Heine, J., Henderson, S., Jacobs, C.A., Johnson, F., Kelly, J., Makhado, A.B., Marais, C., Maroga, J., Mayekiso, M., McClelland, G., Mphepya, J., Muir, D., Ngcaba, N., Ngcobo, N., Parkes, J.P., Paulsen, F., Schoombie, S., Springer, K., Stringer, C., Valentine, H., Wanless, R.M., & Ryan, P.G. 2019. South Africa works towards eradicating introduced house mice from sub-Antarctic Marion Island: the largest island yet attempted for mice. In Veitch, C.R., Clout, M.N., Martin, A.R., Russell, J.C., West, C. (Eds.), *Island invasives: scaling up to meet the challenge,* pp. 40–46. IUCN, Gland, Switzerland.

Raath-Krüger, M.J., McGeoch, M.A., Schöb, C., Greve, M., & le Roux, P.C. 2019. Positive plant-plant interactions expand the upper distributional limits of some vascular plant species. *Ecosphere* 10: e02820.

Rousseeuw, P.J. 1987. Silhouettes - A graphical aid to the interpretation and validation of cluster-analysis. *Journal of Computational and Applied Mathematics* 20: 53–65.

le Roux, P.C., & McGeoch, M.A. 2008a. Changes in climate extremes, variability and signature on sub-Antarctic Marion Island. *Climatic Change* 86: 309–329.

le Roux, P.C., & McGeoch, M.A. 2008b. Rapid range expansion and community reorganization in response to warming. *Global Change Biology* 14: 2950-2962.

le Roux, P.C., & McGeoch, M.A. 2008c. Spatial variation in plant interactions across a severity gradient in the sub-Antarctic. *Oecologia* 155: 831–844.

le Roux, P.C., Ramaswiela, T., Kalwij, J.M., Shaw, J.D., Ryan, P.G., Treasure, A.M. et al. 2013. Human activities, propagule pressure and alien plants in the sub-Antarctic: Tests of generalities and evidence in support of management. *Biological Conservation* 161: 18–27.

Rudolph, E.M., Hedding, D.W., Fabel, D., Hodgson, D.A., Gheorghiu, D.M., Shanks, R., & Nel, W. 2020. Early glacial maximum and deglaciation at sub-Antarctic Marion Island from cosmogenic Cl-36 exposure dating. *Quaternary Science Reviews* 231: 106208.

Ryan, P.G., Smith, V.R., & Gremmen, N.J.M. 2003. The distribution and spread of alien vascular plants on Prince Edward Island. African Journal of Marine Science 25: 555–562.

Saha, S., & Bandyopadhyay, S. 2012. Some connectivity based cluster validity indices. *Applied Soft Computing 12*: 1555–1565.

Scott, D. 1995. Vegetation - a mosaic of discrete communities, or a continuum. *New Zealand Journal of Ecology* 19: 47–52.

Smith, V.R., Avenant, N., & Chown, S.L. 2002. The diet and impact of house mice on a sub-Antarctic island. *Polar Biology* 25: 703–715.

Smith, V.R., & Mucina, L. 2006. Vegetation of sub-Antarctic Marion and Prince Edward Islands. In: Mucina, L., Rutherford, M.C., & Powrie, L.W. (Eds.), Vegetation of South Africa, Lesotho and Swaziland, pp. 699–723. South African National Biodiversity Institute, Pretoria, South Africa.

Smith, V.R., & Steenkamp, M. 1990. Climatic change and its ecological implications at a subantarctic island. *Oecologia* 85: 14-24.

Smith, V.R., Steenkamp, M., & Gremmen, N.J.M. 2001. Terrestrial habitats on sub-Antarctic Marion Island: Their vegetation, edaphic attributes, distribution and response to climate change. *South African Journal of Botany* 67: 641–654.

van Staden, P.J., Bredenkamp, G.J., Bezuidenhout, H., & Brown, L.R. 2021. A reclassification and description of the Waterberg Mountain vegetation of the Marakele National Park, Limpopo province, South Africa. *Koedoe* 63: 1-16.

Tibshirani, R., Walther, G., & Hastie, T. 2001. Estimating the number of clusters in a data set via the gap statistic. *Journal of the Royal Statistical Society Series b-Statistical Methodology* 63: 411–423.

Tsakalos, J.L., Renton, M., Dobrowolski, M.P., Feoli, E., Macintyre, P.D., Veneklaas, E.J., & Mucina, L. 2018. Community patterns and environmental drivers in hyper-diverse Kwongan scrub vegetation of Western Australia. *Applied Vegetation Science* 21: 694–722.

Verboom, G.A., Archibald, J.K., Bakker, F.T., Bellstedt, D.U., Conrad, F., Dreyer, L.L. et al. 2009. Origin and diversification of the Greater Cape flora: Ancient species repository, hot-bed of recent radiation, or both? *Molecular Phylogenetics and Evolution* 51: 44–53.

Weaver, J., & Clements, F. 1929. *Plant Ecology*. McGraw-Hill Book Company, New York, USA.

Wiser, S.K., & De Cáceres Cáceres, M. 2013. Updating vegetation classifications: an example with New Zealand’s woody vegetation. *Journal of Vegetation Science* 24: 80–93.

Wolda, H. 1981. Similarity indices, sample sizes and diversity. *Oecologia* 50: 296–302.

Yang, D., Morrison, B.D., Hantson, W., Breen, A.L., McMahon, A., Li, Q. et al. (2021). Landscape-scale characterization of Arctic tundra vegetation composition, structure, and function with a multi-sensor unoccupied aerial system. *Environmental Research Letters* 16: 085005.

Appendix A

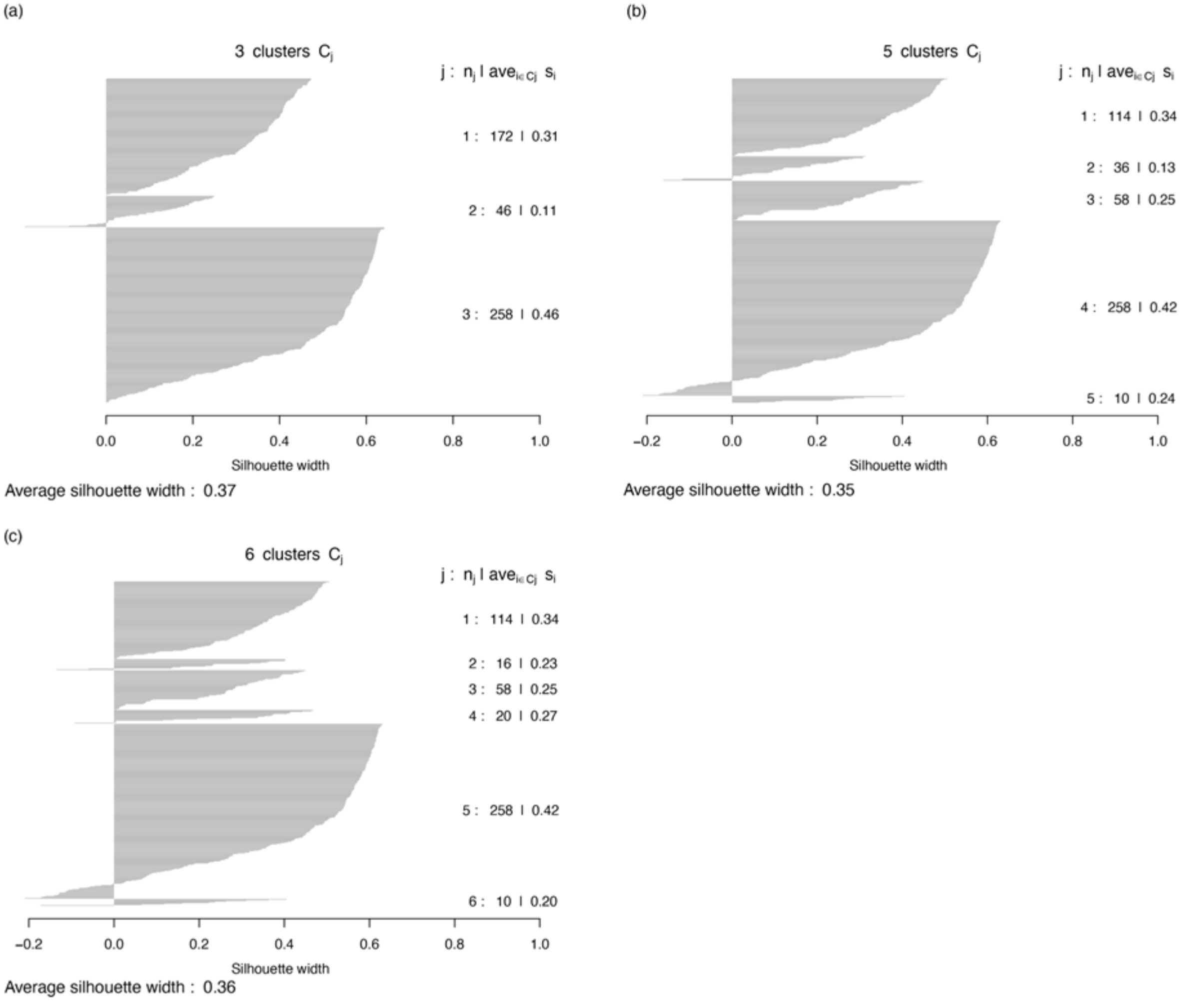


Figure A1. Average silhouette widths calculated for DIANA clustering in a) three groups, b) five groups and c) six groups. The number of clusters were chosen based on the two clustering solutions with highest Average Silhouette Width (ASW) and Dunn statistic, as well as the previously mapped five groups. Each grey horizontal line represents the Silhouette Width of a plot that was allocated to each cluster (j). The number of plots (n_j; n=476) allocated to each cluster and the ASW for each cluster (ave_{ieCiSi}) is shown on the right, as well as the overall average of the entire classification (shown below the graph). Large within-cluster ASW values indicate that plots within a cluster are compositionally similar. A large overall ASW for the entire classification indicates that clusters are well separated and compact. Negative silhouette values indicate plots might have been placed in the incorrect cluster. Ideally, the plots clustered within a group would all have high and similar silhouette widths, i.e., the grey lines would be uniform within a cluster. The overall average would also ideally be high in a well separated and compact grouping of a data set.

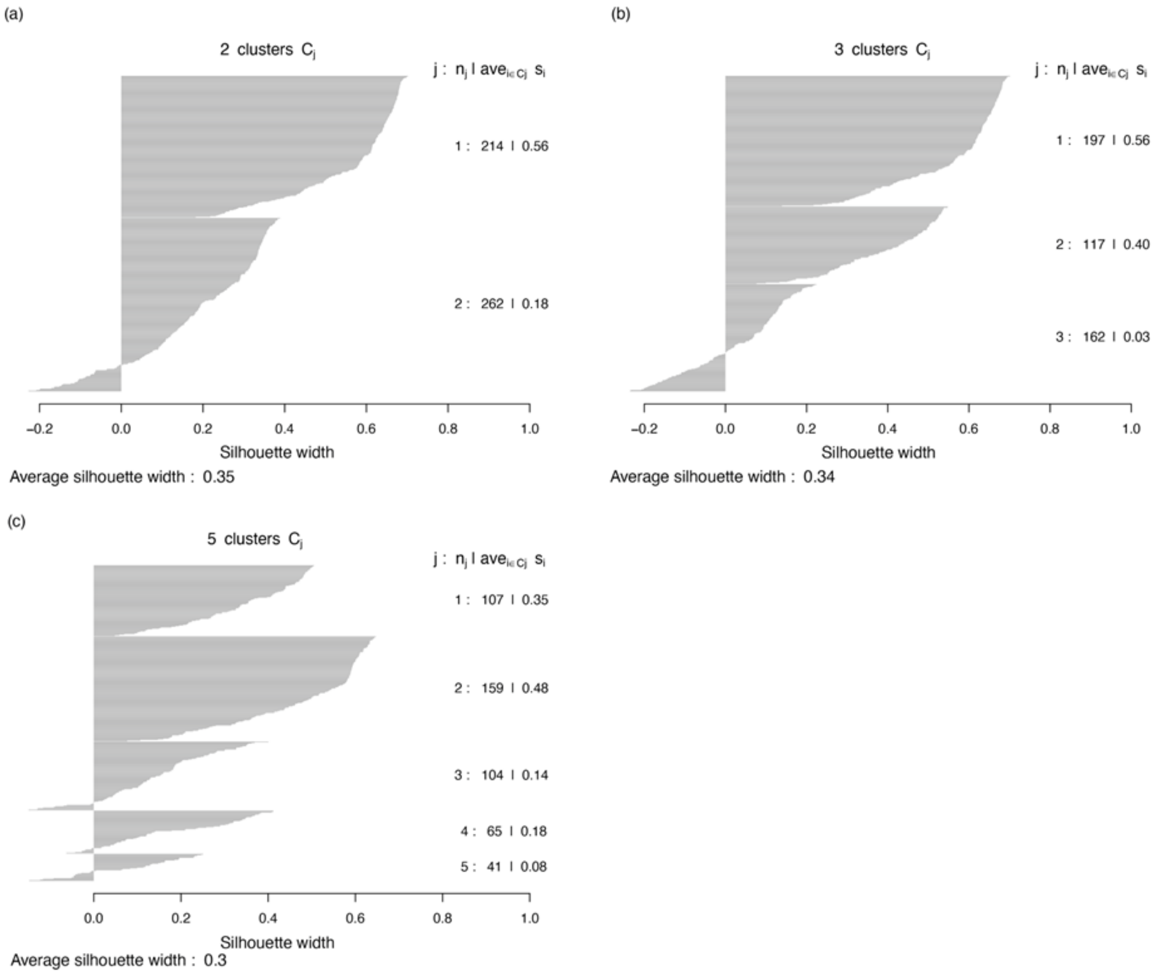


Figure A2. Average silhouette widths calculated for kmeans clustering in a) two, b) three and c) five groups. The number of clusters were chosen based on the two clustering solutions with highest Average Silhouette Width (ASW) and Dunn statistic, as well as the previously mapped five groups. Each grey horizontal line represents the Silhouette Width of a plot that was allocated to each cluster (j). The number of plots (n_j; n=476) allocated to each cluster and the ASW for each cluster (ave_{ieCiSi}) is shown on the right, as well as the overall average of the entire classification (shown below the graph). Large within-cluster ASW values indicate that plots within a cluster are compositionally similar. A large overall ASW for the entire classification indicates that clusters are well separated and compact. Negative silhouette values indicate plots might have been placed in the incorrect cluster. Ideally, the plots clustered within a group would all have high and similar silhouette widths, i.e., the grey lines would be uniform within a cluster. The overall average would also ideally be high in a well separated and compact grouping of a data set.

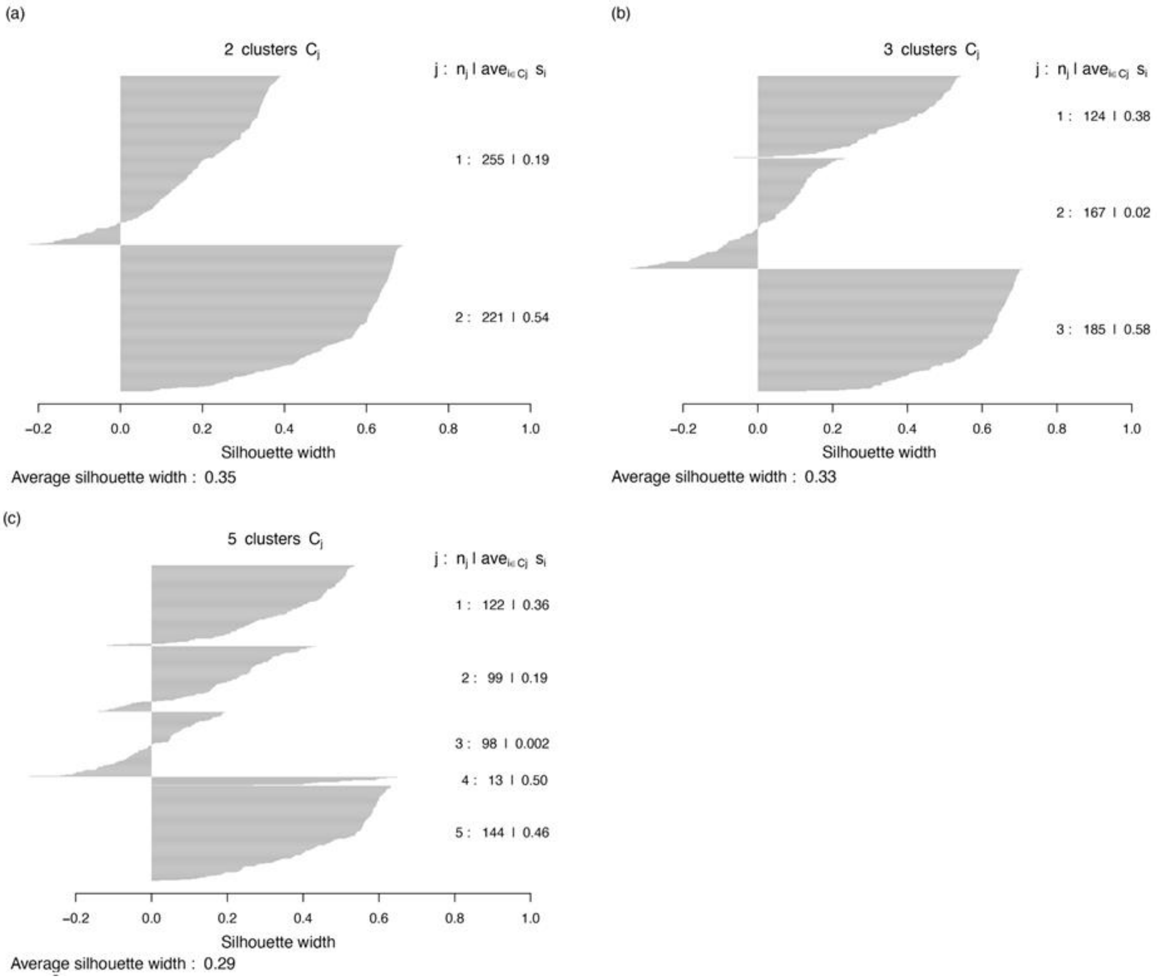


Figure A3. Average silhouette widths calculated for PAM clustering in a) two, b) three and c) five groups. The number of clusters were chosen based on the two clustering solutions with highest Average Silhouette Width (ASW) and Dunn statistic, as well as the previously mapped five groups. Each grey horizontal line represents the Silhouette Width of a plot that was allocated to each cluster (j). The number of plots (n_j; n=476) allocated to each cluster and the ASW for each cluster (ave_{ieCiSi}) is shown on the right, as well as the overall average of the entire classification (shown below the graph). Large within-cluster ASW values indicate that plots within a cluster are compositionally similar. A large overall ASW for the entire classification indicates that clusters are well separated and compact. Negative silhouette values indicate plots might have been placed in the incorrect cluster. Ideally, the plots clustered within a group would all have high and similar silhouette widths, i.e., the grey lines would be uniform within a cluster. The overall average would also ideally be high in a well separated and compact grouping of a data set.

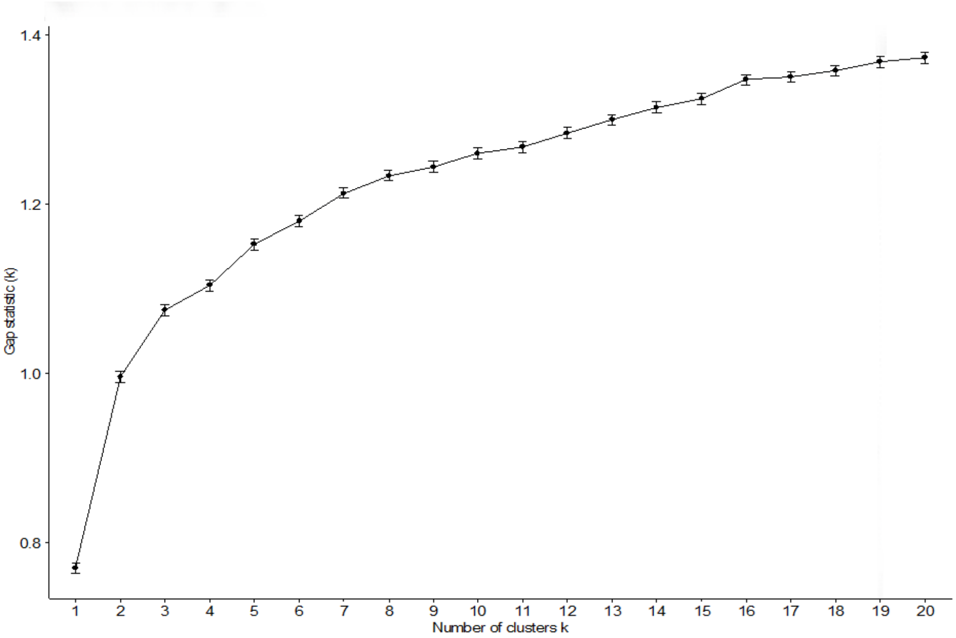


Figure A4. Gap statistic for Ward clustering for 1-20 clusters. The gap statistic compares within-cluster distance to a uniformly distributed null reference distribution with bootstrapping. The optimum cluster number is indicated where the gap curve reaches an inflection point and changes to a higher value.

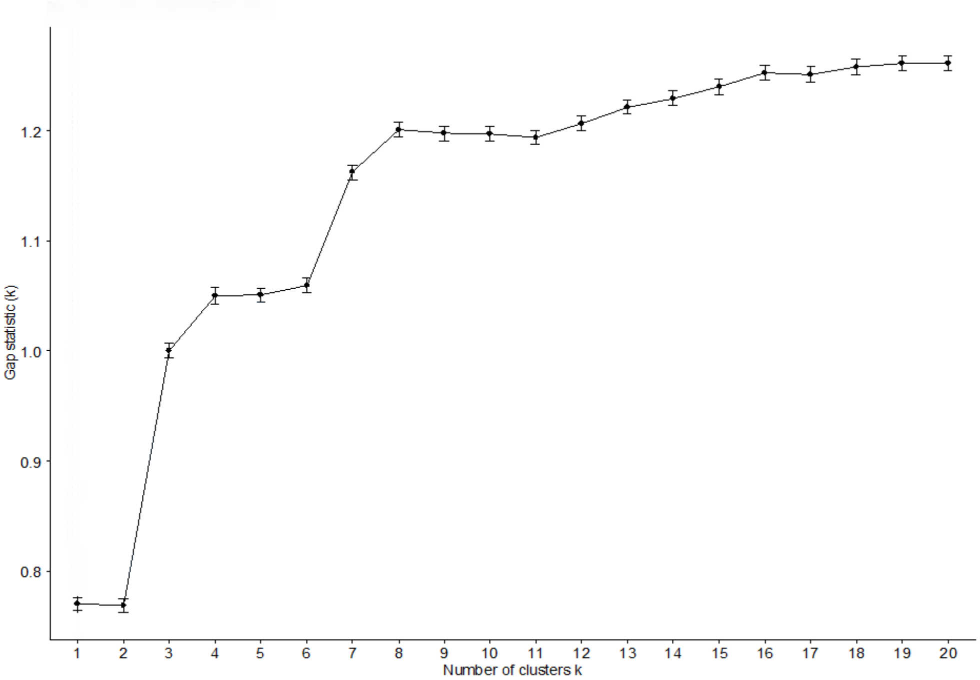


Figure A5. Gap statistic for DIANA clustering for 1-20 clusters. The gap statistic compares within-cluster distance to a uniformly distributed null reference distribution with bootstrapping. The optimum cluster number is indicated where the gap curve reaches an inflection point and changes to a higher value.

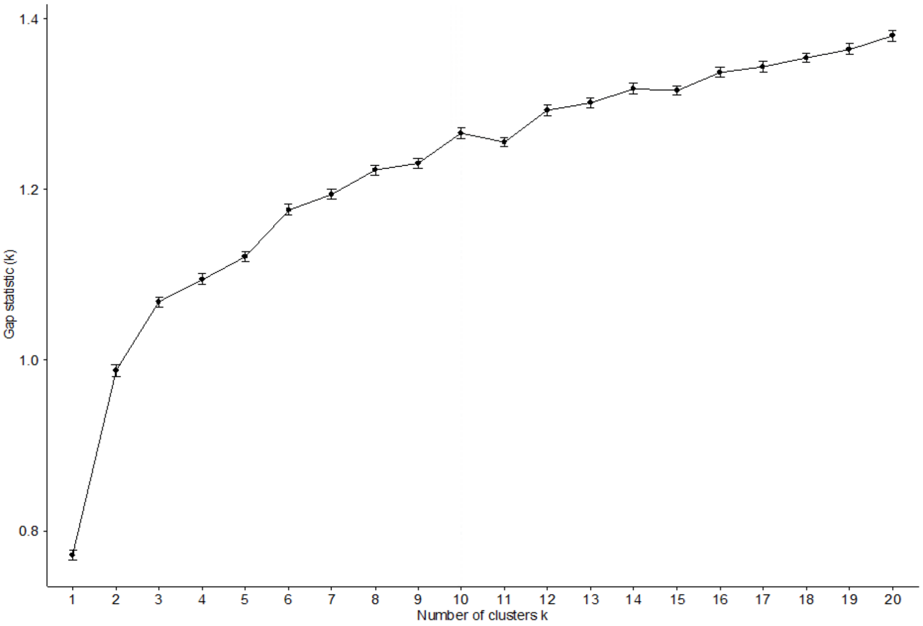


Figure A6. Gap statistic for kmeans clustering for 1-20 clusters. The gap statistic compares within-cluster distance to a uniformly distributed null reference distribution with bootstrapping. The optimum cluster number is indicated where the gap curve reaches an inflection point and changes to a higher value.

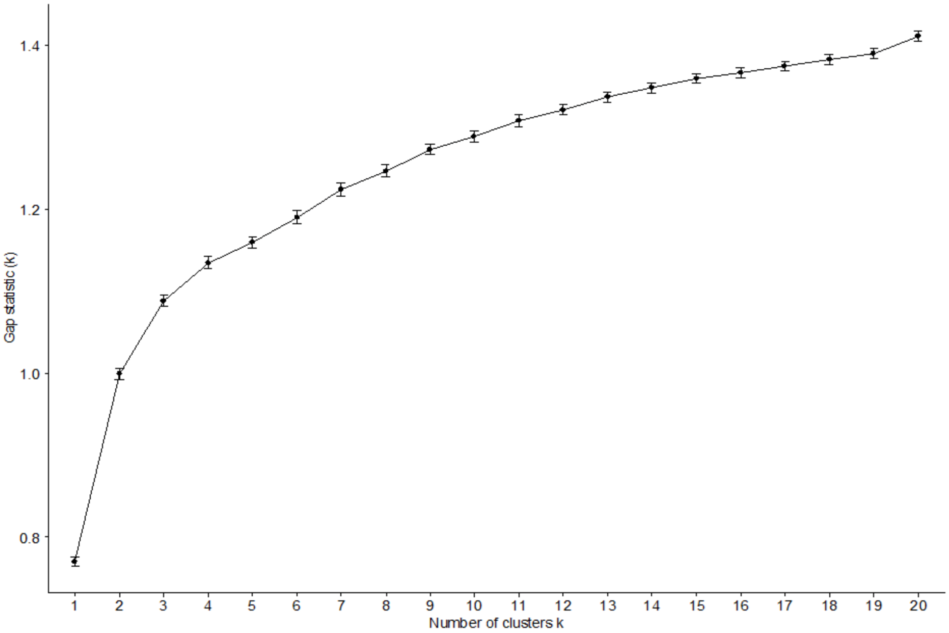


Figure A7. Gap statistic for PAM clustering for 1-20 clusters. The gap statistic compares within-cluster distance to a uniformly distributed null reference distribution with bootstrapping. The optimum cluster number is indicated where the gap curve reaches an inflection point and changes to a higher value.

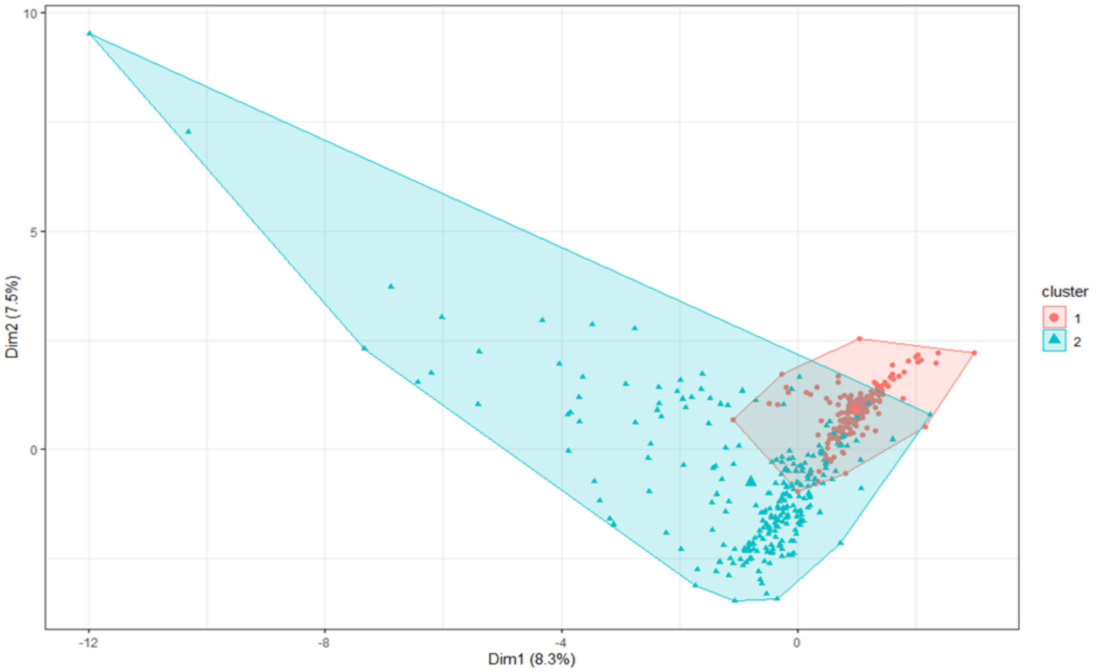


Figure A8. K-means two-cluster solution. Ideally, centroids should be well separated or compact.

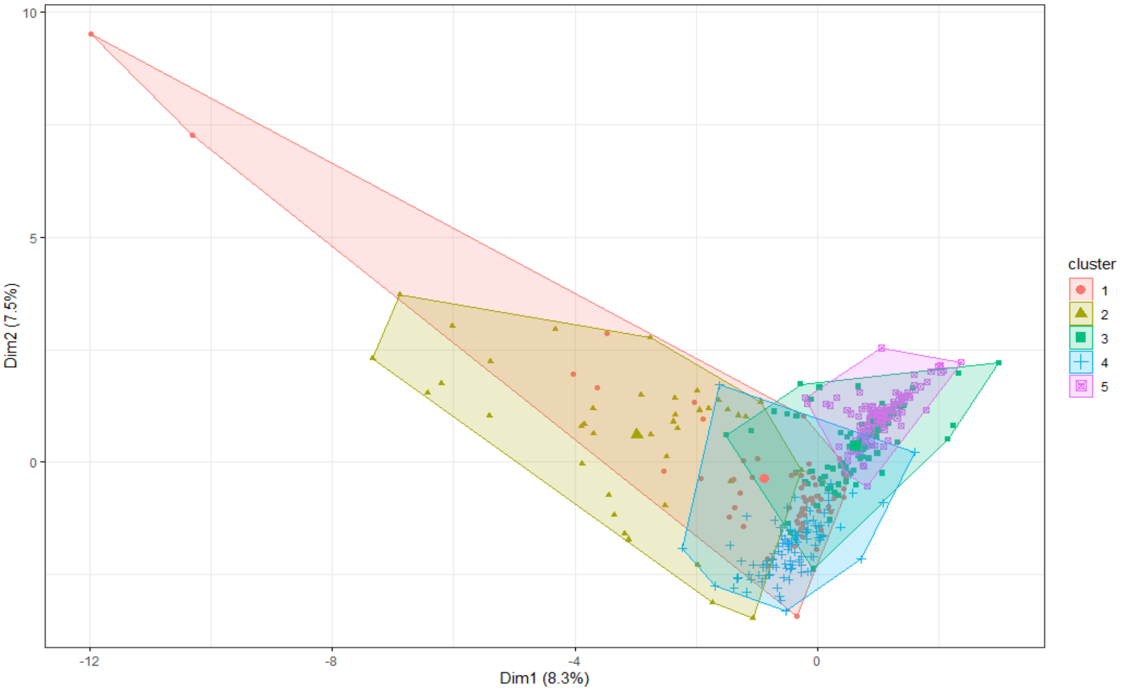


Figure A9. Kmeans five cluster solution. Ideally, centroids should be well separated or compact.

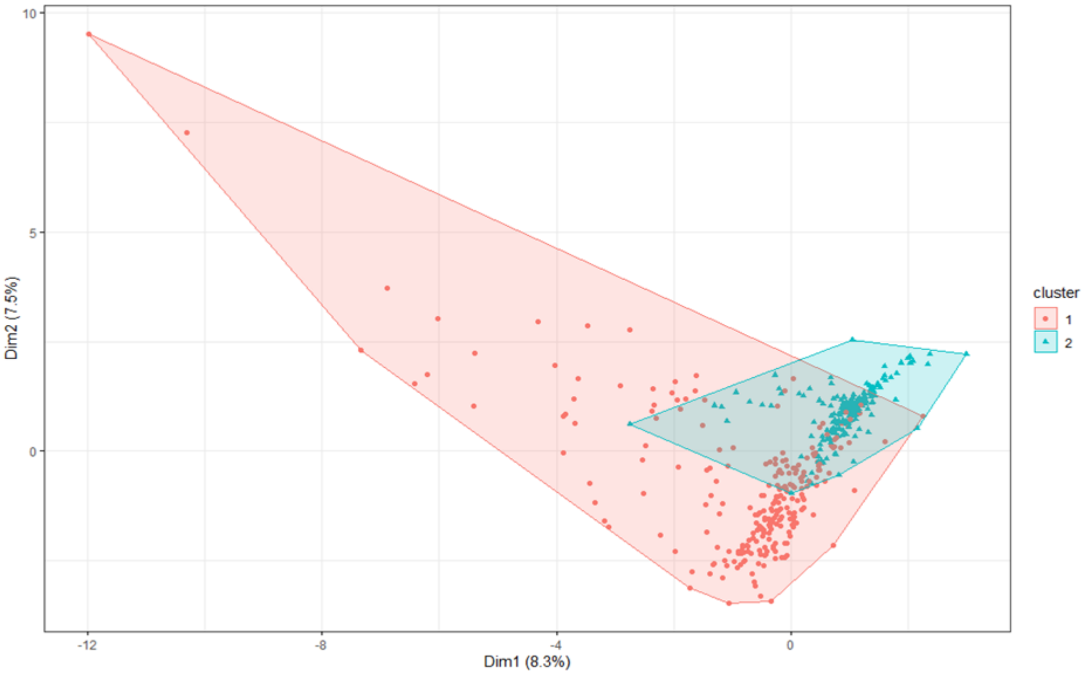


Figure A10. PAM two-cluster solution. Ideally, medoids should be well separated or compact.

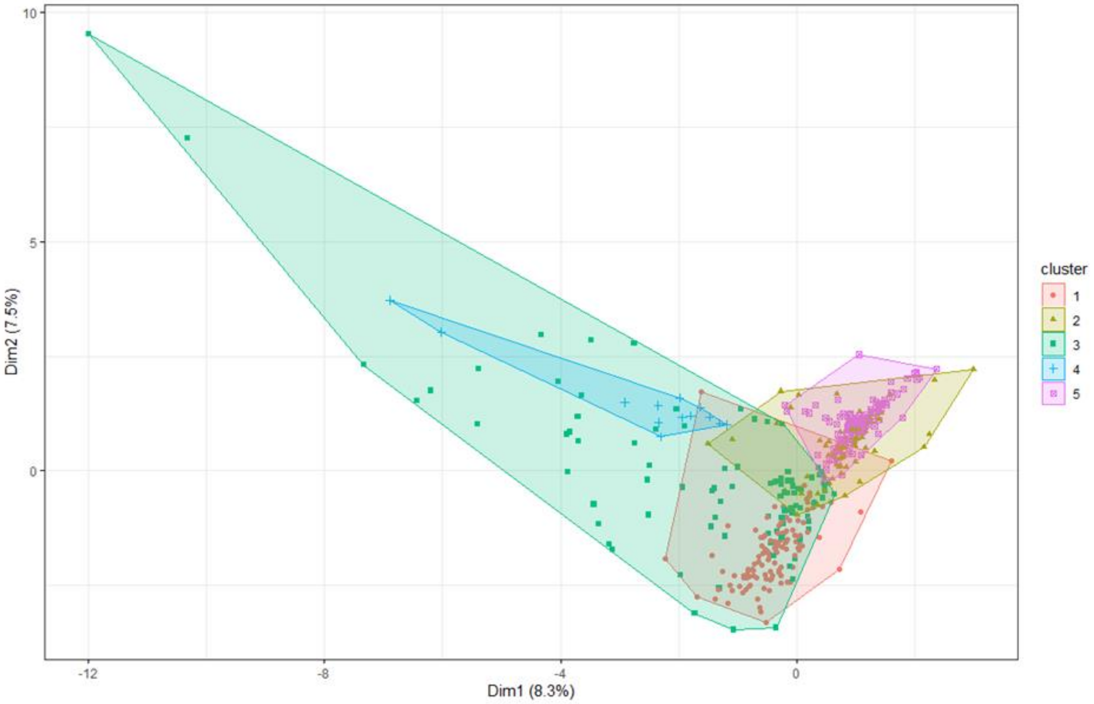


Figure A11. PAM five-cluster solution. Ideally, medoids should be well separated or compact.

Chapter 3

Long-term vegetation change (1965-2020) in response to rapid warming and drying in a sub-Antarctic tundra: evidence from repeat photography

Repeat photography fieldwork being conducted in fellfield vegetation that consists predominantly of *Azorella selago* cushion plants and *Polypogon magellanicus* epiphytic grasses, interspersed by smaller patches of the fern *Austroblechnum penna-marina* and bryophytes, visible in the bottom foreground.

Abstract

At high latitudes, anthropogenic climate change and invasive species particularly threaten biodiversity, often with antagonistic effects. Climate change not only impacts all native plant species directly by driving distribution and abundance of species, but indirectly through the influence on community dynamics and habitat suitability to invasive species. A key obstacle to quantifying vegetation change in the sub-Antarctic is the scarcity of cloud-free satellite imagery in a region with near-permanent cloud cover and lack of historical plot data. I thus quantified vegetation change on Marion Island in the sub-Antarctic between 1965 and 2020, using a repeat photography analysis and analysed the climate trends and invasive plant species cover changes over the same period. Total vegetation cover was significantly higher in 2020 than in 1965 in all habitats, other than in the coastal saltspray habitat, indicating an increase in overall biomass on the island. The more responsive "generalist" plant species, specifically the grass *Polypogon magellanicus* and fern *Austroblechnum penna-marina* have expanded across the island, whilst the more "specialised" plant species have not significantly changed in cover, with the exception of the mire graminoids which have decreased. MI has thus undergone significant vegetation change across most habitats in the last five decades, accompanied by aridification, an increase in mean air temperature, change in wind direction and wind speed. The three most widespread invasive plant species have also expanded their ranges, especially in biotic areas, and invasive mice have rapidly increased in abundance. The two key interactive drivers of vegetation change on MI are thus climate change and invasive species.

Introduction

The composition and structure of vegetation largely governs ecosystem function and thus vegetation change can significantly impact ecosystem function and result in loss of biodiversity (Nolan et al. 2018; Nunez et al. 2019). Drivers of vegetation change vary greatly across regions, with climate change (Nunez et al. 2019), invasive species (Bergstrom & Chown 1999), habitat loss (Skowno et al. 2021), land-use change (Hoffman et al. 2019) and increased CO_2 (Chen et al. 2011) being among the most significant drivers globally. At high latitudes, anthropogenic climate change (Bergstrom et al. 2015; Piao et al. 2020) and invasive species (Frenot et al. 2005; Shaw 2013) particularly threaten biodiversity, often with antagonistic effects. Changes in temperature or rainfall for example, not only impact all native plant species directly by driving distribution and abundance of species (Chen et al. 2011), but indirectly through the influence on community dynamics (Allan et al. 2013; Hoffmann et al. 2019) and habitat suitability to invasive species (Lee et al. 2017).

Most regions around the world have observed negative impacts of climate change, with high latitudes often experiencing disproportionate effects (Myers-Smith et al. 2011; Hoffmann et al. 2019). Warming is the predominant climate trend at high latitudes, with temperatures increasing faster than mid- and low-latitudes in recent decades (Hinzman et al. 2005; Myers-Smith et al. 2011; Xia et al. 2020), accompanied by drying in the southern high latitudes (Bergstrom & Chown 1999; le Roux & McGeoch 2008a). The implications for the indigenous biota that are adapted to the cold, humid conditions, may be severe. For instance, climate change has shifted species distributions (le Roux & McGeoch 2008b), altered species interactions (Allan et al. 2013; Hoffmann et al. 2019), and to a more severe extent, caused ecosystem collapse (Bergstrom et al. 2015) in southern high latitudes. Indeed, the islands in the sub-Antarctic are described as "sentinels of change" to study the impacts of climate change (Ansorge et al. 2017), as they are sensitive to changes in temperature and rainfall (le Roux & McGeoch 2008b). However, the impacts of climate change on vegetation in the sub-Antarctic (Hoffmann et al. 2019) and the southern hemisphere in general (Hoffman et al. 2019), are poorly understood.

The establishment and spread of invasive species has increased in the sub-Antarctic, likely exacerbated by a warming and drying climate (McClelland et al. 2018; Hoffmann et al. 2019), increasing the habitat suitability for invasive species due to the amelioration of the harsh climatic conditions in the sub-Antarctic. The islands in the sub-Antarctic are susceptible to the establishment of alien species (Shaw 2013), due to their geographical isolation distancing the islands from colonising populations, which may result in unfilled niches on islands (Russell et al. 2017). Invasive species are often associated with disturbed environments, with fauna being the key direct non-anthropogenic disturbance on sub-Antarctic islands (Smith et al. 2001). Indeed, on many sub-Antarctic islands, invasive species mostly occur in close proximity to fauna (Haussmann et al. 2013; Hoffmann et al. 2019), such as around seal and penguin colonies (le Roux et al. 2013). Some invasive plant species have also reached dominance in such disturbed environments (Haussmann et al. 2013), outcompeting native plant species (Gremmen et al. 1998), which may cause disruption to biological processes. While the impacts of invasive species in the sub-Antarctic are not well understood, it is likely to worsen with warming.

The key obstacles to quantifying vegetation change in the sub-Antarctic are the scarcity of cloud-free satellite imagery in a region with near-permanent cloud cover (Fitzgerald et al. 2021), lack of historical plot data and limited access to the region. Since modern techniques used for studying vegetation change rely on satellite imagery (Xie et al. 2008) or long-term permanent plot data (De Cáceres et al. 2015), most change detection techniques cannot effectively be implemented in the sub-Antarctic (Bircher 2012; Fitzgerald et al. 2021). Secondly, while the analysis of vegetation change with satellite imagery has been successful in analysing overall vegetation cover in high latitudes such as the Arctic (Stow et al. 2004), it cannot be used to identify change in smaller vegetation units, patches and species composition (Bricher 2012; Fitzgerald et al. 2021). Differentiating vegetation from satellite imagery for change detection is not possible in vegetation that has similar spectral signatures between supposedly distinct vegetation units (Xie et al. 2008). Indeed, this was the case on Macquarie Island in the sub-Antarctic, where the digital signatures were not distinct between the vegetation units studied, and the analysis could thus not effectively detect change from satellite imagery (Fitzgerald et al. 2021). Therefore, a more practical technique to quantify vegetation change is necessary in cloudy environments and in vegetation with no distinct vegetation units.

Repeat photography is one of the most informative and a well-established method available to quantify vegetation change trends (Webb et al. 2010; Hoffman & Rohde 2011; Knight & Fitchett 2020; Bayr 2021). Often, historical photographs are the only available record of past vegetation properties since historical permanent plot data may not exist. An analysis of the changes that are evident in historical views of an environment may allow for the study of long-term vegetation change (Webb et al. 2010) at temporal scales not possible with ecological monitoring (Rohde & Hoffman 2012; Hoffman et al. 2019; Bayr 2021). Hoffman et al. (2019) have shown how repeat photography can be used to contextualise projected vegetation change by studying past vegetation change trajectories and comparing it to projected scenarios. It may be particularly suitable for cloudy environments (Myers-Smith et al. 2011; Bricher 2012; Fitzgerald et al. 2021), where cloud-free satellite imagery is limited. Furthermore, satellite imagery has only been available since the 1970s and initially at very low resolution, making high resolution comparisons challenging. Repeat photography has been used in the sub-Arctic to investigate shrub expansion (Myers-Smith et al. 2011) and on Macquarie Island in the sub-Antarctic to assess vegetation change caused by invasive European rabbits (*Oryctolagus cuniculus;* Fitzgerald et al. 2021). It can thus be useful in analysing vegetation change trends at high latitudes.

Marion Island (MI) in the sub-Antarctic, in consensus with general high latitude trends (Chown et al. 2012; Piao et al. 2020), has two key factors that could potentially contribute to vegetation change. Firstly, records from 1949 onwards show that the climate has been changing on the island. In particular, an increase in air temperatures and dry spells, decrease in precipitation and changes in wind speed have been documented (le Roux & McGeoch 2008a). These changes in climate have only been analysed up to 2003 (le Roux & McGeoch 2008a), and the climate record of the last 19 years has not yet been assessed in detail (although see McClelland et al. 2018). Though it has been speculated for decades that the vegetation will have changed considerably due to climate change (Smith & Steenkamp 1990; Smith et al. 2001), only vascular plant species range expansion and contraction have thus far been documented (le Roux & McGeoch 2008b). Inferences have also been made from a short-term warming experiment (le Roux et al. 2005). Little else is known about the impact of climate change and invasive species on the vegetation.

Secondly, non-native species have established and spread on MI (Chown et al. 2008; le Roux et al. 2013). Six invasive plant species have spread rapidly across the island, especially along the coast, between the 1960s and 2008 and with continued propagule pressure were predicted to spread further (le Roux et al. 2013). While their impacts on native vegetation are not well documented, largely due to lack of data (le Roux et al. 2013), the most widespread invasive plant species have likely negatively impacted the native vegetation. Some invasive plant species, such as *Poa annua* and *Agrostis stolonifera*, can outcompete native plants species (Mathakutha et al. 2019; Ripley et al. 2020) and have become dominant in certain areas, reducing native species richness (Gremmen et al. 1998; Smith et al. 2001). The population of invasive house mice (*Mus musculus*), also increased by 430% between 1980 and 2011 (McClelland et al. 2018) in concert with the extirpation of all invasive cats (*Felis catus*) by 1991 (Bester et al. 2002). Mice have a negative impact on the physical environment and on all aspects of biodiversity (Greve et al. 2020). They have a severe impact on macro-invertebrates (Chown et al. 2002), decreasing their abundance, biomass and body size, leading to changes in nutrient cycling and decomposition in which invertebrates are integral (Smith et al. 2002). Although the impact of mice on vegetation are not well known, mice eat the seeds of some plant species (Smith et al. 2002) and tunnel and burrow through vegetation (Phiri et al. 2009). For example, mice prefer seeds of the sedge *Carex dikei* on MI, where the sedge's cover is significantly reduced in mires compared to the neighbouring Prince Edward Island which is mouse-free (Chown & Smith 1993). The impacts of mice are likely compounded by climate change (McClelland et al. 2018).

Habitat suitability for plant species is determined by differential environmental conditions, with habitat "generalist" species being those that can thrive in a wide range of environmental conditions compared to habitat "specialists" that are adapted to more explicit habitats and thus only occur in a narrow range of environmental conditions (Brouat et al. 2004). Environmental change thus often negatively affects specialist species more than generalists, because generalists can presumably adapt to change by distributing to more suitable habitats or altering their physiology (Denelle et al. 2020). Since the climate has rapidly changed on MI between 1949 and 2003 (le Roux & McGeoch 2008a), and has likely continued to change, with invasive species also spreading (le Roux et al. 2013; McClelland et al. 2018), native plant species may be experiencing novel environmental conditions and interspecific interactions. Specialist species are likely more restricted from range shifts in response to impacts of climate change and invasive species than generalist species, as their habitat suitability is more limited, unless the dominant abiotic or biotic factor determining their distribution changes accordingly.

I aimed to quantify vegetation change on MI between 1965 and 2020, using a repeat photography analysis across a variety of habitats and provide plausible interpretations of these changes given the well documented history of the island. I also related the responses of the vegetation to the changes in climate and invasive species populations over the same period. My hypotheses were that 1) vegetation change is likely due to a combination of climate change and invasive species, 2) habitat generalists have increased in cover in all habitats, 3) habitat specialists have not increased in cover due to their reliance on more explicit environmental conditions, 4) alien plant species have spread on MI with consequent impacts on the distribution and cover of native species.

Methods

Study Site

Marion Island (46°54′ S, 37°45′ E) is a *c.* 290 km^2 remote South African sub-Antarctic island (Fig. 1). The island has a cool, thermally-stable, oceanic climate with mean annual precipitation of *c.* 2000 mm (le Roux & McGeoch 2008a). The mean temperatures of the coldest and warmest months differ by *c.* 3.6°C, and diurnal temperatures vary by *c.* 1.9°C (Smith 2002). The island has a relatively recent origin, *c.* 450 000 years B.P., with the last glacial maximum occurring around 34 500 years ago (Rudolph et al. 2020). The geology consists of pre-glacial grey lava and post-glacial black lava with *c.* 130 more recent red scoriaceous cones scattered around the island (Rudolph et al. 2020).

The flora comprises 21 indigenous species (Chau et al. 2020) and 17 alien vascular plant species (Greve et al. 2017), along with 134 bryophyte species and 100 lichen species (Øvstedal & Gremmen 2001). Plant species have different environmental requirements that determine habitat suitability (Austin & Van Niel 2011). To differentiate between specialists and generalists, species with limited habitat preferences and thus narrow niches (Ainsworth & Drake 2020) which are restricted to specific habitats, such as species limited to high salinity soils, are considered specialist species. On the other hand, habitat generalists may occupy multiple habitat types, because of their broader niche preferences (Denelle et al. 2020). Habitat specialists can be divided into halophilous species (*Crassula moschata* and *Leptinella plumosa*), hygrophilous species (*C. dikei, Juncus scheuchzerioides, Limosella australis*) and coprophilous species (*Callitriche antarctica, Poa cookii, Montia fontana*). All other species (n = 13) are considered habitat generalists (Huntley 1971; le Roux & McGeoch 2008b). Due to the harsh climate on MI, vegetation distribution is closely coupled with abiotic conditions, such as exposure to wind and temperature (Smith & Steenkamp 2001; Cramer et al. 2022). On the coast, in and around seal colonies and seabird breeding sites, such as penguin rookeries, the distribution of plant species is more biotically-driven, by manuring and trampling of animals, where coprophilous species thrive. Wherever saltspray occurs in areas highly exposed to waves, halophytes thrive (Smith et al. 2001). If drainage is impeded, only hygrophilous species are generally able to grow (Huntley 1971). Feral domestic cats were introduced to the island in 1949 to control the increasing mouse population, although were extirpated by 1991 (Bester et al. 2002). Shortly after the cats were introduced, they started predating on seabirds and soon caused severe declines in seabird population, especially in burrowing petrels (Bester et al. 2002). During the same time period, many invasive plant species were introduced to MI, with eight now being invasive (Greve et al. 2017). Four alien plant species are widespread on MI, particularly concentrated in the coastal areas (*P. annua*, *A. stolonifera, Sagina procumbens, Cerastium fontanum*; le Roux et al. 2013).

Repeat photography

Mean annual temperatures on MI increased rapidly from the 1960s and rainfall decreased concurrently (Bergstrom & Chown 1999; le Roux & McGeoch 2008a). Therefore, historical photographs from the 1960s are an ideal baseline for assessing the impact of changes in temperature and rainfall on the vegetation of the island. Sixty-nine historical photographs that encompass all habitats of MI were sourced from researchers that visited the island in 1965 (n = 59; Brian Huntley) and 1980 (n = 10; Marthan Bester). Both the 1965 and 1980 photographs served as the "historical" baseline. The photographs were originally captured as 35 mm colour slides. The sites of the historical photographs (hereafter referred to as being taken in "1965") were relocated in the field in 2019/2020 (hereafter "2020"). The repeat photography approach described by Rohde & Hoffman (2012) was followed. For each historical photograph, the camera position was located as close as possible to the original site to capture the repeat photograph. The GPS location, elevation and photographic information were recorded, and a detailed ecological survey was conducted at each site. This was done by dividing the field of view into general habitats, recording an in-field description of the vegetation, and then identifying all vascular plant species together with an estimate of the aerial percentage cover of each species in each habitat. Water and rock cover were also estimated in each habitat. The repeat photograph was overlaid on the original photograph to obtain an exact match to the original using Adobe Photoshop CS5 (Adobe, CA, USA).

Cover estimates of vegetation change derived from an analysis of photographs

Within each photograph, polygons were drawn around habitats that could be identified from the historical photographs (as was also done in the field). To address the close association of certain range-restricted species (specialists) with specific environmental or biotic factors, which confines them to one particular habitat, plant cover within each habitat was estimated (rather than at the island-scale). The habitats were informed by Smith & Steenkamp's (2001) key to identifying habitats on MI (see Table B1 in Appendix B for a description of these habitats). Cover was estimated based on "plant guild", rather than species, because the inconspicuous species, such as the mat forming herbs that occur around fauna, were difficult to differentiate in the photographs. Therefore, while photographs were divided into habitats to account for specialists species, plant cover changes were still estimated per guild. A plant guild consists of a group of species that utilise resources in a similar manner and since they have similar resource requirements usually occur together in similar habitats (Simberloff & Dayan 1991). It thus includes taxonomic and ecological characteristics. However, most plant guilds are only represented by a single species, due to the low species richness on the island (see Table B2 for a description of plant guilds), thus the analysis was mostly done at a species-level (as suggested in Chapter 2). Within each habitat the cover of each visible plant guild in the historical and repeat photograph was estimated by two researchers with detailed knowledge of the habitats and flora of MI, and the average value was used for each observation. Twelve plant guilds were identified as follows: bryophyte, pteridophyte, mire graminoid, tussock graminoid, epiphytic graminoid, alien grass, alien herb, mat dicotyledon (“dicot” hereafter), cushion dicot, rosette dicot, erect dicot, and suffrutescent herb (Table B2). The cover of bare soil and/or rock and water evident in the photographs was also estimated. In total, 100 paired polygons were recorded in the historical and repeat photographs. In 21 polygons, however, only the total vegetation cover could be estimated, as the field of view was too distant to estimate the cover of different plant guilds in different habitats. Polar desert was the only habitat excluded from the analysis because historical photographs in polar desert are scarce, partially because of extreme weather conditions through most of the year.

The advantage of repeat photography analyses in tundra vegetation, which generally has low vascular species richness, is that plant guilds can easily be identified from photographs. Most species also have distinct colours on MI, and do not show pronounced changes with season compared to more temperate study sites, making identification of plant guilds possible from photographs taken throughout the year. The exception is *Acaena magellanica* which is the only deciduous species on MI (Smith & Steenkamp 2001). This was kept in mind when interpreting change in *A. magellanica* (i.e., the suffrutescent herb plant guild) cover. This is because on slopes where *A. magellanica* is dominant, the fern *Austroblechnum penna-marina* is often co-dominant and may be more pronounced in photographs when *A. magellanica* has lost its leaves. While exact dates for the historical photographs are not known, the season could be identified from *A. magellanica* flowerheads, and grass inflorescences, such as those of *Polypogon magellanicus.* The latter is an abundant grass species throughout the island, whose culms grow much taller in summer, especially in mires, where it reaches its optimum rigour (Huntley 1971). If epiphytic graminoids growing in cushion plants in fellfield increase and cover a larger area in a repeat photograph, the cushion plant cover in the photograph becomes less visible. Consequently, to avoid overestimating total vegetation cover, the cushion plant cover is simultaneously subtracted from the assessment. This does not indicate replacement of cushion plants by epiphytes, but rather overgrowing or shading of cushion plants by epiphytes.

Climate data

The past climate trends have only been analysed up to 2003 in detail (le Roux & McGeoch 2008a; although see also McClelland et al. 2018) and are now outdated. To investigate general climate trends that the vegetation experienced over the study period, temperature, precipitation and wind data were analysed, available from 1949 to 2020, sourced from the National Oceanic and Atmospheric Administration’s Integrated Surface Dataset using package “worldmet” (Carslaw 2023). The data were derived from the MI weather station located to the east of the island at the research station (Fig. 1). Six-hourly temperature (°C) data, taken at 08:00, 14:00, 20:00 and 02:00, were averaged to daily mean, maximum and minimum temperatures. From these data, annual mean, minimum and maximum temperatures were calculated to analyse the trend over the available data period. Daily precipitation, falling mainly as rainfall (mm), was summed to a total rainfall per year. The total number of rain-free days and maximum number of consecutive rain-free days were also calculated to explore dry spells. Rainfall data were missing between 1949 and 1960 and thus only data from 1960 onwards were analysed for rainfall. Six-hourly wind measurements were averaged to mean annual wind speed (m s^{-1}), and wind direction (°) per day was calculated using circular statistics in the “circular” package (Agostinelli & Lund 2022) and averaged to mean annual wind direction. Temperature and wind data were analysed from 1949 to 2020 to include the climate trend preceding 1965 as well. In the exploratory phase of this study, change in seasons, such as season length, was also analysed, but being a hyper-oceanic island, seasonality does not have a strong influence, thus the seasonal variables were not significant and not presented here to limit the study to relevant data.

Mouse data

To assess changes in mouse abundance and density, mouse data were extracted from previous studies that used live trapping to estimate mouse abundance and densities in different seasons in 1980, 1991-1999, 2008 and 2011 (see e.g. McClelland et al. 2018 for detailed methodology).

Statistical analysis

Paired sample “Wilcoxon” tests were run for each polygon pair to determine whether there was a significant difference in cover of each plant guild, as well as total vegetation cover across MI (“combined data”), between 1965 and 2020. Some range-restricted plant species (i.e., specialist species in the tussock graminoid, mat dicot, rosette dicot and erect dicot guilds) do not occur across the entire island, thus a second set of tests were run for each plant guild-habitat combination to determine whether there was a difference in cover of each plant guild within each habitat between 1965 and 2020, using the “car” (Fox et al. 2013) and “PairedData” (Champely 2018) packages.

To analyse the change in climate variables during the study period, the mean, minimum and maximum air temperature, total precipitation falling as rainfall, total number of rain-free days, maximum number of consecutive rain-free days, wind speed and wind direction were explored. General additive models were used to explore non-linear trends of mean, minimum and maximum air temperature, total number of rain-free days, wind speed and wind direction and whether these variables changed significantly over the study period, using the “gam()” function in the “mgcv” package (Wood 2011). A general linear model was run for total rainfall per year and maximum number of consecutive rain-free days, which had a linear trend over time.

All statistical analyses were conducted with R statistical software (R Core Team 2020), while the map (see Chapter 2 for detailed methodology) was created in ArcGIS Desktop 10.4 (Environmental Systems Research Institute, CA, USA).

Results

Repeat photography

In the combined data (n = 100), total vegetation cover was significantly ($p < 0.05$) higher in 2020 than in 1965 in all habitats (Fig. 1), other than in coastal saltspray (Fig. 2). The most pronounced increase in total vegetation cover (by *c.* 18%) occurred in fellfield (Fig. 2). The overall increase in total cover was largely due to the higher cover of pteridophyte, epiphytic graminoid, alien grass, alien herb and bryophyte guilds ($p < 0.05$) in 2020 compared to 1965 (Fig. 2). Bare ground, cushion dicot, tussock graminoid and suffrutescent herb cover were significantly ($p < 0.05$) lower in 2020 than in 1965 (Fig. 2). The remaining guilds (mire graminoid, mat dicot, rosette dicot and erect dicot) did not differ significantly ($p > 0.05$) between years in the combined data (Table 1).

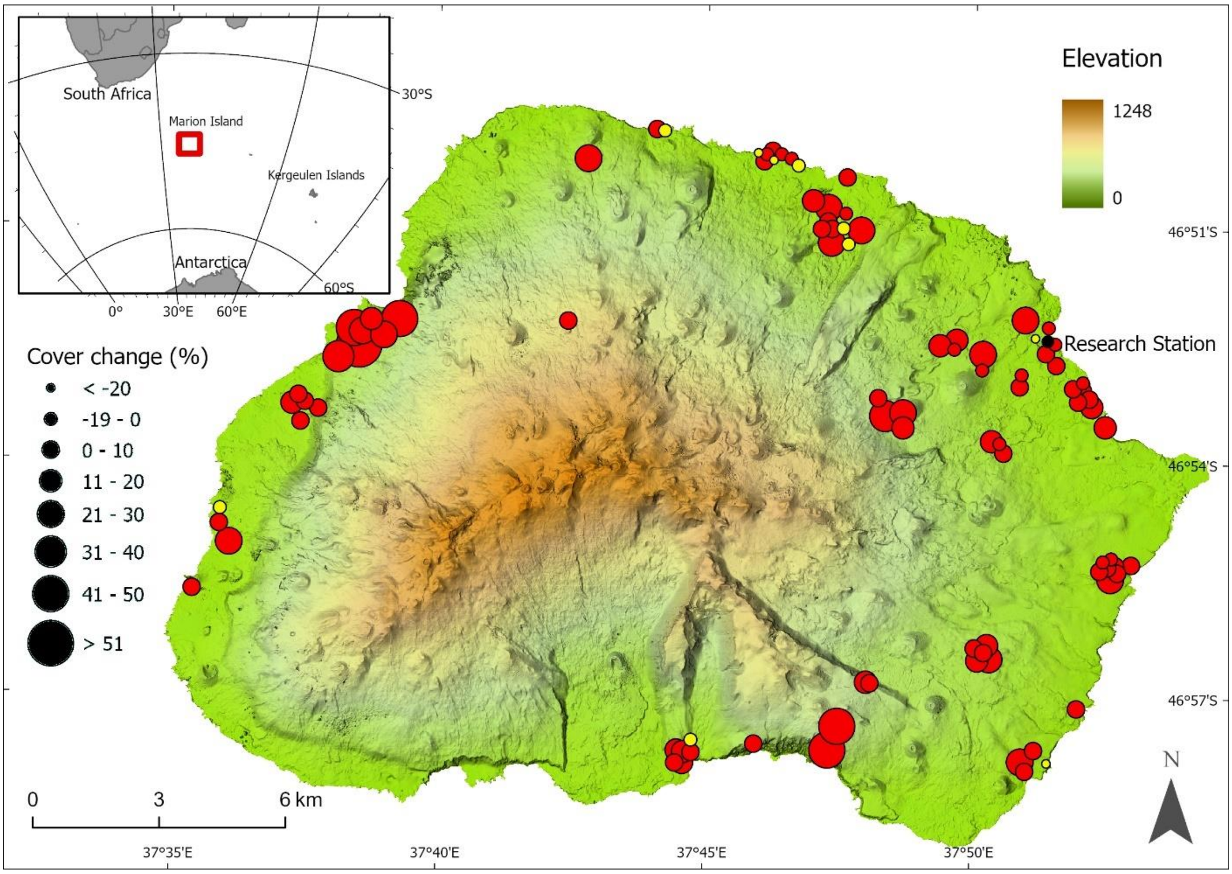


Figure 1. Percentage change in total vegetation cover at each photograph location of the repeat photography analysis across Marion Island between 1965 and 2020. Graduated symbols indicate percentage change from decreasing to increasing total vegetation cover. Yellow indicates the sites with a decrease in cover and red indicates sites with an increase in plant cover. The position of some site symbols has been jittered to improve visibility at this map scale.

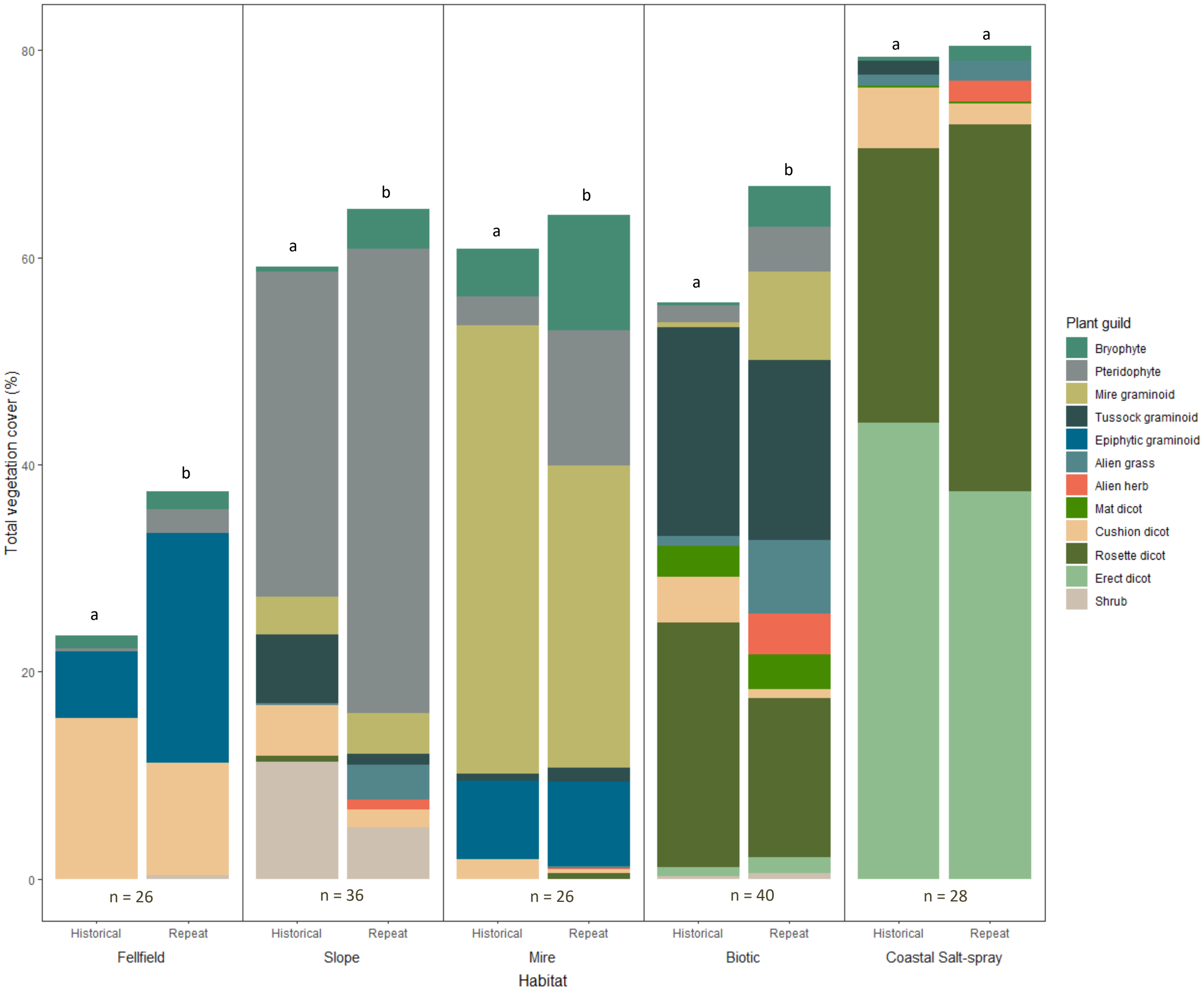
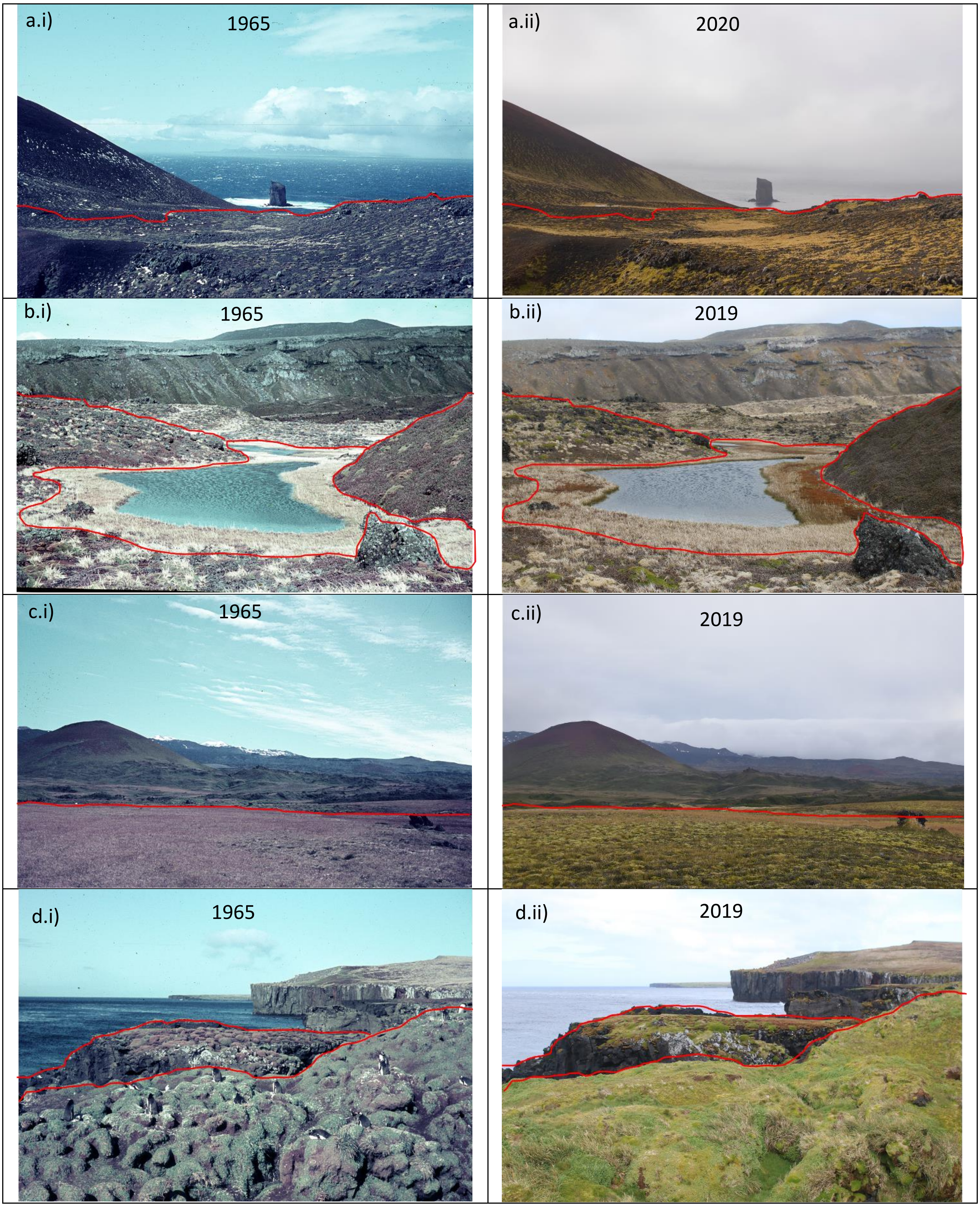


Figure 2. Stacked bar charts showing percentage vegetation cover across habitats on MI between 1965 (“Historical”) and 2020 (“Repeat”). Bars are stacked by mean percentage of each plant guild that made up the total vegetation cover. Bare ground and water habitats were removed to display only vegetation cover. Significant differences ($p < 0.05$) between 1965 and 2020 for total vegetation cover are indicated by letters.

Table 2. Mean percentage change (± SE) of each guild in each habitat on MI between 1965 and 2020. Colours indicate an increase (green) or decrease (orange) in mean cover. Light green indicates a 1-4%, medium green 5-9% and dark green ≥10% increase. Grey cells indicate zero change. Light orange indicates a 1-4%, medium orange 5-9% and dark orange ≥10% decrease. White cells indicate that the guild does not occur in a habitat and thus has no value. Values in bold were significant ($p < 0.05$) according to a Wilcoxon signed rank test.

Guild	Fellfield	Slope	Mire	Biotic	Coastal saltspray
Alien grass		4 ± 12	0 ± 1	**8 ± 14**	1 ± 1
Alien herb		1 ± 4	0 ± 0	**5 ± 9**	2 ± 7
Bare ground	**-19 ± 9**	**-7 ± 8**	**-4 ± 6**	**-15 ± 4**	-2 ± 4
Bryophyte	1 ± 1	**5 ± 7**	**10 ± 9**	**5 ± 9**	1 ± 4
Cushion dicot	**-6 ± 5**	**-4 ± 3**		-4 ± 12	**-4 ± 5**
Epiphytic graminoid	**21 ± 13**				
Erect dicot				1 ± 2	-7 ± 3
Mat dicot				0 ± 5	0 ± 0
Mire graminoid		0 ± 2	**-21 ± 3**	**10 ± 22**	
Pteridophyte	3 ± 9	**18 ± 9**	**15 ± 12**	**3 ± 7**	
Rosette dicot			1 ± 3	-10 ± 8	9 ± 13
Suffrutescent herb		**-8 ± 7**		0 ± 1	
Total vegetation	**18 ± 9**	**8 ± 9**	**5 ± 1**	**14 ± 4**	1 ± 3
Tussock graminoid		**-7 ± 11**	1 ± 2	-4 ± 2	-1 ± 2

In fellfield vegetation ($n = 26$), bare ground and cushion dicot cover were significantly ($p < 0.05$) lower in 2020 than in 1965, whereas epiphytic graminoid cover was higher ($p < 0.05$) in 2020 (Fig. 2; Table 1). No other plant guilds differed significantly between the years in fellfield ($p > 0.05$; Table 1). On slopes ($n = 36$), pteridophyte ($p < 0.05$) cover was significantly higher and tussock graminoid ($p < 0.05$), bryophyte ($p = 0.01$), suffrutescent herb ($p < 0.05$), cushion dicot ($p = 0.02$) and bare ground ($p < 0.05$) were lower in 2020 than in 1965 (Fig. 2; Table 1). In mires ($n = 26$), pteridophyte ($p < 0.05$) and bryophyte cover ($p = 0.02$) was significantly higher in 2020 than 1965 (Table 1). Mire graminoid ($p = 0.02$) and bare ground ($p = 0.01$) were significantly lower in 2020 than in 1965 (Fig. 2). In biotic sites ($n = 40$), pteridophyte ($p = 0.02$), bryophyte ($p = 0.02$), mire graminoid ($p = 0.03$), alien grass cover ($p < 0.05$) and alien herb ($p = 0.01$) were significantly higher in 2020 than in 1965, with lower bare ground cover ($p < 0.05$) in 2020 (Table 1). In coastal saltspray habitat ($n = 28$), only cushion dicot differed significantly ($p = 0.01$), being lower in 2020 than in 1965 (Fig. 2). Examples of the most prominent guild changes in each habitat are shown in Figure 3.


a.i)
1965
a.ii)
2020
b.i)
1965
b.ii)
2019
c.i)
1965
c.ii)
2019
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1965
d.ii)
2019

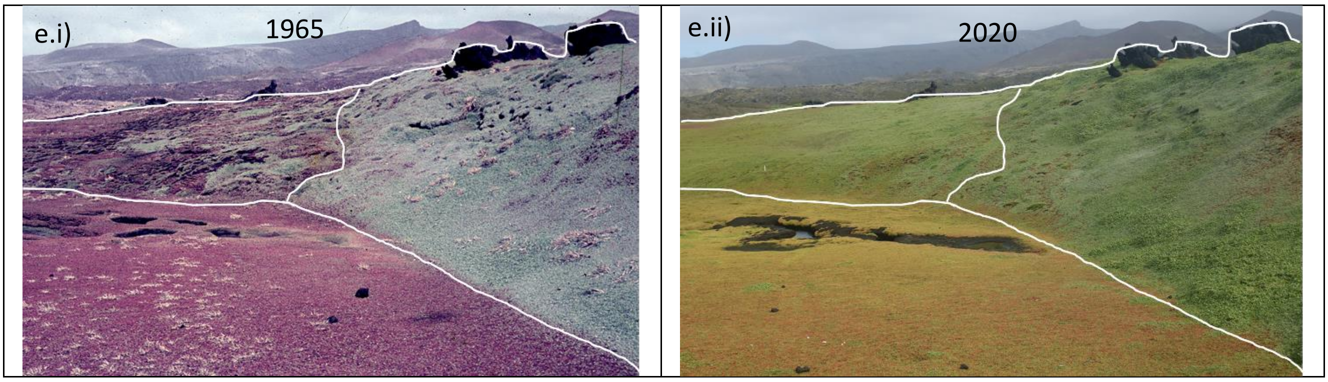


Figure 3. Matched photograph examples showing vegetation change within each vegetation unit on Marion Island. Historical photographs from 1965 are on the left and repeat photographs captured in 2019/2020 are on the right. These are examples of a) epiphytic graminoid cover increase and cushion dicot cover decrease in fellfield where grasses have expanded onto bare ground; b) pteridophyte cover increase and cushion dicot decrease on slopes (on the right). In the mire (centre) bryophytes have expanded where a new foot path was created on the right; c) mire graminoid decrease and bryophyte/pteridophyte increase in mires; d) mat dicot, alien grass and herb cover increase in the biotic habitat. Non-native plant species are present in the repeat photographs, where they were previously absent in the historical photographs; e) slight cushion dicot decrease and rosette dicot increase in coastal salt-spray, although this was not significant.

Climate data

Mean annual temperature increased significantly ($p < 0.05$) over the study period from *c.* 5.8°C in 1949 to *c.* 6.3°C in 2020 (Fig. 4). Mean annual temperatures increased up to *c.* 1999, decreased until *c.* 2010 and increased again from 2011 (Fig. 4). The annual mean monthly maximum temperatures did not change significantly ($p > 0.05$) between 1949 and 2020. Annual mean monthly minimum temperatures changed significantly from *c.* -2.2°C (1949) to *c.* -1.2°C (2020), although a negligible amount of variation (12.0%) was explained by the model. The total rainfall decreased significantly from *c.* 2585 mm p.a. in 1960 to *c.* 1640 mm p.a. in 2020 ($p < 0.05$; Fig. 5). Total number of rain-free days increased significantly from the 1960s to 1990s, then decreased until 2010 and increased again from 2011 (Fig. 5). Although comparing the two years of the repeat photography analysis, there were 86 rain-free days in 1965 and 64 in 2020. The maximum number of consecutive rain-free days (i.e., dry spells) decreased over the study period, but it was not significant ($p > 0.05$). Wind direction changed significantly ($p < 0.05$) from being predominantly NW to predominantly SW (Fig. 6). Wind speed increased until the 1990s, then decreased from the late 1990s, although this was not significant ($p > 0.05$; Fig. 6).

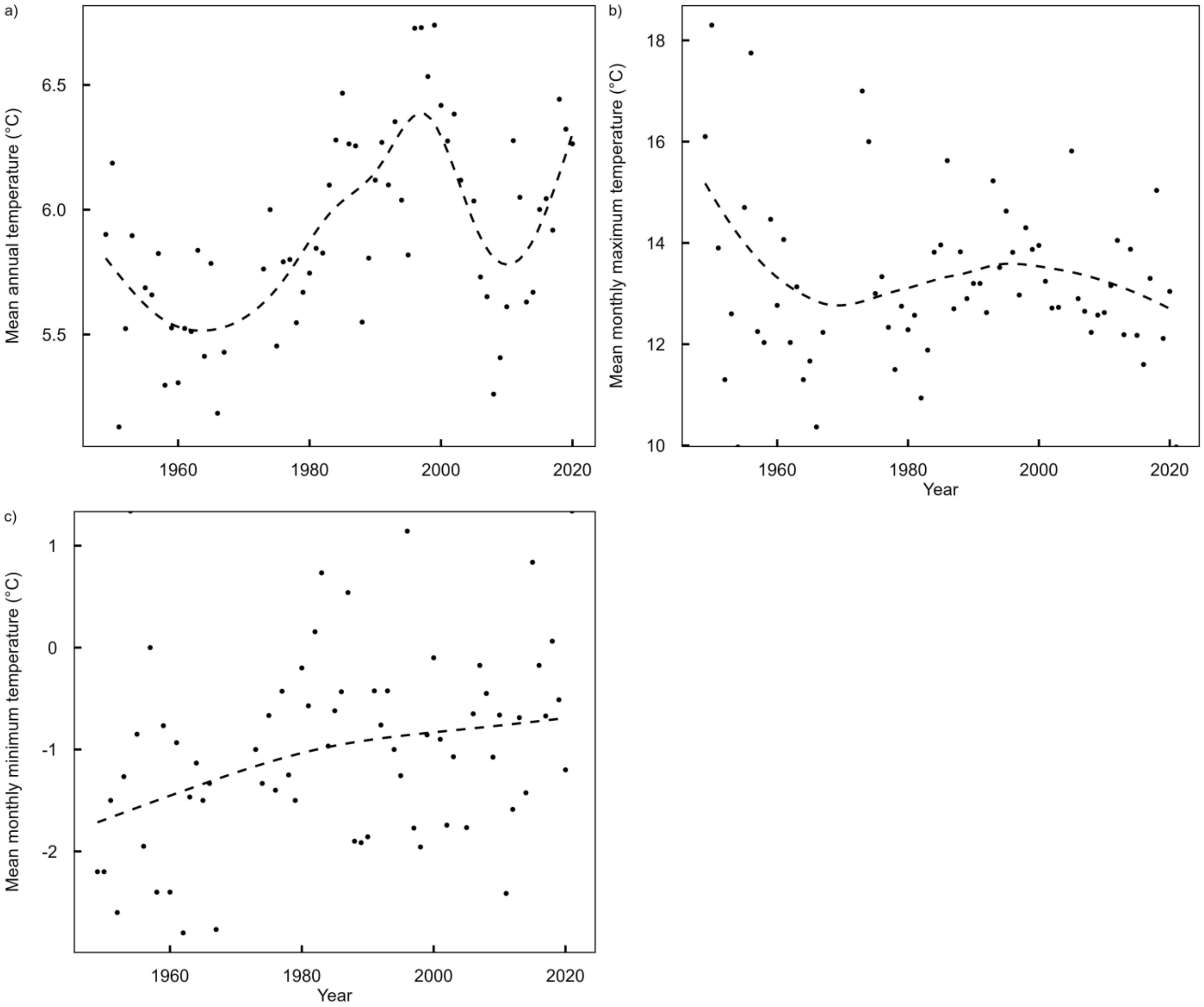


Figure 4. Air temperature change on Marion Island from 1949 to 2020: a) mean annual temperature ($p < 0.05$; deviance explained = 74.6%), b) mean monthly maximum temperature ($p > 0.05$, deviance explained = 28.0%) and c) mean monthly minimum temperature ($p < 0.05$, deviance explained = 12.0%). General additive models were fitted to the graphs.

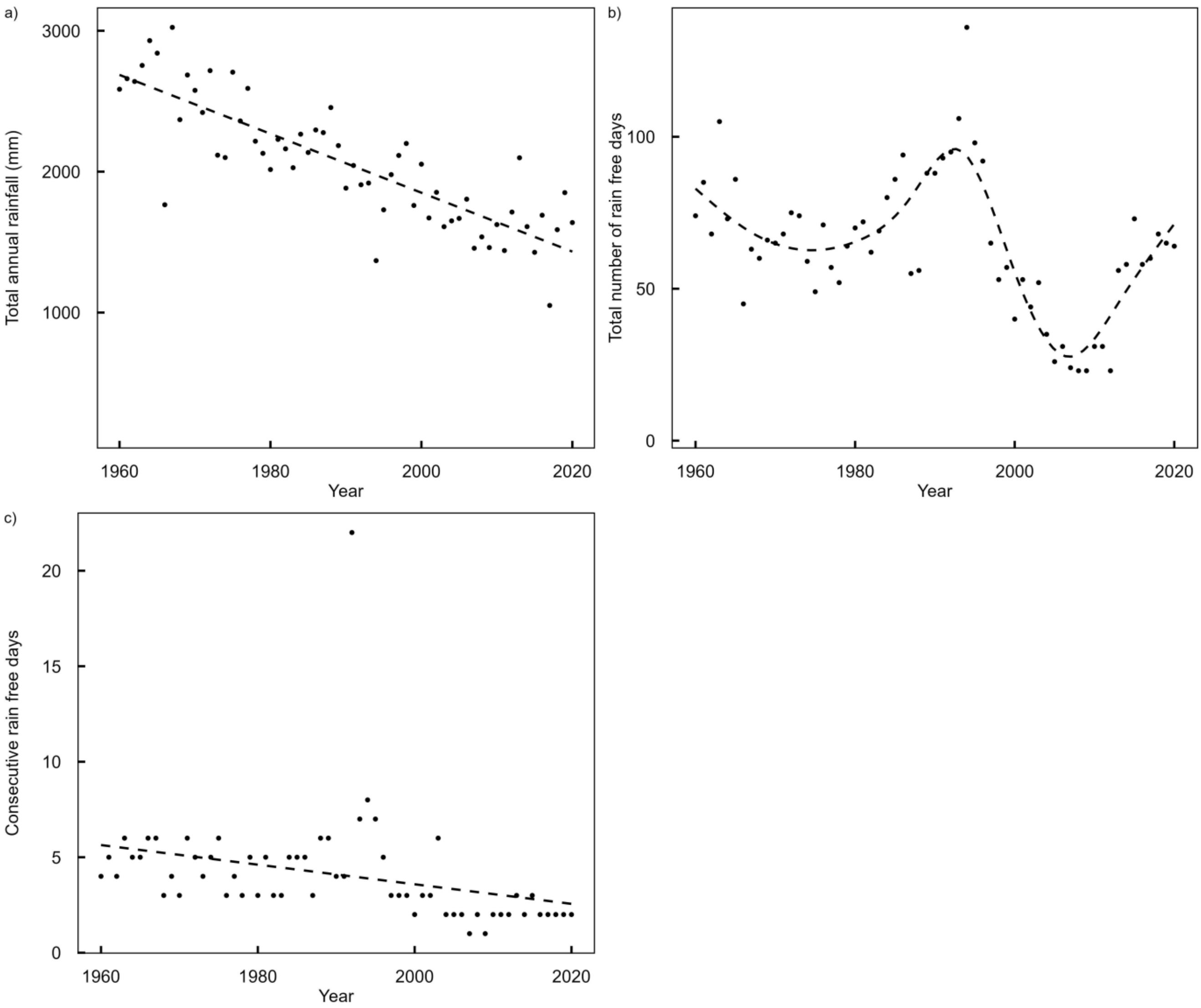


Figure 5. Change in a) total annual rainfall ($p < 0.05$, $R^2 = 70.4\%$); b) total number of rain free days ($p < 0.05$ deviance explained = 14.7%); and c) maximum number of consecutive rain-free days, i.e., dry spells ($p = 0.02$, $R^2 = 8.10\%$), between 1960 and 2020. A general linear model has been fitted to the graph in a) and c) and a general additive model was fitted to b).

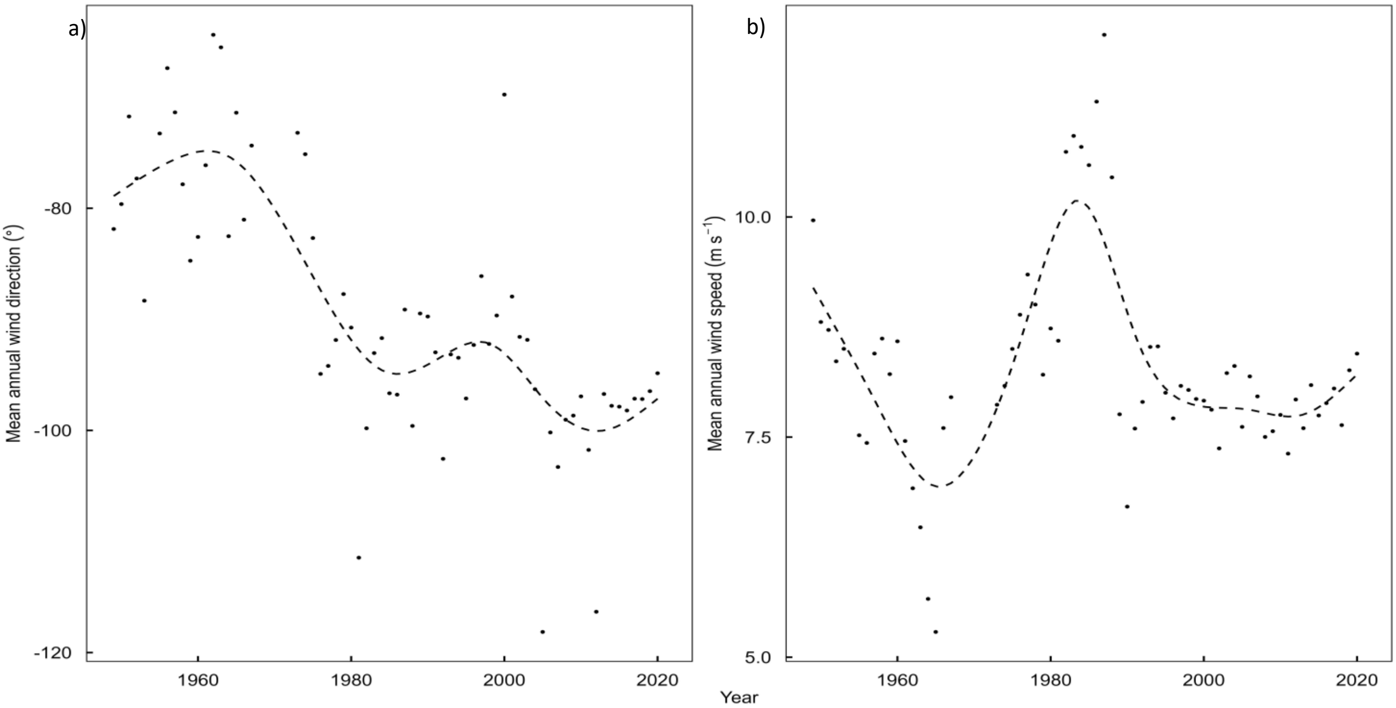


Figure 6. Changes in wind conditions between 1949 and 2020: a) mean annual wind direction ($p < 0.05$; deviance explained = 68.3%) shown as degrees from 360° and b) mean annual wind speed ($p > 0.05$; deviance explained = 68.0%). General additive models were fitted to the graphs.

Mouse data

The total number of mice increased from *c.* 332 220 in 1980 to *c.* 1 760 740 in 2011 (Table 2). Biotic habitats generally had the highest densities of mice (given the smaller area occupied), followed by mires and then slopes. In 2011, peak mouse density in mires and on slopes increased to six times that of 1980. Peak densities in biotic areas were similar between years (Ferreira et al. 2006).

Table 3. Population density and abundance of mice at peak densities, usually in late summer. “b” indicates biotic habitats, “m” mire, and “s” slope. The total number of mice were estimated per grid (n = 1) per habitat. The information was extracted from previous studies indicated in “References”. Total numbers are only available for certain years. Values have been rounded up for display purposes.

Year	Total number of mice at peak density	Peak mouse density (n ha^{-1})	References	Additional information
1979/80	87990 (b), 122500 (m), 121730 (s)	138 (b), 35 (m), 33 (s)	Gleeson 1981	Estimates based on a modified Peterson Index and may have been overestimated
1991/92	-	247 (b), 27 (m), 48 (s)	Ferreira et al. 2006	Cats eradicated in 1991. Estimates based on a modified Peterson Index and may have been overestimated
1993/94	93 882 (b), 227 040 (m), 186 159 (s)	134 (b), 65 (m), 50 (s)	McClelland et al. 2018	Estimates based on spatially explicit capture recapture methods
1996/97	-	143 (b), 51 (m), - (s)	McClelland et al. 2018	Estimates based on spatially explicit capture recapture methods
1998/99	82 214 (b), 430 274 (m), 185 179 (s)	117 (b), 123 (m), 50 (s)	McClelland et al. 2018	Estimates based on spatially explicit capture recapture methods
2008/09	-	115 (b), 22 (m), 43 (s)	McClelland et al. 2018	Estimates based on spatially explicit capture recapture methods
2009/10	-	222 (b), 237 (m), 106 (s)	McClelland et al. 2018	Estimates based on spatially explicit capture recapture methods
2010/11	155 687 (b), 828 150 (m), 776 902 (s)	132 (b), 214 (m), 210 (s)	McClelland et al. 2018	Estimates based on spatially explicit capture recapture methods

Discussion

Following decades of speculation that the vegetation has been changing on MI (Smith & Steenkamp 1990; Chown & Smith 1993; Smith et al. 2001; Smith 2002), this study provides the first vegetation-level, circum-island demonstrations that this is indeed the case (see also le Roux et al. 2008b). Vegetation cover, particularly of alien plant species, has generally increased across MI, suggesting vegetation biomass has also increased. This is consistent with global increases in vegetation greenness (Piao et al. 2020), especially in cold environments, such as the Arctic tundra (Tape et al. 2006), where an increase in biomass is often related to climate change and rising global CO_2 concentrations. These changes are thought to increase photosynthetic rates, especially when combined with warming in cold environments (Marchand et al. 2005; Campioli et al. 2013; Piao et al. 2020) Productivity may thus have increased due to the combination of higher temperatures and less waterlogging of soils which increase microbial activity, followed by a nutrient increase and stimulation of plant growth. However, these responses are context-specific and not straightforward (Körner 2006), thus I cannot confidently attribute the changes on MI to these drivers without experimental data. Concurrent with the increase in vegetation cover, was a rapid change in the climate on MI and invasive plant and mouse abundance have increased. These are thus likely major factors driving vegetation change.

A key limitation of a repeat photography approach is that correlating vegetation change to a specific driver is particularly challenging. However, on MI, direct anthropogenic influence is limited to the research station, overnight huts and footpaths around the island, thus typical continental drivers of vegetation change, such as habitat loss and land-use change, are absent. Other non-anthropogenic change drivers such as fire and herbivory (other than the invasive mice) also do not occur on the island. Therefore, many typical drivers of change can be ruled out. While climate change is likely contributing significantly to vegetation change, changes in climate were more complex than previously believed, as the trends have shifted since the last climate study was conducted on MI in 2003 (le Roux & McGeoch 2008a). While the mean air temperatures increased rapidly until *c.* 2000, it subsequently dropped until the 2010s, after which a warming trend resumed. Although mean minimum temperatures increased by *c.* 1°C between 1949 and 2020, high variation around the mean resulted in negligible explained variance. Nonetheless, overall air temperatures have been warming, with 2020 temperatures being *c.* 0.5°C higher than those recorded in 1949. Wind speed also did not follow a linear trend, increasing between the 1960s and 1990s, decreasing rapidly in the early 2000s and stabilising afterward, with annual windspeeds being similar in 1965 (*c.* 7.7 m s^{-1}) and 2020 (*c.* 7.9 m s^{-1}). However, the change in wind speed was not significant. Wind direction has also changed from more north-westerly winds to predominantly south-westerly winds. However, in contrast to the varying trends of the other climate variables, total rainfall has consistently and rapidly decreased, with 2020 experiencing around 1000 mm less rainfall per year compared to 1960. Therefore, climate change, especially aridification, and invasive species are likely the two key drivers of vegetation change, also proposed as the important drivers at other islands in the sub-Antarctic (Frenot et al. 2005; Bergstrom et al. 2015; Hoffmann et al. 2019), supporting the first hypothesis explored in this study.

In 1965, there was no observable alien plant cover in the photographs, although some alien plant species were present by then (Greve et al. 2017). In 2020, alien plant species were present in biotic sites, coastal saltspray and on slopes. If alien plants are now observable from photographs (with a relative increase of 500% in the study period) but was not in 1965, it suggests that alien species are still spreading on MI. This confirms predictions (Smith et al. 2001; le Roux et al. 2013; Greve et al. 2017) that alien species distributions would increase on MI. There is no evidence that mice consume any part of the alien plants on MI (Smith et al. 2002). Conversely, the disturbance of natural vegetation caused by mice may provide the opportunity for invasive species to spread. Alien species often establish in disturbed and nutrient-enriched environments (Vila et al. 2011). On MI, seals and seabirds are the key agents of nutrient enrichment through manuring and disturbance. Areas where fur seals occur particularly favour the production of *P. annua* lawns, due to nutrient-enrichment and trampling of native species which creates disturbance sites for the establishment of non-native species (Haussmann et al. 2013). The range expansion of alien plants is thus likely due to the synergy between residence time, biotic disturbance and dispersal through seals (Haussmann et al. 2013), humans or seabirds (Ryan et al. 2003) and climatic changes.

While little is known about the impacts of alien plant species on MI, invasive species can more rapidly acquire resources and potentially outcompete native species (Mathakutha et al. 2019) and invasive plant species elsewhere are also known to respond faster to disturbance as a result (Vila et al. 2011). Indeed, the photosynthetic rate of invasive grasses on MI increased in response to experimental warming, whereas native grasses in comparison did not (Ripley et al. 2020). The authors suggested that the native species may be more vulnerable to environmental change, compared to invasive grass species, due to their selection for stress tolerance to the harsh environmental conditions with limited responsiveness to change. The increase in alien grass and alien herb cover here, comprising the three most widespread invasive species, *P. annua, A. stolonifera* and *S. procumbens*, is thus of concern as these species may be more responsive than native species to the rapid changes occurring on the island. Displacement of native plant species in disturbed sites may be the key negative impact of invasive plant species. Indeed, in the biotic site studied here, where faunal disturbance is high, an increase in alien plants coincided with a decrease in native rosette dicots (*L. plumosa*) and tussock grasses (*P. cookii*), suggesting that aliens may play a role in displacing the native species. Similarly, some native *P. cookii* grasslands were also replaced by *P. annua* lawns in a study conducted between 1979 and 2011 on MI

(McClelland et al. 2018). Furthermore, the grass *A. stolonifera* reaches dominance in some habitats where it outcompetes native species (Gremmen et al. 1998). This not only reduces diversity, especially in bryophyte species, but also effectively leads to changes in ecosystem functioning. *Sagina procumbens,* a cushion and mat-forming invasive plant species, has spread rapidly across MI (le Roux et al. 2013), could also be outcompeting and occupying unfilled niches or those of native species that are struggling under climate change and mouse impacts. The management of invasive plant species is thus necessary to avoid further impacts on native plant species, that are already undergoing change on MI due to climate change.

The guilds representing generalist species, i.e., pteridophyte, epiphytic and mire graminoid guilds, accounted for a large proportion of the increase in vegetation cover and thus biomass, indicating range expansion of these generalists. In particular, the cover of *P. magellanicus* which occurs in two forms as epiphytic graminoid in fellfield and mire graminoid in mires and biotic sites*,* and *A. penna-marina,* the dominant pteridophyte, expanded in all habitats where they occur. Pteridophytes in general are hypersensitive to environmental variation and are often used as indicators of change, since their distribution is independent of biotic vectors and thus rather a response to climate and other abiotic conditions (Abotsi et al. 2020). Indeed, mice do not eat *A. penna-marina* (Smith et al. 2002) and alien plant species probably do not compete with the fern. Invertebrates comprise the main component in the diet of mice (Chown & Smith 1993) and invertebrate abundance is low on *A. penna-marina*. Therefore, mice densities are the lowest on *A. penna-marina* dominated slopes, compared to biotic and mire habitats (McClelland et al. 2018). *Austroblechnum penna-marina* is likely sensitive to temperature, reflected in its preference for warmer north facing slopes (Huntley 1971; Gremmen 1981), as well as its habitat suitability being significantly influenced by mean nightly temperatures (Chapter 5). In the 1960s, *A. penna-marina* did not occur above 275 m a.s.l. (Huntley 1971), but by 2006 had moved upslope by 147 m (le Roux & McGeoch 2008b), presumably due to a warmer and drier climate. *Austroblechnum penna-marina* also prefers well-drained soils, never occurring in water-logged peat (i.e., mires; Huntley 1971). The continued decrease in rainfall on MI, may thus have contributed to the range expansion of *A. penna-marina* into mires from 1965 to 2020. This also supports the prediction that mires may be drying out on MI (Hedding & Greve 2018). As species that prefer wetter soils shift or contract their ranges to track the changes in soil moisture, *A. penna-marina* may be able to disperse to marginal habitats such as previously waterlogged peat. Climate change, may thus be driving the range expansion in *A. penna-marina.*

An exception amongst the generalist species, was the decrease in the cushion dicot cover, *Azorella selago*. While we cannot say with certainty that the cushion plant cover is reducing in terms of size with the analysis presented here, the decline in the cover of cushion plants coincided with an increase in more responsive species, such as *P. magellanicus* (epiphytic graminoid) in the higher elevation fellfield and *A. penna-marina* on lower elevation slopes, likely shading the very slow growing cushion plants. Indeed, the interactive effects of shading by more responsive species (epiphytes in particular), changes in wind and decreased rainfall have been shown to increase senescence of *A. selago* in a short term experiment (le Roux et al. 2005). Similarly, the congeneric *Azorella macquariensis* is sensitive to drought and have died back likely as a result of an increase in drought periods and warming on Macquarie Island in the sub-Antarctic, with subsequent overgrowing of cushion remnants by *P. magellanicus* and lichens (Bergstrom et al. 2015). In a longer term study on MI, *P. magellanicus* also increased in cover on 58% of cushion plants studied, although there appeared to be no significant cost of epiphytic growth to the cushion plants (Raath-Krüger et al. 2023). On Kerguelen Island, also in the sub-Antarctic, the cushion plant *Lyallia kerguelensis*, has been shown to exhibit necrosis related to water stress (Marchand et al. 2021). Mechanical damage by mice through tunnelling and burrowing on MI (Phiri et al. 2009) may have also contributed to the decline in cushion plant cover. Therefore, the direct impacts of climate change, including increased temperature, decreased rainfall, and changes in wind speed and/or direction, interact with indirect effects such as shading (le Roux et al. 2005; le Roux & McGeoch 2008b), along with the mechanical damage caused by mice (Phiri et al. 2009). These compounded impacts can significantly affect cushion plants, which have demonstrated sensitivity to climate change in the sub-Antarctic (le Roux et al., 2005; Bergstrom et al., 2015; Dickson et al., 2019).

The implications of *A. selago* being shaded and damaged, with potential dieback, may be severe because it is a pioneer species (Yeloff et al. 2007) and an ecosystem engineer that acts as a keystone species due to its important role in succession, with an abundance of plant species and invertebrates associated with it (le Roux et al. 2005; Mcgeoch et al. 2006; Chau et al. 2019). Cushion plants are fundamental in the colonisation of otherwise unsuitable habitat, such as exposed ridges, scoria cones and toward the polar desert on MI, where other vascular plants reach their environmental limits (Gremmen 1981). The cushion growth form allows resistance to mechanical injury from wind, enhances soil moisture and nutrient content and has the ability to absorb and store radiation (Cavieres et al. 2007), with *A. selago* retaining high temperatures for hours after sunset (Huntley 1971). *Azorella selago* facilitates the successful establishment of other species within its canopy, and thus acts as a nurse plant for vascular species (Haussmann et al. 2010), ameliorating harsh conditions in the more abiotically stressful habitats, such as fellfield (Phiri et al. 2009). Many plant species are expanding their ranges globally to track climate change (Chen et al. 2011). Some species have shown remarkable upslope expansion by as much as 3.4 m yr^{-1} on MI (le Roux & McGeoch 2008b), being facilitated in part by cushion plants which offer a stable substrate for establishment in otherwise loose and exposed soil (Raath-Krüger et al. 2019). Ecosystem transformation generally occurs through changes in vegetation composition and structure by the replacement of dominant plant species, such as *A. selago,* by either native or non-native plants, with mortality in dominant species further accelerating ecosystem change (Allen & Breshears 1998; Nolan et al. 2018). Such transformations may be irreversible following reduction in keystone species or specific groups (le Roux et al. 2008b; Bergstrom et al. 2015) and due to their nurse and ecosystem engineering effects, a change in cushion plants in particular can alter species richness and community composition (Badano & Cavieres 2006). On Macquarie Island, rapid ecosystem collapse has been documented due to the dieback in *A. macquariensis*, also a keystone cushion plant (Bergstrom et al. 2015). On MI, the low recruitment and slow growth rate of *A. selago* (Phiri et al. 2008) will inevitably reduce its ability to regrow after structural damage by mice and to track ongoing climate change and shading by taller and more responsive plants species. *Azorella selago* may follow the same trajectory as *A. macquariensis* (Bergstrom et al. 2015; Dickson et al. 2021), if the interactive impacts of climate change and mice continue.

The specialist plant guilds (tussock graminoid, rosette dicot, mat dicot) whose distribution is dependent on specific biotic or abiotic drivers, did not show marked change in cover. The strong association of these plant guilds with particular habitat conditions, e.g. high nutrient soils that do not change rapidly with climate change, suggests that the ability of the specialists to respond to climate change may be constrained (Cramer et al. 2022). There was, however, a reduction of *P. cookii* grasses (the only species in the tussock graminoid guild) in all biotically-driven systems (i.e., where fauna occur). Although, only on slopes was the decrease of *P. cookii* cover significant between years in the current study. The distribution of *P. cookii* is determined by manuring and trampling (Smith et al. 2001), and thus the understanding of their reduced cover in relation to climate change is not straightforward, because climate change also impacts animal species. Nevertheless, one important difference between 1965 and 2020 is the change that has occurred in the populations of invasive cats and mice. Cats had been present for 19 years at the time the historical photos were taken, but were eradicated by 1991 (Bester et al. 2002). Cats caused a major decline in seabird populations, eating up to 635 000 burrowing petrels and prions per year in the mid-1970s (Bester et al. 2002). *Poa cookii* only occurs inland on slopes where there is guano enrichment around bird burrows (Smith et al. 2001). Reduction in guano enrichment of soils around burrows is the most likely cause of the reduction in *P. cookii* on the abiotically-driven slope system (Smith et al. 2001; Smith & Mucina 2006). Indeed, *A. penna-marina* increased in this study on slopes where *P. cookii* decreased. *Austroblechnum penna-marina* is sensitive to trampling by fauna (Smith & Steenkamp 2001), thus its increase on slopes where *P. cookii* decreased, indicates reduced faunal activity. Fur seal populations have also increased considerably on MI (Haussmann et al. 2013), and could further reduce tussock grasses through trampling. While *P. cookii* could potentially return to previously suitable inland slopes, burrow-nesting birds have not recovered as expected in the absence of cats (Dilley et al. 2017). This is likely due to continued predation on hatchlings by mice that have had to find other sources of protein after depleting invertebrate biomass and abundance (Dilley et al. 2017). Mice also eat *P. cookii* seeds (Chown & Smith 1993), perhaps reducing recruitment potential. While the decrease in *P. cookii* cannot be explained with certainty, the indirect impacts of cats and then mice on burrowing birds and recruitment have likely led to reduced habitat suitability and the potential for more responsive species to dominate where *P. cookii* cover declines.

Two predictions for specific plant species on MI seem to have been realised. Firstly, mire graminoids that include the hygrophilous specialist species, of which the sedge *C. dikei* was an important or even dominant component in the 1960s (Huntley 1971), have decreased significantly in mires. Mice target *C. dikei* seeds and can remove up to 75% of seed heads in mires (Chown & Smith 1993), reducing recruitment. The density of mice increased six fold in mires specifically between 1980 and 2011, indicating diet switching following decreased invertebrate abundance. The seed predation of *C. dikei*, combined with the substantial decline in rainfall drying out the dominant habitat for hygrophilous species, mires, is highly likely the reason for the reduction of mire graminoids on the island, even though *P. magellanicus*, also a mire graminoid, has increased. In fact, *P. magellanicus* only occurs in drier mires (Huntley 1971), thus its increase in cover could also indicate the drying out of mires. Secondly, *Pringlea antiscorbutica* (the Kerguelen Cabbage), a generally conspicuous plant in the 1960s, was not detected in the repeat photography analysis (although it still occurs on the island; pers. obs.). Similarly, van der Merwe et al. (2023) and Smith & Steenkamp (2001) did not detect *P. antiscorbutica* in any of their sites considered for the vegetation classification on MI, even though in the 1970s it was prevalent across MI in most community complexes (Huntley 1971; Gremmen 1981). This species was the only vascular species predicted to disappear from MI due to its intolerance to warming (Smith & Steenkamp 1990). Invasive moths have also infested *P. antiscorbutica*, likely causing further dieback (Smith & Steenkamp 1990). In a species-poor system, the disappearance of even one vascular species, may have far-reaching consequences for the indigenous biota. For example, the decline and potential local extinction of *P. antiscorbutica or C. dikei* may increase the available niche space for alien species.

Repeat photography has some limitations, particularly that a photograph only captures the vegetation properties at one moment in time in a particular season (Hoffman et al. 2020) and is subject to the vagaries of weather conditions (e.g., drought or flooding). It also only captures the vegetation properties that are visible at the angle of the photo. In this study, epiphytes that grow in cushion plants may be more visible from the angle of the photograph and thus seem to overgrow cushion plants, perhaps leading to overestimation of graminoid cover. Investigating more inconspicuous species is also challenging. For example, graminoids were grouped into epiphytic, tussock and mire graminoids to avoid erroneous identification, but *P. magellanicus* was considered an epiphytic grass in fellfield where it mainly grows as small tufts of grass in cushion plants and as a mire graminoid in mires and biotic sites because it grows much taller with increased moisture and nutrients (Smith et al. 2001). The implication was that the cover of *P. magellanicus* in reality increased in mires, consistent with its expansion in all other habitats, but the prominent decrease in the other mire graminoids, *C. dikei* and *J. scheuchzerioides* overshadowed this observation. Bryophyte identification was also not possible from the photographs and was a key gap in this study, since bryophytes, of which *Racomitrium lanuginosum* is the most prominent in photographs, increased in all habitats. Increasing the amount of photo points across the study site, photographing sites at similar times, and only interpreting the vegetation properties visible in the photos can negate some of these limitations. Nevertheless, the paired data of repeated images still provide a comparison of the vegetation properties at the exact same location and at temporal scales not possible with other techniques (Hoffman et al. 2020) other than long term permanent plots or palynological records. If a study site's history is well documented, such as on MI, plausible interpretations of vegetation change are still possible.

Conclusion

MI has undergone significant vegetation change across most habitats in the last five decades, accompanied by rapid aridification, an increase in mean air temperature, change in wind direction and changes in wind speed. The three most widespread invasive plant species have also expanded their ranges, especially in biotic areas, and invasive mice have rapidly increased in abundance and density. The two key interactive drivers of vegetation change on MI are thus climate change and invasive species. The more responsive generalist plant species, specifically *P. magellanicus* and *A. penna-marina*, have expanded across the island, whilst the more specialised plant species have not significantly changed in cover. While climate change impacts are difficult to manage/control, this study provides support for the necessity of eradicating mice and for the management of the three most widespread invasive plant species on MI to allow the chance for the native vegetation to recover and adapt.

References

Abotsi, K.E., Bose, R., Adjossou, K., Deblauwe, V., Rouhan, G., Segla, K.N., Atsri, K.H., & Kokou, K. 2020. Ecological drivers of pteridophyte diversity and distribution in Togo (West Africa). *Ecological Indicators* 108: 105741.

Agostinelli, C., & Lund, U. 2022. R package 'circular': circular statistics. Available at https://r-forge.r-project.org/projects/circular. [Accessed 17 May 2023].

Ainsworth, A., & Drake, D.R. 2020. Classifying Hawaiian plant species along a habitat generalist-specialist continuum: Implications for species conservation under climate change. *PLOS ONE* 15: e0228573.

Allan, E.L., Froneman, P.W., Durgadoo, J. V, McQuaid, C.D., Ansorge, I.J., & Richoux, N.B. 2013. Critical indirect effects of climate change on sub-Antarctic ecosystem functioning. *Ecology and Evolution* 3: 2994–3004.

Allen, C.D., & Breshears, D.D. 1998. Drought-induced shift of a forest-woodland ecotone: Rapid landscape response to climate variation. *Proceedings of the National Academy of Sciences of the United States of America* 95: 14839–14842.

Ansorge, I.J., Skelton, P., Bekker, A., de Bruyn, P.J.N., Butterworth, D., Cilliers, P., Cooper, J., Cowan, D.A., Dorrington, R., Fawcett, S., Fietz, S., Findlay, K.P., Froneman, P.W., Grantham, G.H., Greve, M., Hedding, D., Hofmeyr, G.J.G., Kosch, M., le Roux, P.C., Lucas, M., MacHutchon, K., Meiklejohn, I., Nel, W., Pistorius, P., Ryan, P.G., Stander, J., Swart, S., Treasure, A., Vichi, M., & van Vuuren, B.J. 2017. Exploring South Africa's southern frontier: A 20-year vision for polar research through the South African National Antarctic Programme. *South African Journal of Science* 113: 11–17.

Austin, M.P., & Van Niel, K.P. 2011. Improving species distribution models for climate change studies: variable selection and scale. *Journal of Biogeography* 38: 1–8.

Badano, E.I., & Cavieres, L.A. 2006. Impacts of ecosystem engineers on community attributes: effects of cushion plants at different elevations of the Chilean Andes. *Diversity and Distributions* 12: 388–396.

Bayr, U. 2021. Quantifying historical landscape change with repeat photography: an accuracy assessment of geospatial data obtained through monoplotting. *International Journal of Geographical Information Science* 35: 2026–2046.

Bergstrom, D.M., Bricher, P.K., Raymond, B., Terauds, A., Doley, D., McGeoch, M.A., Whinam, J., Glen, M., Yuan, Z., Kiefer, K., Shaw, J.D., Bramely-Alves, J., Rudman, T., Mohammed, C., Lucieer, A., Visoiu, M., van Vuuren, B.J., & Ball, M.C. 2015. Rapid collapse of a sub-Antarctic alpine ecosystem: the role of climate and pathogens. *Journal of Applied Ecology* 52: 774–783.

Bergstrom, D.M., & Chown, S.L. 1999. Life at the front: history, ecology and change on southern ocean islands. *Trends in Ecology & Evolution* 14: 472–477.

Bester, M.N., Bloomer, J.P., Van Aarde, R.J., Erasmus, B.H., Van Rensburg, P.J.J., Skinner, J.D., Howell, P.G., & Naude, T.W. 2002. A review of the successful eradication of feral cats from sub-Antarctic Marion Island, Southern Indian Ocean. *South African Journal of Wildlife Research* 32: 65-73.

Bricher, P. 2012. Methods for mapping the tundra vegetation of sub-Antarctic Macquarie Island. PhD thesis, University of Tasmania, Tasmania.

Brouat, C., Chevallier, H., Meusnier, S., Noblecourt, T., & Rasplus, J.Y. 2004. Specialization and habitat: spatial and environmental effects on abundance and genetic diversity of forest generalist and specialist Carabus species. *Molecular Ecology* 13: 1815–1826.

De Cáceres, M., Chytrý, M., Agrillo, E., Attorre, F., Botta-Dukát, Z., Capelo, J., Czúcz, B., Dengler, J., Ewald, J., Faber-Langendoen, D., Feoli, E., Franklin, S.B., Gavilán, R., Gillet, F., Jansen, F., Jiménez-Alfaro, B., Krestov, P., Landucci, F., Lengyel, A., Loidi, J., Mucina, L., Peet, R.K., Roberts, D.W., Roleček, J., Schaminée, J.H.J., Schmidtlein, S., Theurillat, J.P., Tichý, L., Walker, D.A., Wildi, O., Willner, W., & Wiser, S.K. 2015. A comparative framework for broad-scale plot-based vegetation classification. *Applied Vegetation Science* 18: 543–560.

Campioli, M., Schmidt, N.M., Albert, K.R., Leblans, N., Ro-Poulsen, H., & Michelsen, A. 2013. Does warming affect growth rate and biomass production of shrubs in the High Arctic? *Plant Ecology* 214: 1049–1058.

Carslaw D. 2023. worldmet: Import surface meteorological data from NOAA integrated surface database (ISD). Available at https://CRAN.R-project.org/package=worldmet [Accessed 17 July 2023].

Cavieres, L.A., Badano, E.I., Sierra-Almeida, A., & Molina-Montenegro, M.A. 2007. Microclimatic modifications of cushion plants and their consequences for seedling survival of native and non-native herbaceous species in the high andes of central Chile. *Arctic Antarctic and Alpine Research* 39: 229–236.

Champely, S. 2018. PairedData: Paired Data Analysis. Available at https://CRAN.R-project.org/package=PairedData. [Accessed 17 May 2023].

Chau, J.H., Born, C., McGeoch, M.A., Bergstrom, D., Shaw, J., Terauds, A., Mairal, M., Le Roux, J.J., & van Vuuren, B.J. 2019. The influence of landscape, climate and history on spatial genetic patterns in keystone plants (*Azorella*) on sub-Antarctic islands. *Molecular Ecology* 28: 3291–3305.

Chau, J.H., Mtsi, N.I.S., Münbergova, Z., Greve, M., le Roux, P.C., Mairal, M., Le Roux, J.J., Dorrington, R.A., & van Vuuren, B. 2020. An update on the indigenous vascular flora of sub-Antarctic Marion Island: taxonomic changes, sequences for DNA barcode loci, and genome size data. *Polar Biology* 43: 1817–1828.

Chen, I.C., Hill, J.K., Ohlemueller, R., Roy, D.B., & Thomas, C.D. 2011. Rapid range shifts of species associated with high levels of climate warming. *Science* 333: 1024–1026.

Chown, S.L., Lee, J.E., Hughes, K.A., Barnes, J., Barrett, P.J., Bergstrom, D.M., Convey, P., Cowan, D.A., Crosbie, K., Dyer, G., Frenot, Y., Grant, S.M., Herr, D., Kennicutt, M.C., Lamers, M., Murray, A., Possingham, H.P., Reid, K., Riddle, M.J., Ryan, P.G., Sanson, L., Shaw, J.D., Sparrow, M.D., Summerhayes, C., Terauds, A., & Wall, D.H. 2012. Challenges to the future conservation of the Antarctic. *Science* 337: 158-159.

Chown, S.L., Lee, J.E., & Shaw, J.D. 2008. Conservation of Southern Ocean Islands: Invertebrates as exemplars. *Journal of Insect Conservation* 12: 277–291.

Chown, S.L., McGeoch, M.A., & Marshall, D.J. 2002. Diversity and conservation of invertebrates on the sub-Antarctic Prince Edward Islands. *African entomology* 10: 67–82.

Chown, S.L., & Smith, V.R. 1993. Climate change and the short-term impact of feral house mice at the sub-Antarctic Prince Edward Islands. *Oecologia* 96: 508-516.

Cramer, M.D., Hedding, D., Greve, M., Midgley, G.F., & Ripley, B.S. 2022. Plant specialisation may limit climate-induced vegetation change to within topographic and edaphic niches on a sub-Antarctic island. *Functional Ecology* 36: 2636–2648.

Denelle, P., Violle, C., Munoz, F., & Consortium, D. 2020. Generalist plants are more competitive and more functionally similar to each other than specialist plants: insights from network analyses. *Journal of Biogeography* 47: 1922–1933.

Dickson, C.R., Baker, D.J., Bergstrom, D.M., Bricher, P.K., Brookes, R.H., Raymond, B., Selkirk, P.M., Shaw, J.D., Terauds, A., Whinam, J., & McGeoch, M.A. 2019. Spatial variation in the ongoing and widespread decline of a keystone plant species. *Austral Ecology* 44: 891–905.

Dickson, C.R., Baker, D.J., Bergstrom, D.M., Brookes, R.H., Whinam, J., & McGeoch, M.A. 2021. Widespread dieback in a foundation species on a sub-Antarctic World Heritage Island: Fine-scale patterns and likely drivers. *Austral Ecology* 46: 52–64.

Dilley, B.J., Schramm, M., & Ryan, P.G. 2017. Modest increases in densities of burrow-nesting petrels following the removal of cats (Felis catus) from Marion Island. *Polar Biology* 40: 625–637.

Elbasiouny, H., El-Ramady, H., Elbehiry, F., Rajput, V.D., Minkina, T., & Mandzhieva, S. 2022. Plant nutrition under climate change and soil carbon sequestration. *Sustainability* 14: 914.

Ferreira, S.M., Van Aarde, R.J., & Wassenaar, T.D. 2006. Demographic responses of house mice to density and temperature on sub-Antarctic Marion Island. *Polar Biology* 30: 83-94.

Fitzgerald, N.B., Kirkpatrick, J.B., & Scott, J.J. 2021. Rephotography, permanent plots and remote sensing data provide varying insights on vegetation change on subantarctic Macquarie Island, 1980-2015. *Austral Ecology* 46: 762–775.

Fox, J., Friendly, M., & Weisberg, S. 2013. Hypothesis tests for multivariate linear models using the car package. *R Journal* 5: 39–52.

Frenot, Y., Chown, S.L., Whinam, J., Selkirk, P.M., Convey, P., Skotnicki, M., & Bergstrom, D.M. 2005. Biological invasions in the Antarctic: extent, impacts and implications. *Biological Reviews* 80: 45–72.

Gremmen, N.J.M. 1981. *The vegetation of the Subantarctic islands Marion and Prince Edward*. Dr W. Junk Publishers, The Hague, Netherlands.

Gremmen, N.J.M., Chown, S.L., & Marshall, D.J. 1998. Impact of the introduced grass *Agrostis stolonifera* on vegetation and soil fauna communities at Marion Island, sub-Antarctic. *Biological Conservation* 85: 223-231.

Greve, M., Mathakutha, R., Steyn, C., & Chown, S.L. 2017. Terrestrial invasions on sub-Antarctic Marion and Prince Edward Islands. *Bothalia* 47: a2143.

Greve, M., von Der Meden, C.E.O., & Janion-Scheepers, C. 2020. Biological invasions in South Africa's offshore sub-Antarctic territories. In van Wilgen, B., Measey, J., Richardson, D., Wilson, J., & Zengeya, T. (Ids.), pp. 207–227. *Biological invasions in South Africa*. Springer.

Haussmann, N.S., McGeoch, M.A., & Boelhouwers, J.C. 2010. Contrasting nurse plants and nurse rocks: The spatial distribution of seedlings of two sub-Antarctic species. *Acta Oecologica-International Journal of Ecology* 36: 299–305.

Haussmann, N.S., Rudolph, E.M., Kalwij, J.M., & McIntyre, T. 2013. Fur seal populations facilitate establishment of exotic vascular plants. *Biological Conservation* 162: 33–40.

Hedding, D.W., & Greve, M. 2018. Decreases in precipitation on sub-Antarctic Marion Island: implications for ecological and geomorphological processes. *Weather* 73: 203.

Hinzman, L.D., Bettez, N.D., Bolton, W.R., Chapin, F.S., Dyurgerov, M.B., Fastie, C.L., Griffith, B., Hollister, R.D., Hope, A., Huntington, H.P., Jensen, A.M., Jia, G.J., Jorgenson, T., Kane, D.L., Klein, D.R., Kofinas, G., Lynch, A.H., Lloyd, A.H., McGuire, A.D., Nelson, F.E., Oechel, W.C., Osterkamp, T.E., Racine, C.H., Romanovsky, V.E., Stone, R.S., Stow, D.A., Sturm, M., Tweedie, C.E., Vourlitis, G.L., Walker, M.D., Walker, D.A., Webber, P.J., Welker, J.M., Winker, K., & Yoshikawa, K. 2005. Evidence and implications of recent climate change in northern Alaska and other arctic regions. *Climatic Change* 72: 251–298.

Hoffman, M.T., & Rohde, R.F. 2011. Rivers through time: Historical changes in the riparian vegetation of the semi-arid, winter rainfall region of South Africa in response to climate and land use. *Journal of the History of Biology* 44: 59–80.

Hoffman, M.T., Rohde, R.F., & Gillson, L. 2020. Further comments on analysing trajectories of vegetation and landscape change in southern Africa from historical fi eld photographs. *Anthropocene* 32: 100274.

Hoffman, M.T., Rohde, R.F., & Gillson, L. 2019. Rethinking catastrophe? Historical trajectories and modelled future vegetation change in southern Africa. *Anthropocene* 25: 100189.

Hoffmann, A.A., Rymer, P.D., Byrne, M., Ruthrof, K.X., Whinam, J., McGeoch, M., Bergstrom, D.M., Guerin, G.R., Sparrow, B., Joseph, L., Hill, S.J., Andrew, N.R., Camac, J., Bell, N., Riegler, M., Gardner, J.L., & Williams, S.E. 2019. Impacts of recent climate change on terrestrial flora and fauna: Some emerging Australian examples. *Austral Ecology* 44: 3–27.

Huntley, B. 1971. Vegetation. In E. M. Van Zinderen Bakker (Ed.), *Marion and Prince Edward Islands,* pp. 98-160, A.A. Balkema, Cape Town, South Africa.

Knight, J., & Fitchett, J. 2020. Analysing trajectories of vegetation and landscape change in southern Africa from historical field photographs. *Anthropocene* 32: 100271.

Körner, C. 2006. Plant CO2 responses: an issue of definition, time and resource supply. *New Phytologist* 172: 393-411.

Lee, J.R., Raymond, B., Bracegirdle, T.J., Chades, I., Fuller, R.A., Shaw, J.D., & Terauds, A. 2017. Climate change drives expansion of Antarctic ice-free habitat. *Nature* 547: 49.

Marchand, F.L., Mertens, S., Kockelbergh, F., Beyens, L., & Nijs, I. 2005. Performance of high Arctic tundra plants improved during but deteriorated after exposure to a simulated extreme temperature event. *Global Change Biology* 11: 2078–2089.

Marchand, L.J., Tarayre, M., Dorey, T., Rantier, Y. & Hennion, F. 2021. Morphological variability of cushion plant *Lyallia kerguelensis* (Caryophyllales) in relation to environmental conditions and geography in the Kerguelen Islands: implications for cushion necrosis and climate change. Polar Biol 44, 17–30.

Mathakutha, R., Steyn, C., le Roux, P.C., Blom, I.J., Chown, S.L., Daru, B.H., Ripley, B.S., Louw, A., & Greve, M. 2019. Invasive species differ in key functional traits from native and non-invasive alien plant species. *Journal of Vegetation Science* 30: 994–1006.

McClelland, G.T.W., Altwegg, R., Van Aarde, R.J., Ferreira, S., Burger, A.E., & Chown, S.L. 2018. Climate change leads to increasing population density and impacts of a key island invader. *Ecological Applications* 28: 212–224.

McGeoch, M.A., le Roux, P.C., Hugo, E.A., & Chown, S.L. 2006. Species and community responses to short-term climate manipulation: Microarthropods in the sub-Antarctic. *Austral Ecology* 31: 719–731.

van der Merwe, S., Greve, M., Skowno, A.L., Hoffman, M.T., & Cramer, M.D. 2023. Can vegetation be discretely classified in species-poor environments? Testing plant community concepts for vegetation monitoring on sub-Antarctic Marion Island. Ecology and Evolution 13: e9681.

Myers-Smith, I.H., Forbes, B.C., Wilmking, M., Hallinger, M., Lantz, T., Blok, D., Tape, K.D., Macias-Fauria, M., Sass-Klaassen, U., Levesque, E., Boudreau, S., Ropars, P., Hermanutz, L., Trant, A., Collier, L.S., Weijers, S., Rozema, J., Rayback, S.A., Schmidt, N.M., Schaepman-Strub, G., Wipf, S., Rixen, C., Menard, C.B., Venn, S., Goetz, S., Andreu-Hayles, L., Elmendorf, S., Ravolainen, V., Welker, J., Grogan, P., Epstein, H.E., & Hik, D.S. 2011. Shrub expansion in tundra ecosystems: dynamics, impacts and research priorities. *Environmental Research Letters* 6: 045509.

Nolan, C., Overpeck, J.T., Allen, J.R.M., Anderson, P.M., Betancourt, J.L., Binney, H.A., Brewer, S., Bush, M.B., Chase, B.M., Cheddadi, R., Djamali, M., Dodson, J., Edwards, M.E., Gosling, W.D., Haberle, S., Hotchkiss, S.C., Huntley, B., Ivory, S.J., Kershaw, A.P., Kim, S.-H., Latorre, C., Leydet, M., Lezine, A.-M., Liu, K.-B., Liu, Y., Lozhkin, A. V, McGlone, M.S., Marchant, R.A., Momohara, A., Moreno, P.I., Mueller, S., Otto-Bliesner, B.L., Shen, C., Stevenson, J., Takahara, H., Tarasov, P.E., Tipton, J., Vincens, A., Weng, C., Xu, Q., Zheng, Z., & Jackson, S.T. 2018. Past and future global transformation of terrestrial ecosystems under climate change. *Science* 361: 920–923.

Nunez, S., Arets, E., Alkemade, R., Verwer, C., & Leemans, R. 2019. Assessing the impacts of climate change on biodiversity: is below 2 degrees C enough? *Climatic Change* 154: 351–365.

Øvstedal, D.O., & Gremmen, N.J.M. 2001. The lichens of Marion and Prince Edward Islands. *South African Journal of Botany* 67: 552–572.

Phiri, E.E., Mcgeoch, M.A., & Chown, S.L. 2009. Spatial variation in structural damage to a keystone plant species in the sub-Antarctic: interactions between *Azorella selago* and invasive house mice. *Antarctic Science* 21: 189–196.

Piao, S., Wang, X., Park, T., Chen, C., Lian, X., He, Y., Bjerke, J.W., Chen, A., Ciais, P., Tommervik, H., Nemani, R.R., & Myneni, R.B. 2020. Characteristics, drivers and feedbacks of global greening. *Nature Reviews Earth & Environment* 1: 14–27.

R Core Team. 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing.

Raath-Krüger, M.J., Schöb, C., McGeoch, M.A., Burger, D.A., Strydom, T., & le Roux, P.C. 2023. Long-term spatially-replicated data show no physical cost to a benefactor species in a facilitative plant-plant interaction. *OIKOS:* e09617.

Raath-Krüger, M.J., McGeoch, M.A., Schöb, C., Greve, M., & le Roux, P.C. 2019. Positive plant-plant interactions expand the upper distributional limits of some vascular plant species. *Ecosphere* 10: e02820.

Ripley, B.S., Edwardes, A., Rossouw, M.W., Smith, V.R., & Midgley, G.F. 2020. Invasive grasses of sub-Antarctic Marion Island respond to increasing temperatures at the expense of chilling tolerance. *Annals of Botany* 125: 765–773.

Rohde, R.F., & Hoffman, M.T. 2012. The historical ecology of Namibian rangelands: Vegetation change since 1876 in response to local and global drivers. *Science of the Total Environment* 416: 276–288.

le Roux, P.C., & McGeoch, M.A. 2008a. Changes in climate extremes, variability and signature on sub-Antarctic Marion Island. *Climatic Change* 86: 309–329.

le Roux, P.C., & McGeoch, M.A. 2008b. Rapid range expansion and community reorganization in response to warming. *Global Change Biology* 14: 2950-2962.

le Roux, P.C., McGeoch, M.A., Nyakatya, M.J., & Chown, S.L. 2005. Effects of a short-term climate change experiment on a sub-Antarctic keystone plant species. *Global Change Biology* 11: 1628–1639.

le Roux, P.C., Ramaswiela, T., Kalwij, J.M., Shaw, J.D., Ryan, P.G., Treasure, A.M., McClelland, G.T.W., McGeoch, M.A., & Chown, S.L. 2013. Human activities, propagule pressure and alien plants in the sub-Antarctic: Tests of generalities and evidence in support of management. *Biological Conservation* 161: 18–27.

Rudolph, E.M., Hedding, D.W., Fabel, D., Hodgson, D.A., Gheorghiu, D.M., Shanks, R., & Nel, W. 2020. Early glacial maximum and deglaciation at sub-Antarctic Marion Island from cosmogenic Cl-36 exposure dating. *Quaternary Science Reviews* 231: 106208.

Russell, J.C., Meyer, J.Y., Holmes, N.D., & Pagad, S. 2017. Invasive alien species on islands: impacts, distribution, interactions and management. *Environmental Conservation* 44: 359–370.

Ryan, P.G., Smith, V.R., & Gremmen, N.J.M. 2003. The distribution and spread of alien vascular plants on Prince Edward Island. *African Journal of Marine Science* 25: 555–562.

Shaw, J.D. 2013. Southern Ocean Islands invaded: Conserving biodiversity in the world's last wilderness. In Foxcroft, L., Pyšek, P., Richardson, D., & Genovesi, P. (Eds.), *Plant Invasions in Protected Areas. Invading Nature - Springer Series in Invasion Ecology, vol 7*, Springer, Dordrecht.

Simberloff, D., & Dayan, T. 1991. The plant guild concept and the structure of ecological communities. *Annual Review of Ecology, Evolution and Systematics* 22: 115–143.

Skowno, A.L., Jewitt, D., & Slingsby, J.A. 2021. Rates and patterns of habitat loss across South Africa's vegetation biomes. *South African Journal of Science* 117: 1-5.

Smith, V.R., Avenant, N., & Chown, S.L. 2002. The diet and impact of house mice on a sub-Antarctic island. *Polar Biology* 25: 703–715.

Smith, V.R., & Mucina, L. 2006. Vegetation of sub-Antarctic Marion and Prince Edward Islands. In Mucina, L., Rutherford, M.C., & Powrie, L.W. (eds.), *Vegetation of South Africa, Lesotho and Swaziland*, pp. 699–723. South African National Biodiversity Institute, Pretoria, South Africa.

Smith, V.R., & Steenkamp, M. 1990. Climatic change and its ecological implications at a subantarctic island. *Oecologia* 85: 14-24.

Smith, V.R., & Steenkamp, M. 2001. Classification of the terrestrial habitats on Marion Island based on vegetation and soil chemistry. *Journal of Vegetation Science* 85: 14-24.

Smith, V.R., Steenkamp, M., & Gremmen, N.J.M. 2001. Terrestrial habitats on sub-Antarctic Marion Island: Their vegetation, edaphic attributes, distribution and response to climate change. *South African Journal of Botany* 67: 641–654.

Stow, D.A., Hope, A., McGuire, D., Verbyla, D., Gamon, J., Huemmrich, F., Houston, S., Racine, C., Sturm, M., Tape, K., Hinzman, L., Yoshikawa, K., Tweedie, C., Noyle, B., Silapaswan, C., Douglas, D., Griffith, B., Jia, G., Epstein, H., Walker, D., Daeschner, S., Petersen, A., Zhou, L.M., & Myneni, R. 2004. Remote sensing of vegetation and land-cover change in Arctic Tundra Ecosystems. *Remote Sensing Of Environment* 89: 281–308.

Tape, K., Sturm, M., & Racine, C. 2006. The evidence for shrub expansion in Northern Alaska and the Pan-Arctic. *Global Change Biology* 12: 686–702.

Vila, M., Espinar, J.L., Hejda, M., Hulme, P.E., Jarosik, V., Maron, J.L., Pergl, J., Schaffner, U., Sun, Y., & Pysek, P. 2011. Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. *Ecology Letters* 14: 702–708.

Webb, R.H., Boyer, D.E., & Turner, R.M. 2010. *Repeat Photography: Methods and Applications in the Natural Sciences*. Island Press, Washington, USA.

Wood, S.N. 2011. Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *Journal of the Royal Statistical Society (B)* 73: 3-36.

Xia, Y., Xu, W., Hu, Y., & Xie, F. 2020. Southern-Hemisphere high-latitude stratospheric warming revisit. *Climate Dynamics* 54: 1671–1682.

Xie, Y., Sha, Z., & Yu, M. 2008. Remote sensing imagery in vegetation mapping: a review. *Journal of Plant Ecology* 1: 9–23.

Yeloff, D., Mauquoy, D., Barber, K., Way, S., van Geel, B., & Turney, C.S.M. 2007. Volcanic ash deposition and long-term vegetation change on subantarctic Marion Island. *Arctic Antarctic and Alpine Research* 39: 500–511.

Appendix B

Table B1. Description of habitat complexes and their key plant characteristics. "Prominent species" include only one or two vascular species with distinct traits, such as colour or growth form, and which were used for the identification of habitats in the photographs. The information in the table has been adapted from Smith & Steenkamp (2001) and Smith & Mucina (2006).

Habitat complex	Dominant plant guild/s	Prominent species	Notes on identifying habitats in photographs
Fellfield	Cushion dicot and epiphytic graminoid	*Azorella selago, Polypogon magellanicus*	The cushion growth form, with low abundance of other growth forms, is the identifying character for fellfield.
Slope	Pteridophyte or suffrutescent herb	*Austroblechnum penna-marina, Acaena magellanica*	*A. penna-marina* dominates most slopes in photographs. *A. penna-marina* slopes have a conspicuous dark green colour in summer and dark brown in winter, which stands in stark contrast to the yellow brown mires which usually surround slopes. *A. magellanica* is the only deciduous species, and thus may not be as conspicuous in photographs.
Mire	Mire graminoid and bryophyte	*Polypogon magellanicus, Juncus scheuchzerioides, Carex dikei*	Mire vegetation occurs in two layers, with yellow (*P. magellanicus*) and reddish brown graminoids being the only visible layer in photographs.
Coastal saltspray	Erect dicot	*Crassula moschata*	This is the only habitat where the small, succulent herb, *C. moschata* cover exceeds 1% and is conspicuously red/orange in many areas, although may also be green.
Biotic	Tussock graminoid, rosette dicot, mat dicot	*Poa cookii, Leptinella plumosa, Callitriche antarctica*	*Poa cookii* is the only large tussock species on the island to identify biotic areas and biotic herbfields are easily identified by the small herbaceous plants, forming mats and continuous stands of herbs.

Table B2. Description of plant guilds used in repeat photography analysis. "Species" incudes all species categorised under each plant guild. "Dominant species" which are named first in the list of characteristic species are those species that have the highest cover within each guild that would ecologically be the most important and that could easily be identified in the repeat photography analysis. The information in the Table has been adapted from Smith & Steenkamp (2001) and Smith & Mucina (2006).

Plant guild	Characteristic species in the guild	Notes
Bryophyte	*Racomitrium lanuginosum.* All bryophytes species	Bryophytes were not easily identified in photographs and were thus grouped into one category, although *Racomitrium lanuginosum* is white and the most prominent bryophyte visible in photographs

Pteridophyte	*Austroblechnum penna-marina, Elaphoglossum randii, Lycopodium saururus, Lycopodium magellanicum, Polystichum marionensis, Hymenophyllum peltatum, Grammitis kergeulensis.*	*A. penna-marina* overwhelmingly dominates pteridophyte cover. All other ferns and clubmosses have very low cover in most habitats, and only in those where *A. penna-marina* is dominant, thus they would not be visible in photographs. *A. penna-marina* ecologically and phenologically acts like a dwarf shrub, not a typical fern, and should be considered separately from other ferns. *A. penna-marina* discolours in winter but is easily distinguished by its brown colour in winter and dark green in summer.
Mire graminoid	*Polypogon magellanicus, Carex dikei, Juncus scheuchzerioides*	*P. magellanicus* is abundant in mires and in fellfield, where it grows epiphytically in cushion plants. It can thus be considered as different guilds depending on the substrate it grows in. It has a conspicuous yellow/brown colour.
Tussock graminoid	*Poa cookii*	*P. cookii* is a large robust grass with dark green leaves and dense inflorescences, which easily distinguishable from other grasses. It occurs in areas influence by animals.
Epiphytic graminoid	*P. magellanicus, P. cookii* that grow in *Azorella selago* cushion plants	*P. magellanicus* is abundant in fellfield, where it grows epiphytically in cushion plants. It has a conspicuous yellow colour. *P. cookii* occurs less frequently in cushion plants
Alien grass	*Poa annua, Agrostis stolonifera, Poa pratensis*	*P. annua* has invaded most coastal areas with manuring by seals and penguins. Alien grasses are easily distinguishable, especially where *P. annua* forms dense lawns as a result of trampling. *A. stolonifera* also form dense patches in areas it invades.
Alien herb	*Sagina procumbens, Stellaria media, Cerastium fontanum*	*S. procumbens* is a mat and cushion-forming invasive plant species and the only alien herb species easily identified in photographs. The other two alien herbs are less conspicuous, but were detected in field notes.
Mat dicot	*Callitriche antarctica, Montia fontana, Ranunculus biternatis*	All species in this guild occur in wet areas, often in areas influenced by animals.
Cushion dicot	*Azorella selago, Collobanthus kergeulensis*	*C. kergeulensis* was not observed in the photographs, thus cushion dicot always refers to *A. selago,* which is a dense cushion-forming species important in tundra vegetation. The cushion growth form is capable of withstanding mechanical damage by wind.
Rosette dicot	*Leptinella plumosa*	*L. plumosa* is abundant in the coastal zone influenced by either saltspray or in soil enriched by animals.
Erect dicot	*Crassula moschata*	*C. moschata* is restricted to the coastal zone influenced by saltspray.
Shrub	*Acaena magellanica*	*A. magellanica* is the only semi-woody species on the island, however it is challenging to estimate its cover from photographs, as *A. penna-marina* is often co-dominant and has higher cover even in habitats where *A. magellanica* may be important. *A. magellanica* distribution is determined by drainage patterns.

Chapter 4

Spatial variability in soil properties on sub-Antarctic Marion Island: an example of the utility of predictive soil mapping

Mire vegetation in the foreground in waterlogged soils, with bryophytes and graminoids growing on top. In the midground, the fern *Austroblechnum penna-marina* is prevalent on the well-drained soils on the slopes interspersed by smaller mires. A scoria cone, made up of loose scoria gravel, and thus no soil, is visible in the background centre.

Abstract

More detailed knowledge of the variation and drivers of soil properties are needed to provide a more comprehensive understanding of the impacts of the rapidly changing climate of the sub-Antarctic region, as the associations of the biota with soil properties are likely to change accordingly. The assumption that all ecologically-relevant environmental data are included in species distribution models is often violated because soils data are seldom included. Therefore, spatially interpolated locally-derived soil data at fine spatial scales are needed to accurately reflect the niches occupied by plant species. The spatial variation of key soil properties (pH, N, P, K, C, Ca, loss on ignition, Mg, Na and Mn) across sub-Antarctic Marion Island (MI) was modelled using boosted regression trees (BRTs) including all ecologically-relevant and available environmental and biotic predictor variables. To assess whether soil properties could perhaps differentiate the three vegetation units classified in Chapter 2, soil properties were compared between units using an analysis of variance. Soil properties showed considerable spatial variation across MI and the BRT models highlighted that the biotic influences, of which NDVI and distance to fauna were the key proxies, as well as elevation were most strongly associated with soil properties. The predictive power of the BRT models was generally high, explaining a large proportion of the observed deviance. The soil properties did not differ significantly between inland and coastal vegetation, supporting the findings of weak differentiation between the composition of inland and coastal vegetation. However, in comparison, fellfield had significantly lower nutrient content, higher pH and higher concentration of cations than coastal and inland vegetation. The addition of spatially explicit maps of soil data is a significant step forward for the exploration of spatial biodiversity patterns in the sub-Antarctic. For example, species distribution models may now investigate the influence of soil properties in determining the spatial distribution of plant species.

Introduction

Spatially explicit distribution modelling has advanced substantially in recent decades (Henderson et al. 2014; Caradima et al. 2019), becoming an important tool in forecasting anthropogenic effects on biodiversity patterns (Guisan & Thuiller 2005; Qazi et al. 2022). Access to freely available geospatial data has made it possible for biologists to address various ecological questions over large scales, especially pertaining to drivers of species distributions and consequences of changes in drivers under different scenarios (Austin & Van Niel 2011; Guillaumot et al. 2018). High resolution climate, topography and satellite-derived data are now available across most regions of the world. However, the accuracy of distribution models are based on the assumption that all ecologically-relevant environmental data are included in the models (Guisan & Thuiller 2005), within the confines of data accessibility limitations. This assumption is often violated because soil data are seldom included (Cramer et al. 2019; Roe et al. 2022). Global soil data are available at relatively fine resolutions, e.g. the SoilGrids database (250 m resolution;

Hengl et al. 2017), but with limited accuracy and poor representation of regions with low sampling density (Cramer et al. 2019), including remote regions such as the sub-Antarctic. Therefore, spatially interpolated locally-derived soil data at fine spatial scales are needed to accurately reflect the niches occupied by species in a region.

Variation in soil properties are determined by a complex interaction famously encapsulated by Jenny (1980) in an equation that defined soil formation as the result of regional climate, potential biota present, relief, parent material and time. In the sub-Antarctic region, the few land masses are scattered, relatively undisturbed and young islands, most of volcanic origin. Soil nutrient inputs in the sub-Antarctic apart from those derived from parent geology are thus largely through saltspray, marine mammals and seabirds and terrestrial organic matter decomposition (Smith 1978; Smith & Steenkamp 2001; Wilson et al. 2019). Recent research from sub-Antarctic Macquarie Island suggests that topography, elevation and drainage are important drivers of soil properties such as soil organic C and total N (Wilson et al. 2019). Environments that are the same age, and have a similar climate and organisms acting on parent material, as well as topography, are expected to have similar soil properties (Hengl & MacMillan 2019). Therefore, other sub-Antarctic islands may have comparable soil properties where topography, climate and biota are similar. More detailed knowledge of the variation and drivers of soil properties may provide a more comprehensive understanding of the impacts of the rapidly changing climate of the sub-Antarctic region (Chapter 3; le Roux & McGeoch 2008; Bergstrom et al. 2015), as the associations of the biota with soil properties are likely to change accordingly.

At Marion Island (MI), in the sub-Antarctic, geospatial data was previously limited, and thus the utility of spatial modelling was restricted. More recently, climate (Leihy et al. 2018; Goddard et al. 2022) and geospatial data (Rudolph et al. 2022) has been made publicly available, and advances in satellite imagery has made the use of remotely-sensed data possible, although still limited, in a region with near-permanent cloud cover. Therefore, more accurate and comprehensive spatial environmental data can now be used to investigate species-environmental relationships. However, soil spatial data are not available for the sub-Antarctic. In a rapidly changing system due to changing climate and alien species invasions (Chapter 3), there is a requirement for accurate and up to date soil information to monitor changes in soil properties and the biota associated with it (Mahmoudzadeh et al. 2022). Modelling soil properties accurately can be challenging due to the complex nature of soil development (McBratney et al. 2003; Hengl et al. 2017), especially in remote and difficult to access environments, such as MI. However, modelling and mapping soil properties on MI, may provide valuable insights into the unique and complex environmental conditions of this region, as well as its role in the ecology and evolutionary history of the island. Soil maps may thus also assist in conservation planning (Hengl & MacMillan 2019).

Cations, K, Na, Mg and Ca are presumably transferred to the island largely through precipitation (Smith 2008), strongly influenced by saltspray from the ocean that can reach far inland with the strong winds experienced on MI (Smith 1977). Furthermore, leaching due to consistent heavy rains on MI may also play a key role in the concentration of soil nutrients (Smith 2008). An approximation of rock weathering on MI estimated rates of mass loss of clasts placed in the field for three years of up to 0.1% 1 yr^{-1} (grey lava) and 0.7% 1 yr^{-1} (black lava; (Sumner 2004), and thus nutrient input through weathering may also play a role in nutrient concentrations, especially in the interior of the island. However, several components of nutrient cycling including chemical weathering and leaching, are poorly understood on MI (Smith 2008).

Soil properties inherently influence the vegetation that is able to grow at specific locations (Gessler et al. 1995) and may result in patchy vegetation, since soil properties can vary over short distances. Some plant species for instance do not grow in the waterlogged soils in mires or in the high salinity of the coastal saltspray zone on MI (Smith et al. 2001). van der Merwe et al. (2023) could not robustly classify the vegetation on MI with the plant species cover alone and suggested that if vegetation had to be considered at the plant community-level, only three units, fellfield, inland and coastal vegetation could be differentiated, albeit weakly, based on the aerial cover of plant species (Chapter 2). They suggested that soil properties may differ significantly between units and perhaps differentiate the vegetation on MI more clearly to help elucidate whether vegetation in species-poor environments can indeed be viewed as assemblages of species that vary together.

Here, I aimed to model and map the spatial variation of key soil properties across MI and determine whether soil properties differ between vegetation units. The main purpose of this modelling attempt was for its utility in environmental predictions, especially to improve plant species distribution models (SDMs). I predict that there is considerable spatial variation in soil properties across MI which can be explained by a combination of biotic, topographic, hydrological and climatic variables.

Methods

Study site

Marion Island (46°54′ S, 37°45′ E) is situated in the sub-Antarctic, is *c.* 290 km^2 in area and has a relatively recent origin, dated to *c.* 450 000 years B.P. (Rudolph et al. 2021). It is the peak of a shield volcano, with Pleistocene grey basalts that have been overlain by younger Holocene black lavas and scoria cones (Rudolph et al. 2021). The climate is hyper-oceanic, cool, windy, with little seasonal or diurnal temperature variation and has high mean annual rainfall, although rainfall has rapidly decreased in recent decades (Chapter 3). The prevailing wind directions are NW, W and SW (Goddard et al 2022). Soils are generally acidic, shallow and high in organic content (Smith 1978). Plant species richness is low, with 39 vascular plant species on the island, of which 21 are native and 17 non-native. Vegetation is concentrated within 300 m of the coast, although some species can grow up to 850 m a.s.l.

The south and west coasts of the island have steep slopes and cliffs with terrain not easily accessible to animals (Fig. 1). The north and east coasts slope gently from the coast toward the interior, creating easier access for fauna to reach further inland than the south and east coasts. Seals and penguins are the major faunal influence on the island due to nutrient-input and trampling (Smith & Steenkamp 2001). Three species of seal, the southern elephant seal (*Mirounga leonine*), Antarctic fur seal (*Arctocephalus gazella*) and sub-Antarctic fur seal (*Arctocephalus tropicalis*) breed on the island. Elephant seals mainly occur along sheltered beaches on the east coast whereas fur seals can move further inland and visit less sheltered beaches (Ryan & Bester 2008). Four penguin species, namely king (*Aptenodytes patagonicus*), gentoo (*Pygoscelis papua*), rockhopper (*Eudyptes chrysocome*) and macaroni (*Eudyptes chrysolophus*) also breed on MI (Ryan & Bester 2008). Furthermore, the invasive house mouse (*Mus musculus*) occurs on the island and have impacted all aspect of the ecosystem (McClelland et al. 2018).

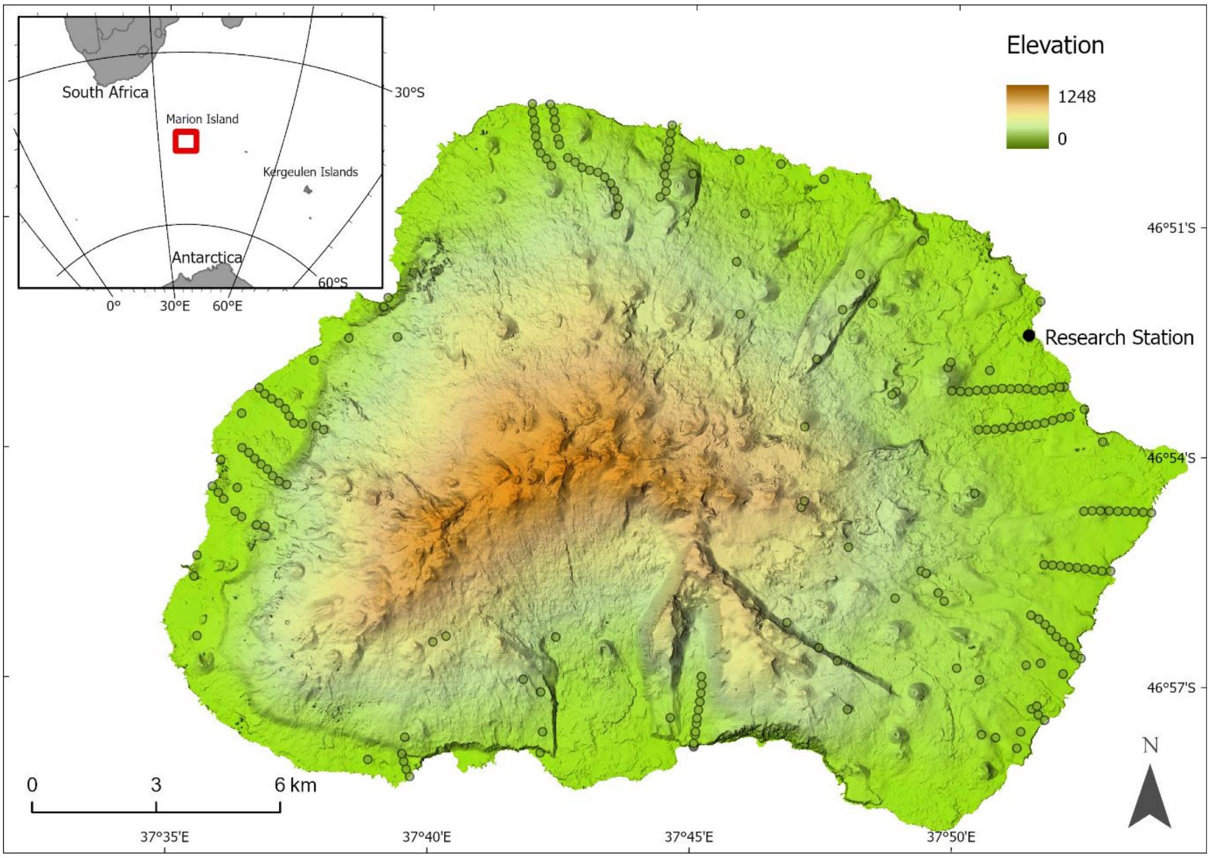


Figure 1. Topography of the volcanic Marion Island. The coastal plain on the north and east coasts is *c.* 5 km wide and gently slopes from the coast to the mountainous interior. The south-west and west coasts form a narrow plain of less than 1 km, after which it steeply slopes toward the central rocky interior. The south coast has sheer cliffs and a discontinuous and narrow coastal plain. The vegetation on the island is mostly concentrated below 300 m a.s.l., with sparse vegetation and high rock cover above 300 m a.s.l and polar desert with no vascular vegetation above 850 m a.s.l. Green points indicate the locations where soil samples were taken.

Soil sampling

We collected 210 soil samples in 2018-2019 along elevational transects orientated perpendicular to the coast on the north, east, south and west coasts of MI (Fig. 1), from the densely vegetated coastal plains to the sparsely vegetated higher elevations (i.e., upper limit of vascular plant growth), thus including a wide range of habitats across the island. Transects coincided with permanent vegetation transects placed over the island for future monitoring, where permanent plots were located every 20m along each transect, starting at the coast and ending in fellfield. Soil samples were taken at the lower left corner of each plot. Soil samples from the unvegetated polar desert and areas in between the transects were sampled randomly (Fig. 1), although the south coast is inaccessible in many areas due to steep topography. The top 20 cm of the soil, or as much as possible where soil depth was lower, was collected using a trowel. The pH was estimated for all samples using an equal volume of soil to 1 M KCl solution. The samples were ground and milled to a fine powder with a ball mill prior to being fused to a glass disc in preparation for the elemental analysis to ensure homogenous sampling. The samples were combusted at 1 000^{0}C in a furnace for 2 h to estimate loss on ignition (LOI) and a separate sample was also combusted to remove organic matter before elemental analysis. Major element compositions (P, K, Ca, Mg, Na, Mn) were determined by XRF spectrometry at the Central Analytical Facilities, Stellenbosch University, South Africa using a Axios Wavelength Dispersive X-Ray Fluorescence spectrometer (Malvern Pananalytical, UK). To estimate total C and total N, a known weight of dried homogenous sample was introduced to a Vario EL Cube Elemental Analyzer (Elementar, Germany). The analyser combusts the samples and measures the total C and total N present in the samples.

Climate, topographic and remote sensing data

The most common environmental covariates used in predictive soil mapping were considered when determining the environmental data: digital elevation model-derivates, raw multispectral images, climate maps, vegetation or land cover covariates, land use information and expert-based maps such as geology maps (Hengl & MacMillan 2019).

Topographic variables included a digital surface model (DSM, 1 m resolution) developed by the National Geo-spatial Information Directorate of the South African Department of Rural Development and Land Reform, resampled to 5 m resolution (Rudolph et al. 2022). Topographic information, including “slope” and “aspect”, were extracted from the DSM in ArcGIS Pro 2.9 (Environmental Systems Research Institute, CA, USA), at 5 m resolution (see Table C1 in Appendix C for layer descriptions). Aspect was converted to northness and eastness by calculating the sine of the slope, multiplied by the cosine and sine of aspect respectively, resulting in a circular variable that is transformed into a continuous variable from -1 to 1. A northness value of 1 represents a northern steep slope with high solar radiation and -1 a steep southern slope exposed to low solar radiation (Amatulli et al. 2018). Drainage lines were generated from the DSM with the ”Hydrology” toolset in ArcGIS, by first generating “Fill” (z-limit=unspecified), then “Flow Direction” (method = D8) and lastly “Flow Accumulation” using a >50 000 flow accumulation parameter. A “distance to drainage lines” layer was created in ArcGIS using the “Euclidean distance” tool. To approximate potential soil moisture, a topographic wetness index (TWI) was generated in ArcGIS using “Slope” (converted to radians) and “Flow Accumulation” in the “Raster Calculator” to fit the TWI equation suggested by Beven & Kirkby (1979). Climate variables included temperature and wind. High resolution monthly temperature data, developed by Leihy et al. (2018), were downloaded at 1 km resolution. The mean, minimum and maximum annual monthly temperatures of both day and night were extracted. Temperature range was calculated by subtracting the minimum annual nightly temperature from the maximum annual daily temperature. A wind speed layer was downloaded from Goddard et al. (2022) at 30 m resolution. No spatial data are available for precipitation on MI, as precipitation is recorded at a single point at the meteorological station only. Given the hyper-oceanic climate at MI, rainfall is likely similar across the island, although wind may influence how rainfall is distributed.

Copernicus Sentinel 2 2019 and 2020 satellite imagery, processed by the European Space Agency was downloaded using Google Earth Engine. This imagery has 13 spectral bands between 10 m and 60 m resolution ranging from ultra-blue coastal aerosol (443 nm) to short wave infrared (2190 nm). Clouds are present throughout most of the year (especially on the south west coast) but these were masked out using the “QA60” cloud mask band where bit 10 and 11 were filtered to contain no opaque or cirrus clouds. The median of each band over 2019 and 2020 was then used. Because the aim of modelling soil properties was to improve plant species distribution models, I did not include vegetation types as predictors, as plant species were used to inform vegetation types and may result in circularity. A normalized difference vegetation index (NDVI) layer was created with the red (Sentinel band 4, 665 nm) and near infrared (Sentinel band 8, 842 nm) bands using the “raster” package (Hijmans 2023) in R (R Core team 2020), and served as the inclusion of vegetation in predicting soil properties. I excluded NDVI from models to test what the effect would be of excluding all vegetation indices, but this reduced model performance considerably and NDVI was therefore retained. The 13 satellite bands and NDVI layer were added to the environmental data. “Distance to coast” was generated with the “Euclidean distance” tool, using a coastline digitised in ArcGIS at 1:1000 m resolution based on the RGB ESRI basemap imagery in ArcGIS. “Distance to lakes” was generated from a digitised lakes layer (Rudolph et al. 2022) using the “Euclidean distance” tool. A geology map was obtained from Rudolph et al. (2021). All environmental layers were rasterised and resampled (using “nearest neighbour” for categorical data and “bilinear” for continuous data), to the same extent and resolution (5 m) as the DSM (Table B1), and then “stacked” with the “raster” package in R.

Faunal distributions

Distance to the location of rookeries and beaches where seals occur served as a proxy for faunal influence (Table B1). The census locations of seals on MI were obtained from the Marion Marine Mammal Programme, published in Rudolph et al. (2022) and Wege et al. (2016). The largest penguin colonies, which were visible on satellite imagery were digitised in ArcGIS using the ESRI World Imagery at 1:1000 m scale. These were mainly king and macaroni penguins which breed in dense colonies and cause severe erosion, with 80% of macaroni penguins occurring in two colonies at Kildalkey and Bullard Bay (Crawford et al. 2003). A buffer was created around nesting sites, colonies and beaches frequented by seals and penguins. The size of the buffers, i.e., area of influence, was informed by the accessibility of the landscape to seals and penguins, by using “Profile Curvature” in ArcGIS, which is the rate of change of slope. Curvature is a well-established parameter of land surface topography, often used to help identify flood or land slide risk (Pradhan & Lee 2010). Curvature determines how different a slope is to a flat surface, visible as convex or concave "curves". The buffer was drawn around the nearest curve around beaches, rookeries and colonies, i.e., where the slope increases suddenly. This increase in slope was assumed to be inaccessible to seals and penguins (although I acknowledge that rockhopper and macaroni penguins are able to access steep slopes and cliffs at some parts of the island). Other penguins and seabirds occur more sporadically and/or more localised around the coast or further inland and thus could not be detected in satellite imagery. Grey-headed and sooty albatross occur on steep, near-vertical cliffs, and thus are not visible from above, making digitising in such areas challenging. These sites were thus excluded, although the largest ridges where albatross nest (such as Grey Headed Ridge) would be detected in the NDVI layer, as plant species, such as *Leptinella plumosa* and *Poa cookii* with strong digital signatures are associated with the nests.

Boosted regression trees

Boosted regression trees (BRTs) were used to associate soil variables with environmental drivers using the "dismo" (Hijmans et al. 2022) and "gbm" (Greenwell et al. 2022) packages, following Elith et al. (2008). BRTs are a machine learning approach with non-linear interactive models that are able to select the most important variables, identify and model interactions between variables, accurately predict the response variable and thus allow the determination of the most important correlations in the data. BRTs have been shown to have predictive advantages over generalised linear models and generalised additive models (Elith et al. 2008; Leathwick et al. 2009). BRTs have also successfully been used to model plant associations with environmental data at the study site (Momberg et al. 2021; Cramer et al. 2022). Various factors, such as topography, climate, manuring by animals, cushion plants and bryophytes likely play an important role in soil development (Smith & Mucina 2006; Lubbe 2010). I thus initially included all environmental data as predictors of soil variables. To assess collinearity of the environmental variables, variable inflation factors (threshold=10) were calculated for all environmental layers with the "usdm" package (Naimi et al. 2014), after which "distance to coast", maximum and minimum daily temperature, maximum and minimum nightly temperature and sentinel satellite bands 1 and 5-12 were removed from the environmental data due to collinearity (see Figure C1). The data in "distance to coast" would be represented by "distance to animals", as seals and penguins occur along the coast, and partly by elevation (DSM), which increases from the coast to the interior of the island.

Parameter optimisation of the BRTs was conducted for each model, testing the combination of tree complexities in the range 1 - 5 and learning rates of 0.1, 0.05, 0.01, 0.005, 0.001 and 0.0001 informed by guidelines for BRT parameters by Elith et al. (2008), after which "Gaussian" BRT models were run with tree complexity = 5, learning rate = 0.001 and bagging fraction = 0.7. The models were simplified with “gbm.simplify” in the “dismo” package, with only the most important predictor variables retained, ranked with the “gbm.step” function. Model simplification runs various models until the average change in predictive deviance exceeds its original standard error (calculated in the previous step). The final models were guided by the model simplification, resulting in more parsimonious models without degradation of model fit (Elith et al. 2008).

Given that geology, a categorical variables, is included in the predictor variables, an ordinary least squares approach cannot be used to evaluate model performance. The predictive power of the models were thus evaluated by a combination of pseudo R^2 (McFadden 1979) and the correlation between the predicted *vs.* observed values. This approach follows Cramer et al. (2019) and is frequently used to evaluate BRT models (Becker et al. 2020; Yu et al. 2020). “McFadden’s” pseudo R^2, also called log likelihood-ratio index, calculates the deviance explained as 1 - (residual cross-validation deviance/total deviance), where a pseudo R^2 of 0.2 - 0.4 is considered an excellent fit (McFadden 1979; Hemmert et al. 2018). After model evaluation, each soil variable was predicted to a raster layer using the BRT models and the environmental data used to build the models for the entire island at 5 m resolution in R, using the “predict” function in the “dismo” package.

Soil variability between vegetation units

The soil properties were compared between the three vegetation units identified by van der Merwe et al. (2023) (i.e., fellfield, inland and coastal vegetation). The vegetation units were classified with plant species cover plot data using random systematic sampling (see Chapter 2 for further detail). The predicted soil maps were combined using “stack” in the “raster” package. For the 467 vegetation plots used in the classification by van der Merwe et al. 2023, the soil properties were extracted from the soil raster layers, using the “extract” function in the “raster” package. Soil properties were then compared between vegetation units using an analysis of variance (ANOVA).

Results

Here, the results for soil properties most relevant to plant growth are presented (pH, N, P, K, C, Ca; see Appendix C for statistical details of LOI, Mg, Na and Mn). Overall, the BRT models performed well, with pseudo R^2 ranging from 0.33 (pH) to 0.48 (LOI), and large proportions of the deviance being explained by the predictor variables (Fig. 2, Table C2), indicating good model precision. The comparison between the predicted and observed values showed a good fit of the predicted soil properties for pH, N, K, C, Ca (Fig. 2), as well as LOI, Mg, Na and Mn (Fig. C2). The accuracy of the models indicated by how close the slope is to one, was also fairly high, except for P (Fig. 2, Fig. C2)

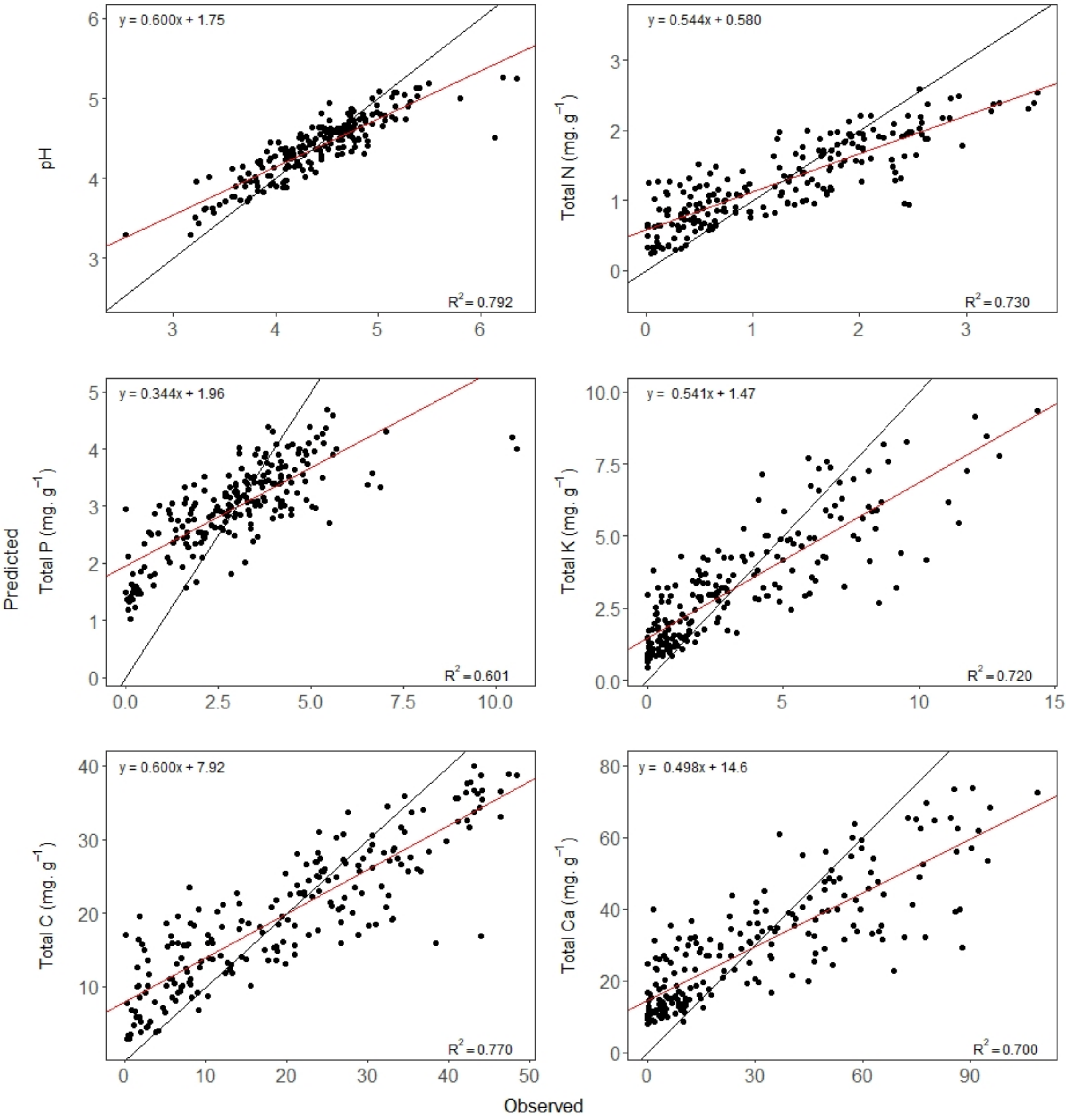


Figure 2. Plots showing the boosted regression tree model precision and accuracy of the six soil variables most relevant to plant growth. Observed values are plotted against predicted values. The red line indicates the linear

regression of predicted to observed values, while the black line indicates the 1:1 line. The R^2 of the linear models are indicated at the bottom right. Other soil properties are shown in Fig. C3.

Following model simplification, the most important predictors were retained for each model (Fig. 3). The BRT models consistently identified NDVI as the most influential predictor for all soil properties (Fig. 3; Fig. C3:C6). pH (Fig. 4) decreased, whereas N (Fig. 5), C (Fig. 6) and LOI (Fig. C3) increased with NDVI. pH was the lowest and N, C and LOI the highest in densely vegetated areas on the coastal plains, where faunal influence also occurs. Indeed, distance to fauna was associated with N, C and LOI (Fig. 3), increasing with proximity to faunal influence while pH decreased with proximity to animals. The cations, P (Fig. 7), K (Fig. 8), Ca (Fig. 9), Mg (Fig. C4) and Na (Fig. C5) decreased with NDVI and increased with distance to fauna. The importance of NDVI and distance to animals as predictors of most soil properties indicates the important influence of biotic effects on soil properties.

Elevation (DSM) was strongly associated with all soil properties, being in the first six most important predictors for all variables (Fig. 3). N, C and LOI was the highest at low elevations and P, K, Ca, Mg, Na and Mn increased with elevation. Temperature range was associated with N, P, K, Ca, LOI, Na, and Mn. N (Fig. 5) and LOI (Fig. C3) decreased and P (Fig. 7), K (Fig. 8), Ca (Fig. 9), Na (Fig. C5), and Mn (Fig. C6) increased with temperature range. pH was strongly associated with temperature range and mean nightly and daily temperatures (Fig. 4). Eastness was associated with N (Fig, 5), C (Fig. 6), LOI (Fig. C3), Mg (Fig. C4) and Mn (Fig. C6) with higher values of N, C and LOI on more east facing slopes. Wind speed was associated with P, K, Ca, LOI, Mg, Na and Mn. Slope was associated with P, K and Na, increasing with steeper slopes. Geology was not a strong predictor of soil properties.

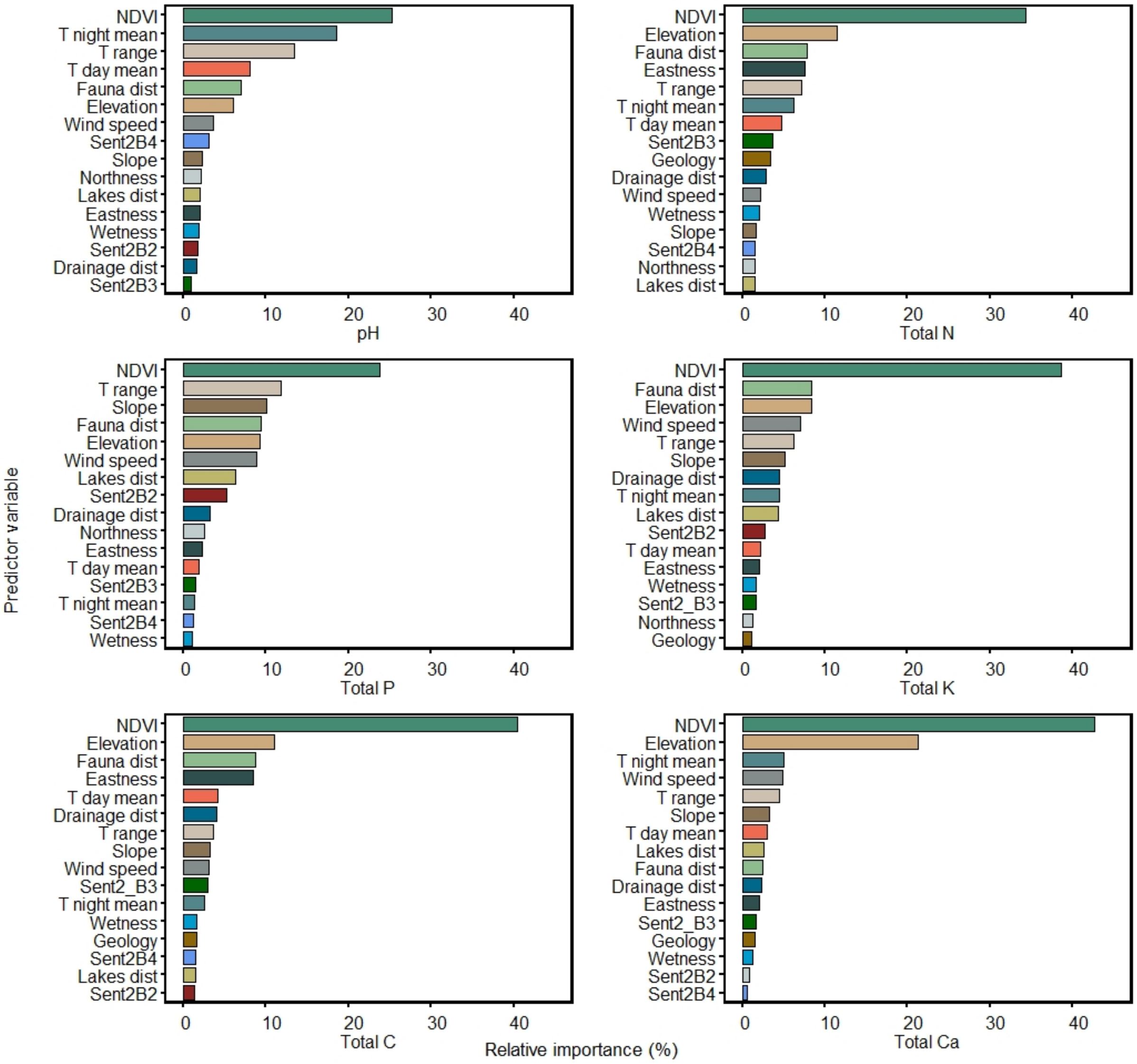


Figure 3. Variable relative importance showing the percentage that each predictor variable (indicated by colours), retained after model simplification, contributed to explaining the deviance of soil models. “Fauna dist” = distance to fauna, “T range” = temperature range, “T night mean” = mean nightly temperature, “T day mean” = mean daily temperature, “Drainage dist” = distance to drainage, “Lakes dist” = distance to lakes, “Sent2B2-4” = Sentinel 2 band 2-4.

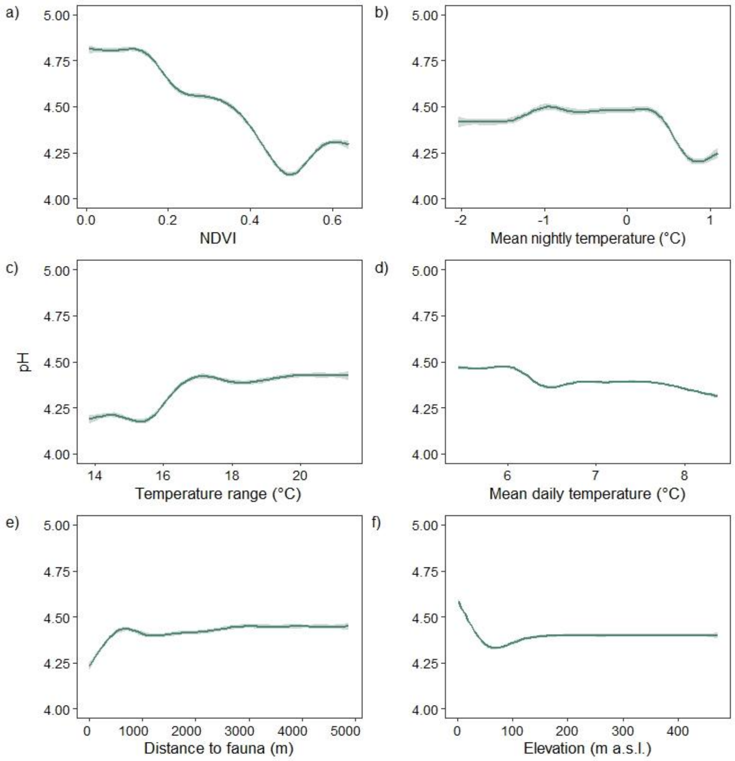


Figure 4. Partial dependence plots showing the relationship (± SE) between pH and the six most important predictor variables a) NDVI, b) mean nightly temperature, c) temperature range, d) mean daily temperature, e) distance to fauna and f) elevation. Standard error is shown, although is not visible in most graphs due to the small standard error.

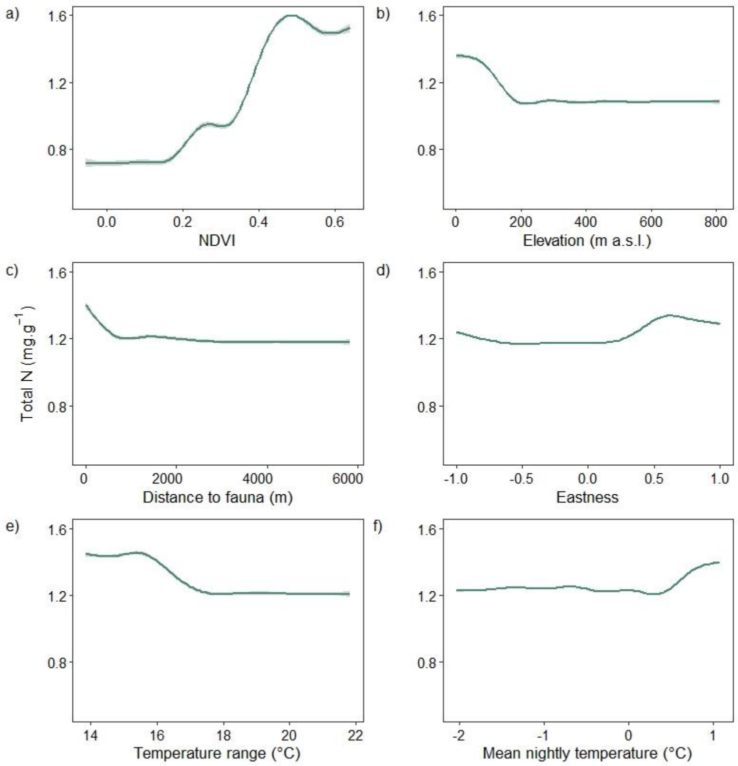


Figure 5. Partial dependence plots showing the relationship (± SE) between total N and the six most important predictor variables a) NDVI, b) elevation, c) distance to fauna, d) eastness, e) temperature range and f) mean

nightly temperature. Standard error is shown, although is not visible in most graphs due to the small standard error.

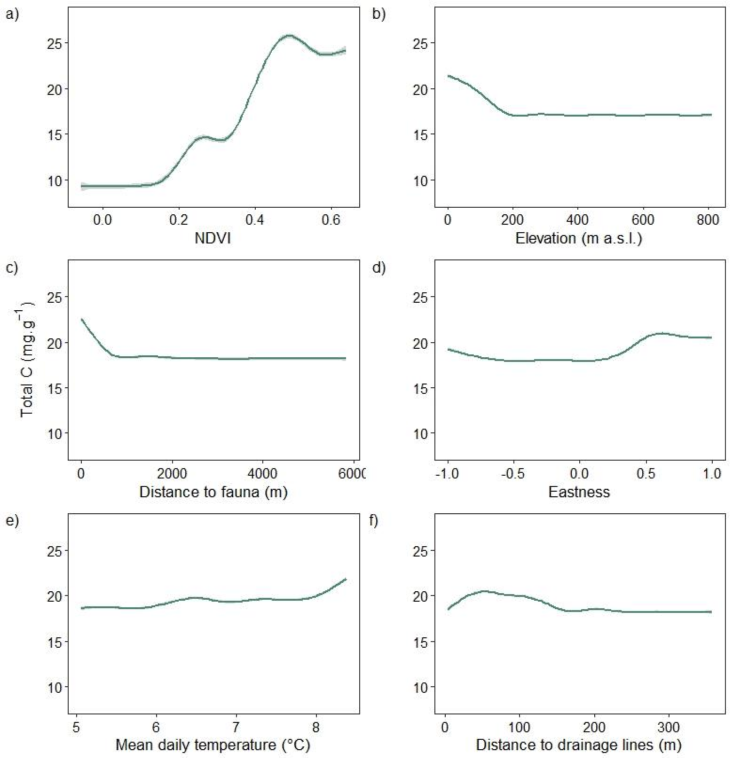


Figure 6. Partial dependence plots showing the relationship (± SE) between total C and the six most important predictor variables a) NDVI, b) elevation, c) distance to fauna, d) eastness, e) main daily temperature and f) distance to drainage lines. Standard error is shown, although is not visible in most graphs due to the small standard error.

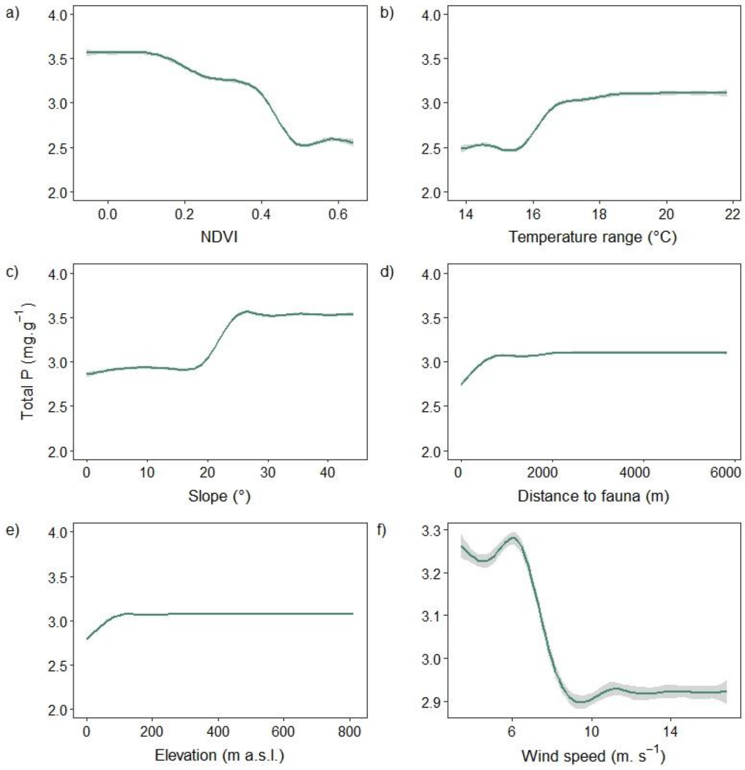


Figure 7. Partial dependence plots showing the relationship (± SE) between total P and the six most important predictor variables a) NDVI, b) temperature range, c) slope , d) distance to fauna, e) elevation and f) wind speed. Standard error is shown, although is not visible in most graphs due to the small standard error.

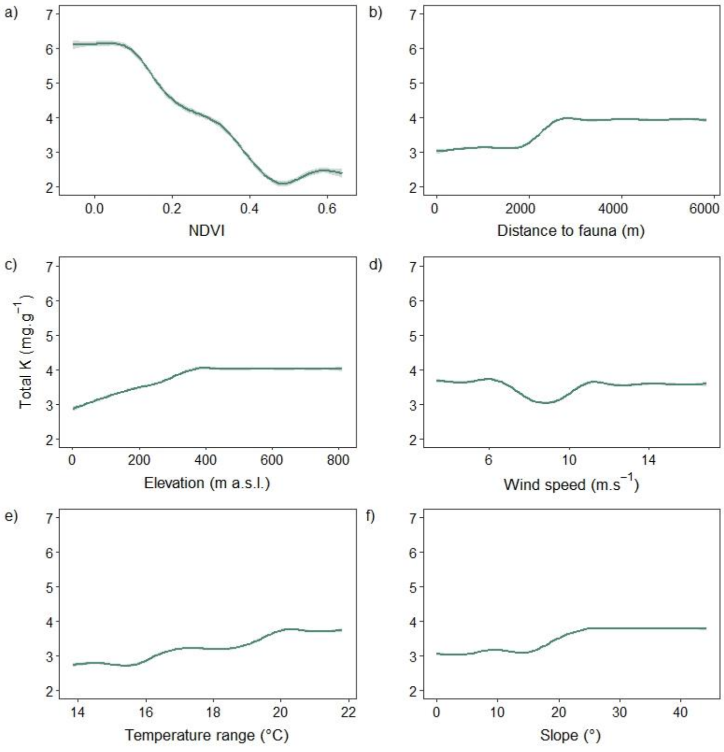


Figure 8. Partial dependence plots showing the relationship (± SE) between total K and the six most important predictor variables a) NDVI, b) distance to fauna, c) elevation, d) wind speed, e) temperature range and f) slope. Standard error is shown, although is not visible in most graphs due to the small standard error.

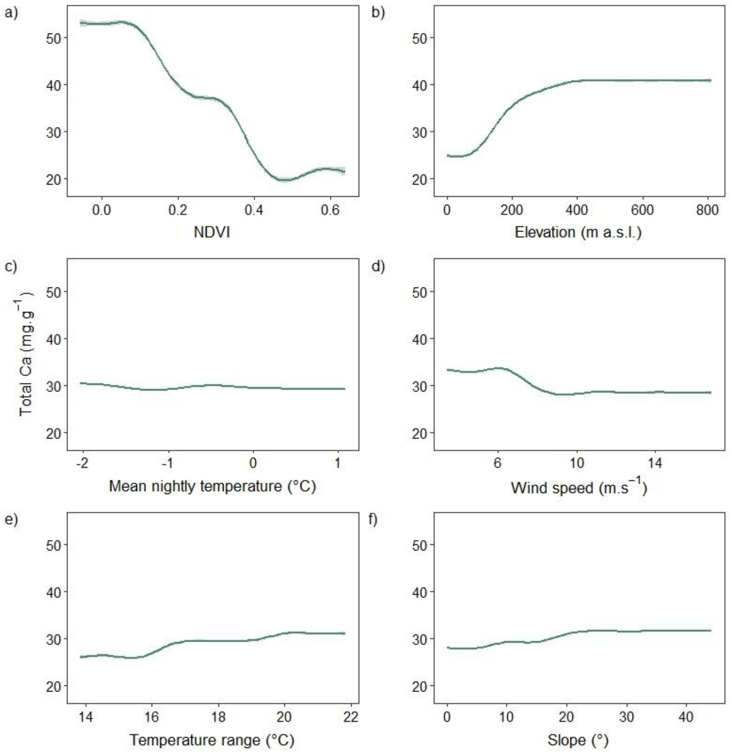


Figure 9. Partial dependence plots showing the relationship (± SE) between total Ca and the six most important predictor variables a) NDVI, b) elevation, c) mean nightly temperature, d) wind speed, e) temperature range and f) slope. Standard error is shown, although is not visible in most graphs due to the small standard error.

pH was higher on the west and north coasts than the east and south coasts of MI as well as on the coastal plains, visible in the prediction maps (Fig. 10). N and C (Fig. 10) and LOI (Fig. C7) concentrations were lower on the interior and south coast and higher on the east, north and west coasts as well as the coastal plains (Fig. 10). P, K, Ca (Fig. 10), Mg, Na and Mn (Fig. C7) had higher concentrations on the interior, scoria cones and south coast, as well as lower concentrations on the coastal plains of the island.

All soil properties differed significantly ($p < 0.05$) between fellfield and coastal vegetation, as well as fellfield and inland vegetation (Fig. 11; Fig. C8). Coastal and inland vegetation did not differ significantly for any soil property (Fig. 11; Fig. C8). Fellfield had lower N, C and LOI and higher pH, cation concentration and Mn than coastal and inland vegetation.

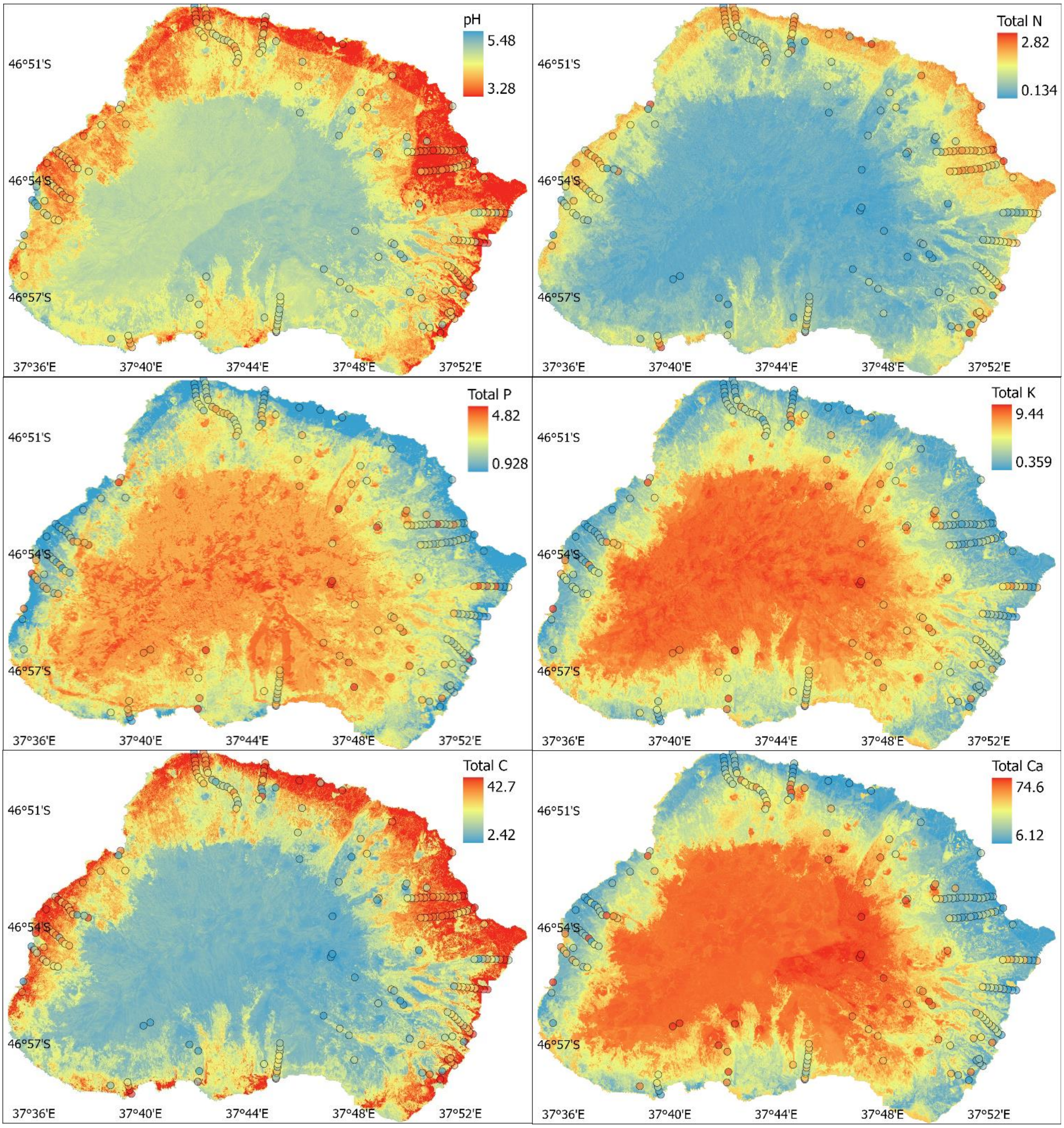


Figure 10. Spatial prediction maps of soil properties on MI. Observed values at each sampling location are indicated on the maps as points in the same colour gradient as the prediction maps. Where the colours of these points differ from the background the observed values differ from the modelled values. All soil properties, other than pH are indicated as mg g^{-1} soil dry weight. The six soil properties most relevant to plants are shown. Other soil properties are presented in Figure C7 in Appendix C.

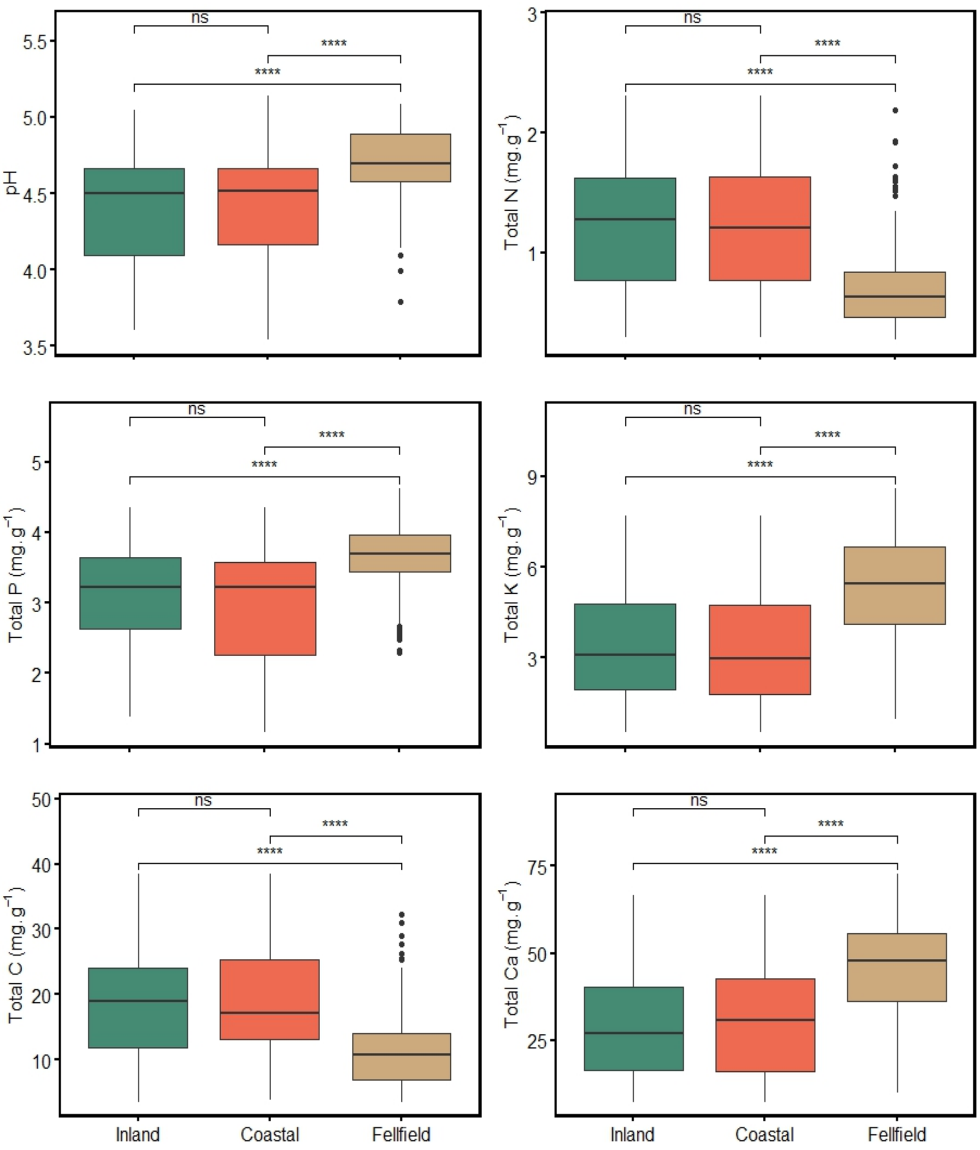


Figure 11. Comparison of soil properties most relevant to plant growth between inland (n = 130), coastal (n = 140) and fellfield (n = 192) vegetation on MI. “ns”= not significant, “*” = $p < 0.05$, “****”= $p < 0.001$. Other soil properties are shown in Figure C8 in Appendix C.

Discussion

The soil models that were produced here provide a key component of spatial environmental data, that was previously not available for MI (although see Lubbe 2010). Soil properties showed considerable spatial variation across MI and the BRT models highlighted the key associations between soil properties and climatic, topographic and biotic variables. The predictive power of the BRT models was generally high, explaining a large proportion of the observed deviance, indicating that the environmental data chosen was sufficient.

The objective of this paper was to develop accurate models for predicting soil characteristics to include in SDMs and other ecological applications, and not to explain the environmental dependencies of soil properties. I thus do not explain the drivers of each soil property in detail which would have to be based on rather speculative associations. However, from these models it is clear that the combination of climatic, biotic and topographic variables provided relatively accurate predictions of soil properties, confirming the importance of including all possible aspects of the environment for predicting soil characteristics, while keeping in mind the principles of parsimony (Austin & Van Niel 2011). I recognise that given the volcanic origin, and thus shape, of the island, many environmental variables covary from the coast toward the interior. For example, environmental severity increases from the coast to the central interior. Thus as distance to the coastline increases, temperature, NDVI and faunal influence decreases, whereas wind speed increases (le Roux & McGeoch 2008b). However, only predictor variables with a variable inflation factor smaller than ten were included to avoid any multicollinearity effects. BRTs are able to deal with complex models containing numerous continuous and categorical predictor variables, and does well in selecting the most relevant predictor variables, considering the interactions between them (De'ath 2007; Elith et al. 2008). Therefore, BRTs are a rather flexible regression modelling technique that can handle predictor interactions well and identify important interactions between them (De'ath 2007; Elith et al. 2008; Leathwick et al. 2009; Becker et al. 2020), such as soil nutrient content being higher in close proximity to fauna and low elevations on MI.

While all parameters were optimised to avoid overfitting, such as varying the permitted interaction complexity with the "learning rate" or using different proportions of the data to randomly subset with the "bagging fraction", there was some overprediction of the extreme (i.e., highest and lowest) values of soil properties. This phenomenon is common in machine learning techniques because having many trees and complex predictor interactions may reduce training errors and increase performance, but also increases the chances of overfitting (Park & Ho 2021). This delicate balance between best performance and overfitting is a challenge for any modeller (Park & Ho 2021; Pichler & Hartig 2023). However, BRTs are specifically utilised to reduce model overfitting, because it averages many decision trees through boosting, rather than using individual trees (De'ath 2007). I thus argue that some overfitting would always occur when complex machine learning models are utilised, although less so than traditional statistical methods (Pichler & Hartig 2023). Nonetheless, the predictions for the extremes should still be interpreted with caution. Additionally, the models were trained on only few samples of the high elevation, rocky interior of the island, and thus the accuracy of the soil predictions over this area may be low. However, the interior is mostly made up of exposed rock where only bryophytes and lichens are able to grow and accumulate litter (Smith & Steenkamp 2001); therefore, little soil is present in this region. Researchers are urged to keep these points in mind when interpreting the prediction maps.

The BRT models were successful in identifying key predictors of each soil property. The biotic influence, of which NDVI and distance to animals were key proxies, were strongly associated with most soil properties. The strong relative importance of NDVI in all models indicates the strong association between vegetation greenness and soil properties. N, C and LOI were higher where vegetation greenness was high, i.e., along the coastal plains where conditions are more suited to plant growth and nutrient input from animals and the ocean is higher, compared to the harsh and rocky interior. Nutrient input by marine mammals and seabirds that occur along the coast contribute considerably to soil fertility on MI (Smith et al. 2001). Furthermore, the decomposition of leaf litter is an important terrestrial nutrient input (Smith 2008) and thus N, C and LOI would be higher in denser vegetation on the coastal plains and around seal and seabird colonies.

The cations decreased with NDVI, which decreases from the coast toward the interior of the island, whilst being higher on scoria. Areas with low NDVI lack vegetation and thus posses high rock cover. Therefore, the cations increase with rock cover and may indicate the uptake of these nutrients by the vegetation which is denser on the coastal plains. This may also indicate the role of weathering in determining the concentrations of K, Ca, Mg and Na. The wind direction on MI is mainly west and south-west (Goddard et al. 2022), with wind speed being the highest on the south-west corner of the island (see Table C1). The high values of K, Ca, Mg and Na at the south-west of the island may thus reflect the prevailing wind direction, and the resultant blowing of saltspray from the south-west coast inland. On the south and west coasts, the cations are also higher at exposed sites near the coastline. Rock cover and wind speed increase while temperature decreases with elevation, which in turn forms a gradient from the coast toward the interior. Therefore, the importance of NDVI and elevation in predicting the cation concentrations likely indicate the combined role of saltspray (highest on the south-west coast) and weathering (increasing with elevation). Geology was not an important predictor for soil properties, confirming that parent material is not an important determinant of soil properties on MI, likely due to the young age of the island. Similarly, le Roex et al. (2012) found little difference in chemical composition between grey and black lava types on MI.

The soil properties did not differ significantly between inland and coastal vegetation. However, in comparison, fellfield has significantly lower nutrient content, higher pH and higher concentration of cations than coastal and inland vegetation. The fact that soil characteristics of coastal and inland vegetation did not differ significantly, supports the findings of weak differentiation between the composition of inland and coastal vegetation (see Chapter 2). The difference between soil properties of fellfield and the two other vegetation units could be driven by fellfield occurring in areas with high rock cover and sparse vegetation. The lack of accumulation of organic material and low trapping of nutrient deposition results in a lower nutrient content in fellfield (Smith & Mucina 2006) compared to coastal and inland vegetation. This provides further support that the vegetation on MI does not occur as assemblages of species, but rather as species that respond individualistically to the environment.

An important consideration when assessing soil fertility and nutrient status is the choice of how nutrient concentration are expressed (Weil & Brady 2016). Expressing soil nutrient content either on the basis of soil weight, soil mineral content or soil volume can have significant implications, particularly in soils with high organic matter content (Lehmann & Kleber 2015), such as those in the sub-Antarctic. Organic matter can increase soil volume considerably without contributing proportionally to nutrient availability, especially in peat soils found on MI, resulting in misleading overestimations of actual nutrient availability to plants. Expressing soils as only the mineral content, and thus excluding the organic matter which is presumably unavailable to plants, may be used as a solution to overestimation of organic-rich soils when expressed by volume (Weil & Brady 2016). However, it may also disregard the key role of organic matter in nutrient retention, cation exchange, microbial activity and nutrient cycling (Lehmann & Kleber 2015). Therefore, expressing soil nutrient content on the basis of weight (here as mg g^{-1}) was chosen in this study as it accounts for variations in the bulk density caused by organic matter content, thus considers the actual amount of nutrients per unit dry weight which plant roots are exposed to.

Conclusion

The addition of spatially explicit maps of soil data is a significant step forward for the exploration of spatial biodiversity patterns in the sub-Antarctic. For example, species distribution models may now investigate the influence of soil properties in determining the spatial distribution of plant species, since it has been demonstrated that including soil properties significantly improves habitat suitability estimations for plant species (Roe et al. 2022). This was the first spatial modelling of soil properties for the sub-Antarctic, thus future research may improve the accuracy of models. For MI, this can be done by increasing soil sample size, especially in the central interior, and/or by including other vegetation variables which may influence soil nutrient content.

References

Amatulli, G., Domisch, S., Tuanmu, M.-N., Parmentier, B., Ranipeta, A., Malczyk, J., & Jetz, W. 2018. A suite of global, cross-scale topographic variables for environmental and biodiversity modeling. *Scientific Data* 5: 180040.

Austin, M.P., & Van Niel, K.P. 2011. Improving species distribution models for climate change studies: variable selection and scale. *Journal of Biogeography* 38: 1–8.

Becker, E.A., Carretta V, J., Forney, K.A., Barlow, J., Brodie, S., Hoopes, R., Jacox, M.G., Maxwell, S.M., Redfern V, J., Sisson, N.B., Welch, H., & Hazen, E.L. 2020. Performance evaluation of cetacean species distribution models developed using generalized additive models and boosted regression trees. *Ecology and Evolution* 10: 5759–5784.

Bergstrom, D.M., Bricher, P.K., Raymond, B., Terauds, A., Doley, D., McGeoch, M.A., Whinam, J., Glen, M., Yuan, Z., Kiefer, K., Shaw, J.D., Bramely-Alves, J., Rudman, T., Mohammed, C., Lucieer, A., Visoiu, M., van Vuuren, B.J., & Ball, M.C. 2015. Rapid collapse of a sub-Antarctic alpine ecosystem: the role of climate and pathogens. *Journal of Applied Ecology* 52: 774–783.

Beven, K.J., & Kirkby, M.J. 1979. A physically based, variable contributing area model of basin hydrology. *Hydrological Sciences Journal* 24: 43-69.

Caradima, B., Schuwirth, N., & Reichert, P. 2019. From individual to joint species distribution models: A comparison of model complexity and predictive performance. *Journal of Biogeography* 46: 2260–2274.

Cramer, M.D., Hedding, D., Greve, M., Midgley, G.F., & Ripley, B.S. 2022. Plant specialisation may limit climate-induced vegetation change to within topographic and edaphic niches on a sub-Antarctic island. *Functional Ecology* 36: 2636–2648.

Cramer, M.D., Wootton, L.M., van Mazijk, R., & Verboom, G.A. 2019. New regionally modelled soil layers improve prediction of vegetation type relative to that based on global soil models. *Diversity and Distributions* 25: 1736–1750.

Crawford, R.J.M., Cooper, J., Dyer, B.M., Greyling, M.D., Klages, N.T.W., Ryan, P.G., Petersen, S.L., Underhill, L.G., Upfold, L., Wilkinson, W., De Villiers, M.S., Du Plessis, S., Du Toit, M., Leshoro, T.M., Makhado, A.B., Mason, M.S., Merkle, D., Tshingana, D., Ward, V.L., & Whittington, P.A. 2003. Populations of surface-nesting seabirds at Marion Island, 1994/95-2002/03. *African Journal of Marine Science* 25: 427–440.

De'ath, G. 2007. Boosted trees for ecological modeling and prediction. *Ecology* 88: 243–251.

Elith, J., Leathwick, J.R., & Hastie, T. 2008. A working guide to boosted regression trees. *Journal of Animal Ecology* 77: 802–813.

Gessler, P.E., Moore, I.D., Mckenzie, N.J., & J, R.P. 1995. Soil-landscape modeling and spatial prediction of soil attributes. *International Journal of Geographical Information Systems* 9: 421–432.

Goddard, K.A., Craig, K.J., Schoombie, J., & le Roux, P.C. 2022. Investigation of ecologically relevant wind patterns on Marion Island using Computational Fluid Dynamics and measured data. *Ecological Modelling* 464: 109827.

Greenwell, B., Boehmke, B., Cunningham, J., & Developers, G. 2022. gbm: generalized boosted regression models. Available at https://CRAN.R-project.org/package=gbm. [Accessed 15 May 2023].

Guillaumot, C., Martin, A., Eleaume, M., & Saucede, T. 2018. Methods for improving species distribution models in data-poor areas: example of sub-Antarctic benthic species on the Kerguelen Plateau. *Marine Ecology Progress Series* 594: 149–164.

Guisan, A., & Thuiller, W. 2005. Predicting species distribution: offering more than simple habitat models. *Ecology Letters* 8: 993–1009.

Hemmert, G.A.J., Schons, L.M., Wieseke, J., & Schimmelpfennig, H. 2018. Log-likelihood-based pseudo-R2 in logistic regression: Deriving sample-sensitive benchmarks. *Sociological Methods & Research* 47: 507–531.

Henderson, E.B., Ohmann, J.L., Gregory, M.J., Roberts, H.M., & Zald, H. 2014. Species distribution modelling for plant communities: stacked single species or multivariate modelling approaches? *Applied Vegetation Science* 17: 516–527.

Hengl, T., de Jesus, J.M., Heuvelink, G.B.M., Gonzalez, M.R., Kilibarda, M., Blagotic, A., Shangguan, W., Wright, M.N., Geng, X., Bauer-Marschallinger, B., Guevara, M.A., Vargas, R., MacMillan, R.A., Batjes, N.H., Leenaars, J.G.B., Ribeiro, E., Wheeler, I., Mantel, S., & Kempen, B. 2017. SoilGrids250m: Global gridded soil information based on machine learning. *PLOS ONE* 12: e0169748.

Hengl, T., & MacMillan, R.A. 2019. *Predictive soil mapping with R*. OpenGeoHub foundation, Wageningen, Netherlands.

Hijmans, R. 2023. raster: Geographic data analysis and modeling. Available at https://CRAN.R-project.org/package=raster. [Accessed 17 May 2023].

Hijmans, R.J., Phillips, S.J., Leathwick, J., & Elith, J. 2022. dismo: Species distribution modeling. Available at https://CRAN.R-project.org/package=dismo. [Accessed 11 May 2023].

Jenny, H. 1980. *The Soil Resource, origin and Behaviour*. Springer New York, NY.

Leathwick, J.R., Elith, J., Rowe, D., & Julian, K. 2009. Robust planning for restoring diadromous fish species in New Zealand's lowland rivers and streams. *New Zealand Journal of Marine and Freshwater Research* 43: 659–671.

Lehmann, J., & Kleber, M. 2015. The contentious nature of soil organic matter. *Nature* 528: 60–68.

Leihy, R.I., Duffy, G.A., Nortje, E., & Chown, S.L. 2018. High resolution temperature data for ecological research and management on the Southern Ocean Islands. *Scientific Data* 5: 180177.

Lubbe, N.R. 2010. Soil characteristics and pedogenesis on sub-Antarctic Marion Island. PhD thesis, University of Pretoria, Pretoria, South Africa.

Mahmoudzadeh, H., Matinfar, H.R., Kerry, R., Eskandari, S., Ebrahimi-Khusfi, Z., & Taghizadeh-

Mehrjardi, R. 2022. New hybrid evolutionary models for spatial prediction of soil properties in Kurdistan. *Soil Use and Management* 38: 191–211.

McBratney, A.B., Santos, M.L.M., & Minasny, B. 2003. On digital soil mapping. *Geoderma* 117: 3–52.

McClelland, G.T.W., Altwegg, R., Van Aarde, R.J., Ferreira, S., Burger, A.E., & Chown, S.L. 2018. Climate change leads to increasing population density and impacts of a key island invader: *Ecological Applications* 28: 212–224.

McFadden, D. 1979. Quantitative Methods for Analysing Travel Behaviour of Individuals: Some Recent Developments. In Hensher D. A., S.P.R. (Ed.), *Behavioural Travel Modelling*, pp. 279–318. London, UK.

van der Merwe, S., Greve, M., Skowno, A.L., Hoffman, M.T., & Cramer, M.D. 2023. Can vegetation be discretely classified in species-poor environments? Testing plant community concepts for vegetation monitoring on sub-Antarctic Marion Island. Ecology and Evolution 13: e9681.

Momberg, M., Hedding, D.W., Luoto, M., & le Roux, P.C. 2021. Species differ in their responses to wind: the underexplored link between species fine-scale occurrences and variation in wind stress. *Journal of Vegetation Science* 32: e13093.

Naimi, B., Hamm, N.A., Groen, T.A., Skidmore, A.K., & Toxopeus, A.G. 2014. Where is positional uncertainty a problem for species distribution modelling. *Ecography* 37: 191-203.

Park, Y., & Ho, J.C. 2021. Tackling overfitting in boosting for noisy healthcare data. *IEEE Transactions on Knowledge and Data Engineering* 33: 2995–3006.

Pichler, M., & Hartig, F. 2023. Machine learning and deep learning-A review for ecologists. *Methods in Ecology And Evolution* 14: 994–1016.

Pradhan, B., & Lee, S. 2010. Landslide susceptibility assessment and factor effect analysis: backpropagation artificial neural networks and their comparison with frequency ratio and bivariate logistic regression modelling. *Environmental Modelling & Software* 25: 747–759.

Qazi, A.W., Saqib, Z., & Zaman-ul-Haq, M. 2022. Trends in species distribution modelling in context of rare and endemic plants: a systematic review. *Ecological Processes* 11: 40.

Roe, N.A., Ducey, M.J., Lee, T.D., Fraser, O.L., Colter, R.A., & Hallett, R.A. 2022. Soil chemical variables improve models of understorey plant species distributions. *Journal of Biogeography* 49: 753–766.

le Roex, A.P., Chevallier, L., Verwoerd, W.J., & Barends, R. 2012. Petrology and geochemistry of Marion and Prince Edward Islands, Southern Ocean: Magma chamber processes and source region characteristics. *Journal of Volcanology and Geothermal Research* 223: 11–28.

le Roux, P.C., & McGeoch, M.A. 2008a. Changes in climate extremes, variability and signature on sub-Antarctic Marion Island. *Climatic Change* 86: 309–329.

le Roux, P.C., & McGeoch, M.A. 2008b. Spatial variation in plant interactions across a severity gradient in the sub-Antarctic. *Oecologia* 155: 831–844.

Rudolph, E.M., Hedding, D.W., De Bruyn, P.J.N., & Nel, W. 2022. An open access geospatial database for the sub-Antarctic Prince Edward Islands. *South African Journal of Science* 118:.

Rudolph, E.M., Hedding, D.W., & Nel, W. 2021. The surface geology of the Prince Edward Islands: refined spatial data and call for geoconservation. *South African Journal of Geology* 124: 627–638.

Ryan, P., & Bester, M. 2008. Pelagic predators. In Chown, S. & Froneman, P. (Eds.), *The Prince Edward Islands: land-sea interactions in a changing ecosystem*, pp. 121–164. Sun Press, Stellenbosch, South Africa.

Smith, V.R. 1977. The chemical composition of Marion Island soils, plants and vegetation. *South African Journal of Antarctic Research* 8: 32–39.

Smith, V.R. 1978. Animal-plant-soil nutrient relationships on Marion Island (Subantarctic). *Oecologia* 32: 239–253.

Smith, V.R. 2008. Energy flow and nutrient cycling in the Marion Island terrestrial ecosystem: 30 years on. *Polar Record* 44: 211–226.

Smith, V.R., & Mucina, L. 2006. Vegetation of sub-Antarctic Marion and Prince Edward Islands. In Mucina, L., Rutherford, M.C., & Powrie, L.W. (Eds.), *Vegetation of South Africa, Lesotho and Swaziland*, pp. 699–723. South African National Biodiversity Institute, Pretoria, South Africa.

Smith, V.R., & Steenkamp, M. 2001. Classification of the terrestrial habitats on Marion Island based on vegetation and soil chemistry. *Journal of Vegetation Science* 85: 14-24.

Smith, V.R., Steenkamp, M., & Gremmen, N.J.M. 2001. Terrestrial habitats on sub-Antarctic Marion Island: Their vegetation, edaphic attributes, distribution and response to climate change. *South African Journal of Botany* 67: 641–654.

Sumner, P.D. 2004. Rock weathering rates on subantarctic Marion Island. *Arctic Antarctic and Alpine Research* 36: 123–127.

Wege, M., Etienne, M.-P., Oosthuizen, W.C., Reisinger, R.R., Bester, M.N., & de Bruyn, P.J.N. 2016. Trend changes in sympatric Subantarctic and Antarctic fur seal pup populations at Marion Island, Southern Ocean. *Marine Mammal Science* 32: 960–982.

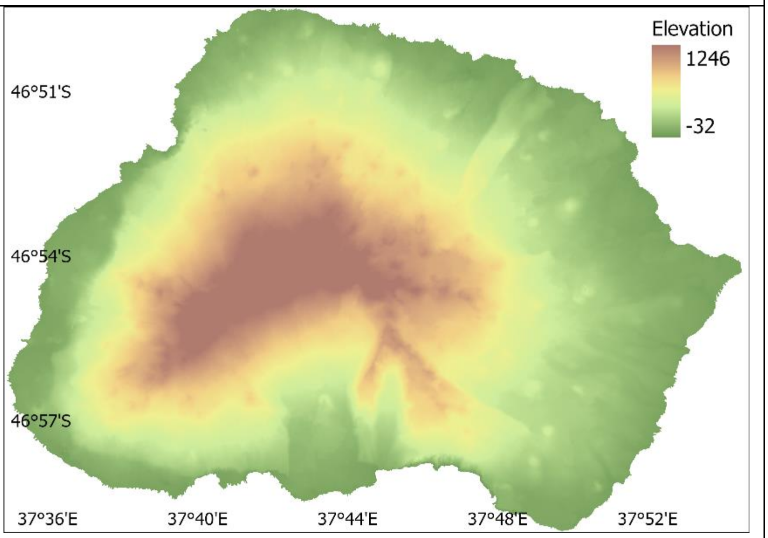
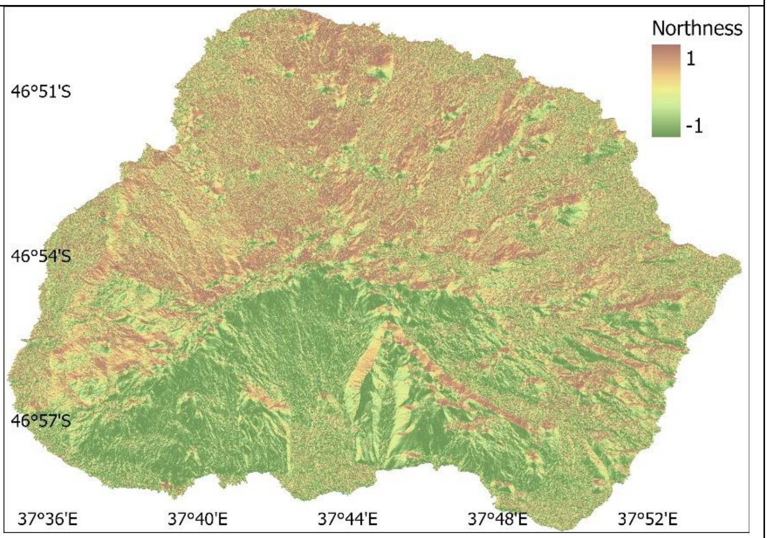
Weil, R.R., & Brady, N.C. 2016. *The nature and properties of soils,* 15th edition. Pearson, London, UK.

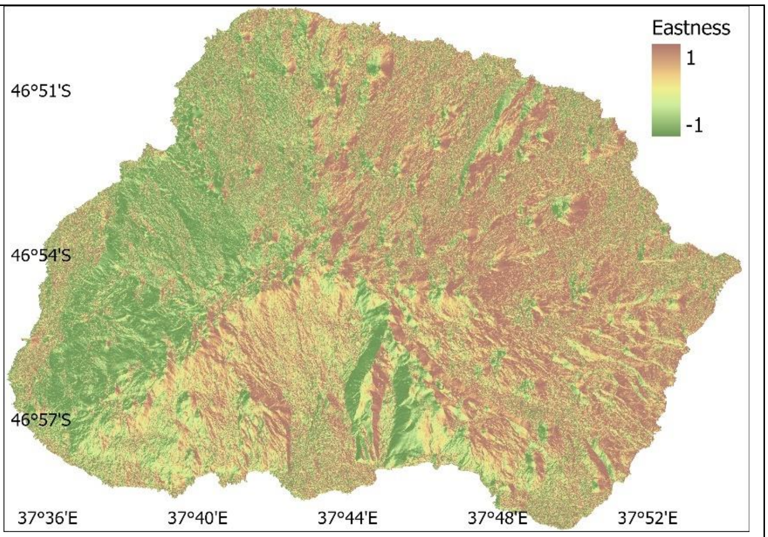
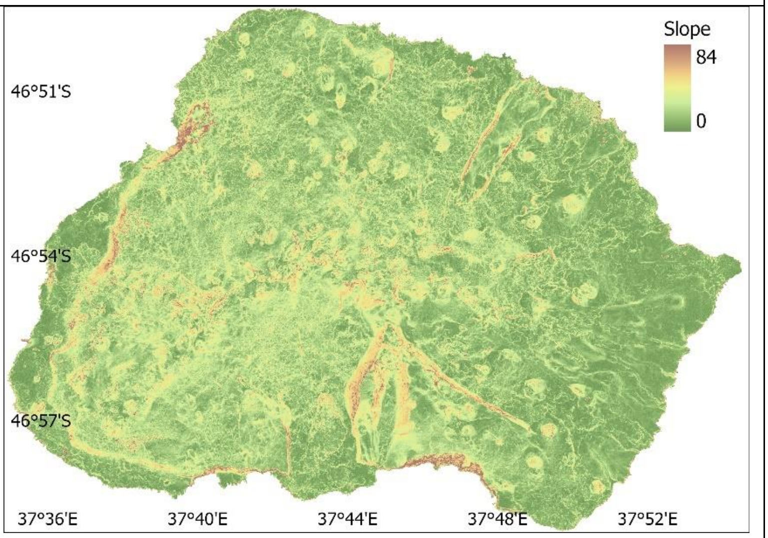
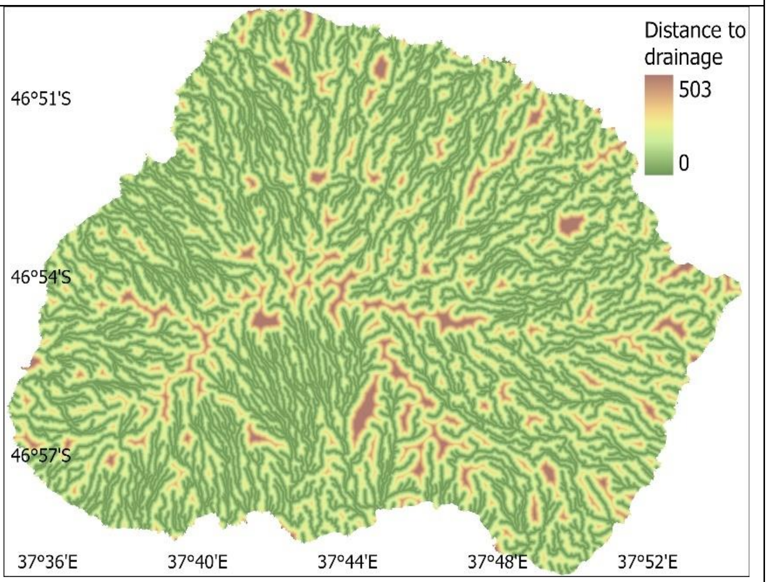
Wilson, B.R., Wilson, S.C., Sindel, B., Williams, L.K., Hawking, K.L., Shaw, J., Tighe, M., Hua, Q., & Kristiansen, P. 2019. Soil properties on sub-Antarctic Macquarie Island: Fundamental indicators of ecosystem function and potential change. *Catena* 177: 167–179.

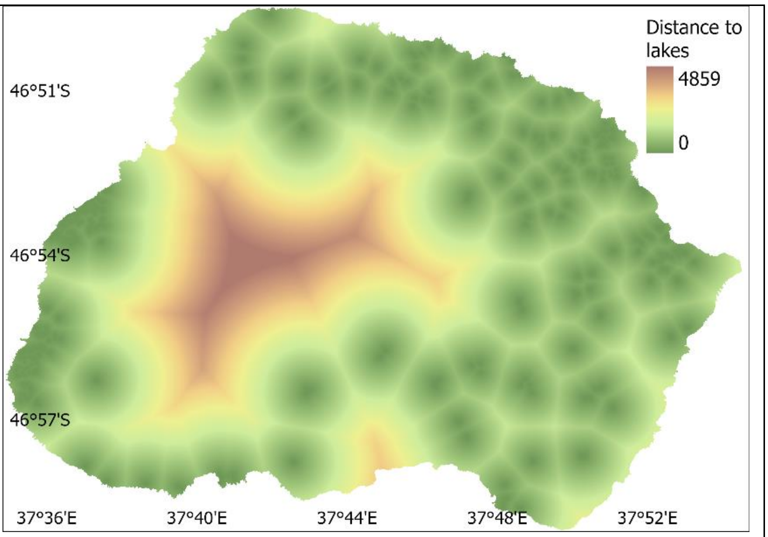
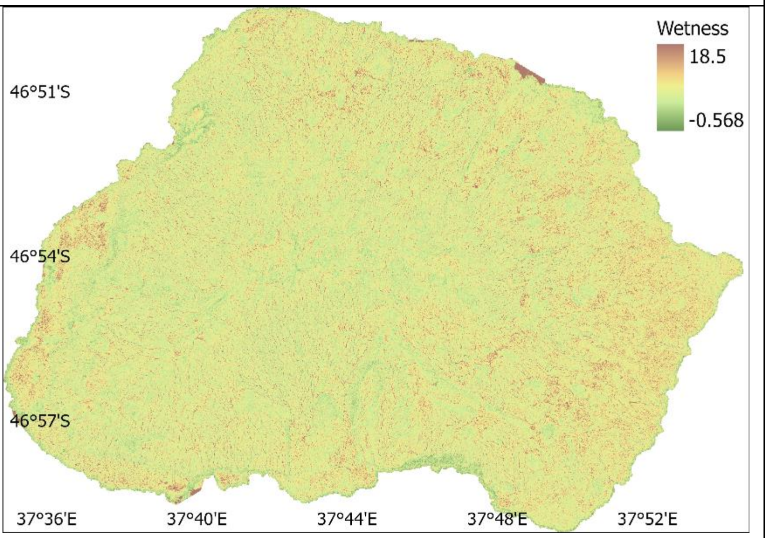
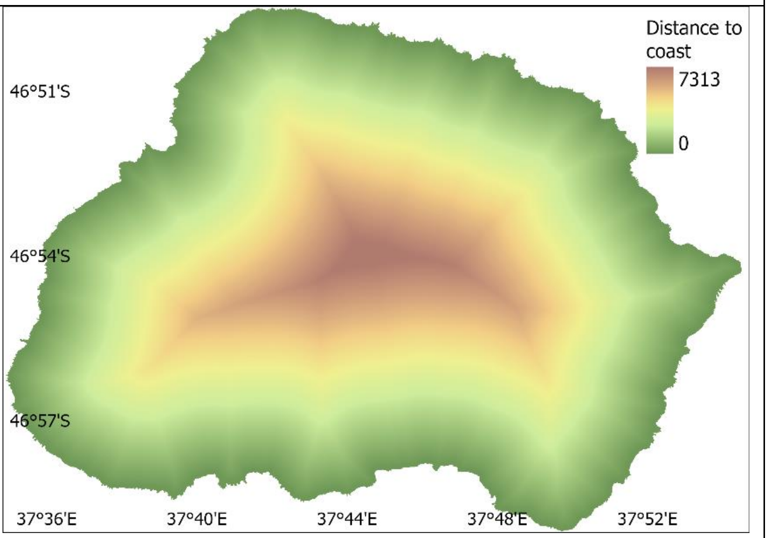
Yu, H., Cooper, A.R., & Infante, D.M. 2020. Improving species distribution model predictive accuracy using species abundance: Application with boosted regression trees. *Ecological Modelling* 432: 109202.

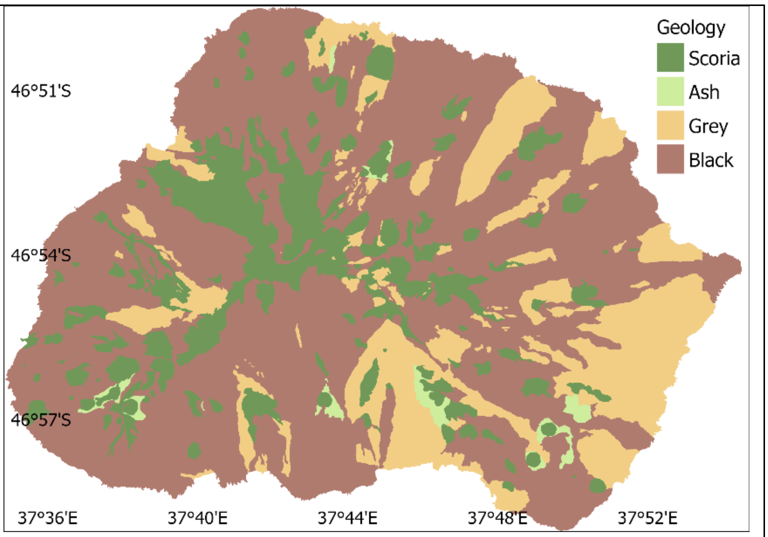
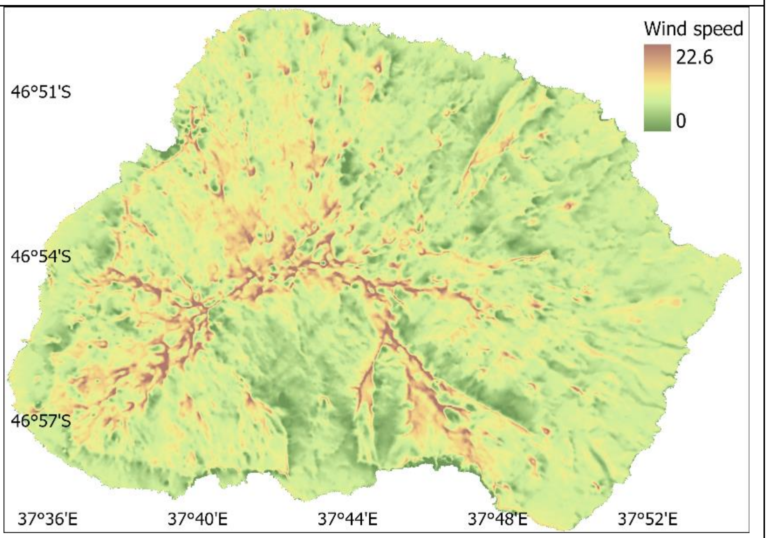
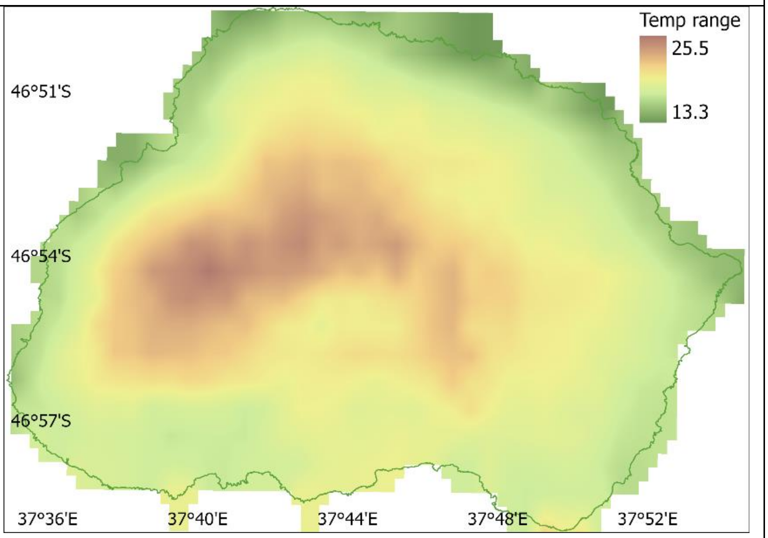
Appendix C

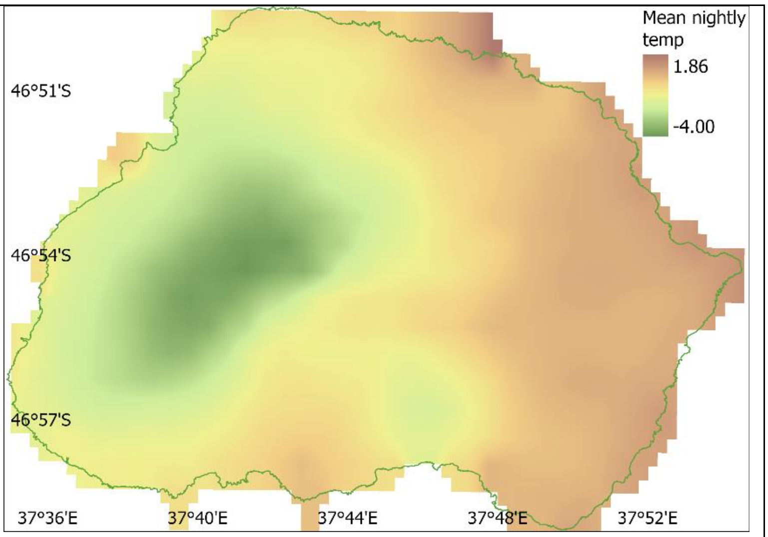
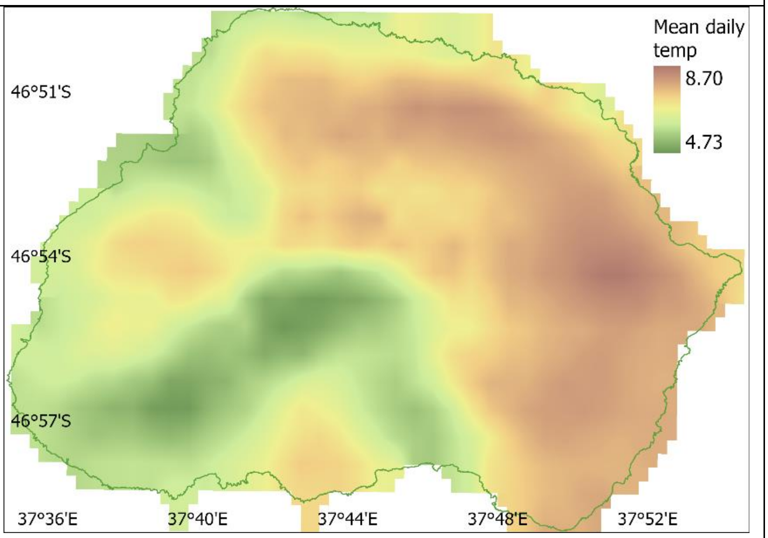
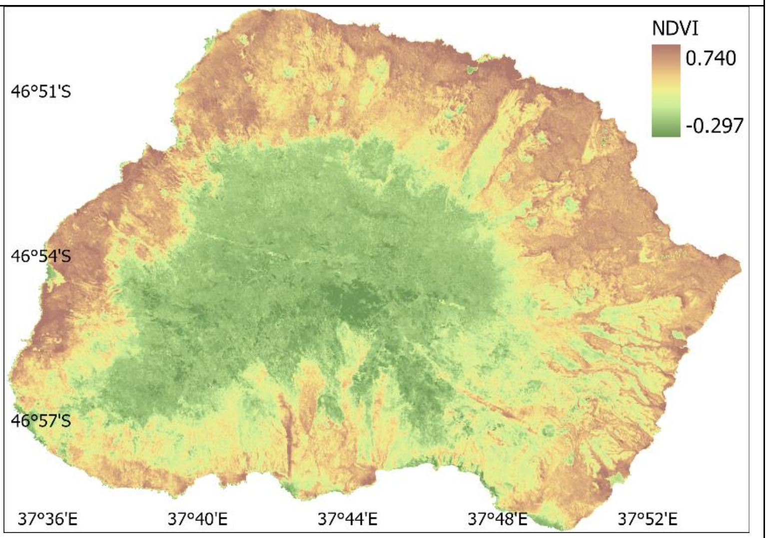
Table C1. Description of environmental variables used to develop models of soil properties on MI. “Ecological information” describes the ecological characteristic of the predictor variables that may influence soil properties. To save space, satellite bands are not presented here.

Predictor variable	Map
Topography: Layer: Elevation Source: Digital Surface Model (DSM) in meters above sea level Ecological information: influence of elevation	
Topography: Layer: Northness Source: aspect generated from DSM Ecological information: influence of solar radiation	

Topography: Layer: Eastness Source: aspect generated from DSM Ecological information: influence of solar radiation	
Topography: Layer: Slope Source: slope in degrees generated from DSM Ecological information: influence of terrain. Indirectly includes the influence solar radiation	
Hydrology: Layer: Drainage dist Source: distance to drainage lines in meters Ecological information: influence of drainage	

Hydrology: Layer: Lakes dist Source: distance to lakes in meters Ecological information: influence of water bodies	
Hydrology: Layer: Wetness Source: Topographic Wetness Index (TWI) Ecological information: influence of soil moisture	
Topography: Layer: Coast dist Source: distance from the coastline in meters Ecological information: influence of the ocean (saltspray)	

Geology: Layer: Geology Source: geology map, shown as the four geological types that occur on the island: Holocene scoria; Ash cones; Grey lava; Black lava Layer name: Geo Ecological information: influence of parent material	
Climate: Layer: Wind speed Source: wind speed map in in meters per second Ecological information: influence of wind speed	
Climate: Layer: T range Source: temperature range in degrees Celsius derived from temperature maps Ecological information: influence of temperature	

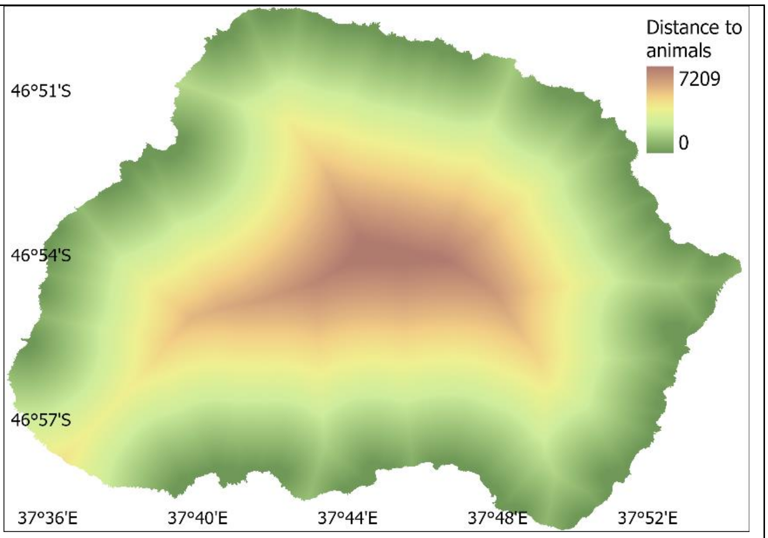
<u>Climate:</u> Layer: T night mean Source: mean annual nightly temperature in degrees Celsius derived from temperature maps Ecological information: influence of temperature	
<u>Climate:</u> Layer: T day mean Source: mean annual daily temperature in degrees Celsius derived from temperature maps Ecological information: influence of temperature	
<u>Biotic:</u> Layer: NDVI Source: Normalized difference vegetation index (NDVI) calculated from Sentinel2 infrared and red satellite bands Ecological information: influence of vegetation density	

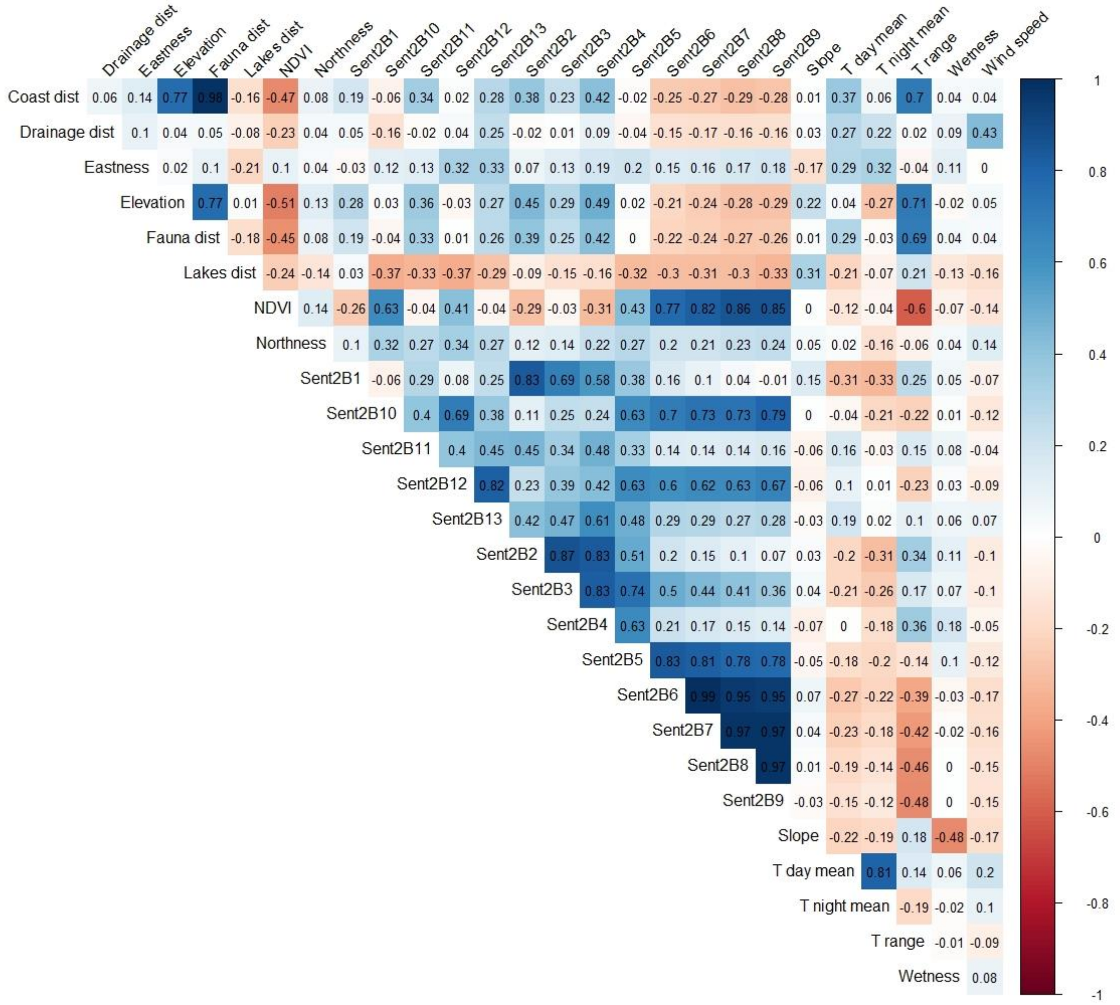
Biotic:

Layer: Fauna dist

Source: distance to seal and penguin colonies and rookeries mapped from satellite imagery

Ecological information: faunal influence





	Drainage dist	Eastness	Elevation	Fauna dist	Lakes dist	NDVI	Northness	Sent2B1	Sent2B10	Sent2B11	Sent2B12	Sent2B13	Sent2B2	Sent2B3	Sent2B4	Sent2B5	Sent2B6	Sent2B7	Sent2B8	Sent2B9	Slope	T day mean	T night mean	T range	Wetness	Wind speed
Coast dist	0.06	0.14	0.77	0.98	-0.16	-0.47	0.08	0.19	-0.06	0.34	0.02	0.28	0.38	0.23	0.42	-0.02	-0.25	-0.27	-0.29	-0.28	0.01	0.37	0.06	0.7	0.04	0.04
Drainage dist		0.1	0.04	0.05	-0.08	-0.23	0.04	0.05	-0.16	-0.02	0.04	0.25	-0.02	0.01	0.09	-0.04	-0.15	-0.17	-0.16	-0.16	0.03	0.27	0.22	0.02	0.09	0.43
Eastness			0.02	0.1	-0.21	0.1	0.04	-0.03	0.12	0.13	0.32	0.33	0.07	0.13	0.19	0.2	0.15	0.16	0.17	0.18	-0.17	0.29	0.32	-0.04	0.11	0
Elevation				0.77	0.01	-0.51	0.13	0.28	0.03	0.36	-0.03	0.27	0.45	0.29	0.49	0.02	-0.21	-0.24	-0.28	-0.29	0.22	0.04	-0.27	0.71	-0.02	0.05
Fauna dist					-0.18	-0.45	0.08	0.19	-0.04	0.33	0.01	0.26	0.39	0.25	0.42	0	-0.22	-0.24	-0.27	-0.26	0.01	0.29	-0.03	0.69	0.04	0.04
Lakes dist						-0.24	-0.14	0.03	-0.37	-0.33	-0.37	-0.29	-0.09	-0.15	-0.16	-0.32	-0.3	-0.31	-0.3	-0.33	0.31	-0.21	-0.07	0.21	-0.13	-0.16
NDVI							0.14	-0.26	0.63	-0.04	0.41	-0.04	-0.29	-0.03	-0.31	0.43	0.77	0.82	0.86	0.85	0	-0.12	-0.04	-0.6	-0.07	-0.14
Northness								0.1	0.32	0.27	0.34	0.27	0.12	0.14	0.22	0.27	0.2	0.21	0.23	0.24	0.05	0.02	-0.16	-0.06	0.04	0.14
Sent2B1									-0.06	0.29	0.08	0.25	0.83	0.69	0.58	0.38	0.16	0.1	0.04	-0.01	0.15	-0.31	-0.33	0.25	0.05	-0.07
Sent2B10										0.4	0.69	0.38	0.11	0.25	0.24	0.63	0.7	0.73	0.73	0.79	0	-0.04	-0.21	-0.22	0.01	-0.12
Sent2B11											0.4	0.45	0.45	0.34	0.48	0.33	0.14	0.14	0.14	0.16	-0.06	0.16	-0.03	0.15	0.08	-0.04
Sent2B12												0.82	0.23	0.39	0.42	0.63	0.6	0.62	0.63	0.67	-0.06	0.1	0.01	-0.23	0.03	-0.09
Sent2B13													0.42	0.47	0.61	0.48	0.29	0.29	0.27	0.28	-0.03	0.19	0.02	0.1	0.06	0.07
Sent2B2														0.87	0.83	0.51	0.2	0.15	0.1	0.07	0.03	-0.2	-0.31	0.34	0.11	-0.1
Sent2B3															0.83	0.74	0.5	0.44	0.41	0.36	0.04	-0.21	-0.26	0.17	0.07	-0.1
Sent2B4																0.63	0.21	0.17	0.15	0.14	-0.07	0	-0.18	0.36	0.18	-0.05
Sent2B5																	0.83	0.81	0.78	0.78	-0.05	-0.18	-0.2	-0.14	0.1	-0.12
Sent2B6																		0.99	0.95	0.95	0.07	-0.27	-0.22	-0.39	-0.03	-0.17
Sent2B7																			0.97	0.97	0.04	-0.23	-0.18	-0.42	-0.02	-0.16
Sent2B8																				0.97	0.01	-0.19	-0.14	-0.46	0	-0.15
Sent2B9																					-0.03	-0.15	-0.12	-0.48	0	-0.15
Slope																						-0.22	-0.19	0.18	-0.48	-0.17
T day mean																							0.81	0.14	0.06	0.2
T night mean																								-0.19	-0.02	0.1
T range																									-0.01	-0.09
Wetness																										0.08

Figure C1. Correlation plot showing the collinearity between predictor variables. “Sent2B1-B13” = Sentinel2 Band 1-13 satellite imagery, “Coast dist” = distance to coast, “Drainage dist” = distance to drainage lines, “Fauna dist” = distance to fauna, “Lakes dist” = distance to lakes, “T range” = Temperature range, “T day mean” = mean daily temperature, “T night mean” = mean nightly temperature, “Wetness” = topographic wetness index. “Northness” and “Eastness” are continuous measures of aspect.

Table C2. Boosted regression tree model statistics for each soil property. The number of trees show the amount of regression trees that were chosen by the BRT models after model simplification. The linear model statistics of the predicted over observed values are also shown with the R^2 of the linear models. Pseudo R^2 of each model was also used as an indicator of model fit.

Soil property	Number of trees	Linear model equation	df	p-value	R^2 linear model	Pseudo R^2
pH	4150	y = 0.600x + 1.75	196	<0.001	0.792	0.311
N	3000	y = 0.544x + 0.580	204	<0.001	0.730	0.375
P	2050	y = 0.344x + 1.96	209	<0.001	0.601	0.172
K	2950	y = 0.541x + 1.47	209	<0.001	0.720	0.352
C	3150	y = 0.600x + 7.92	204	<0.001	0.770	0.413
Ca	2450	y = 0.498x + 14.6	209	<0.001	0.700	0.361
LOI	2750	y = 0.580x + 19.6	208	<0.001	0.753	0.438
Na	2750	y = 0.511x + 4.12	209	<0.001	0.703	0.340
Mg	2400	y = 0.460x + 12.6	209	<0.001	0.672	0.328
Mn	2900	y = 0.462x + 0.483	209	<0.001	0.630	0.289

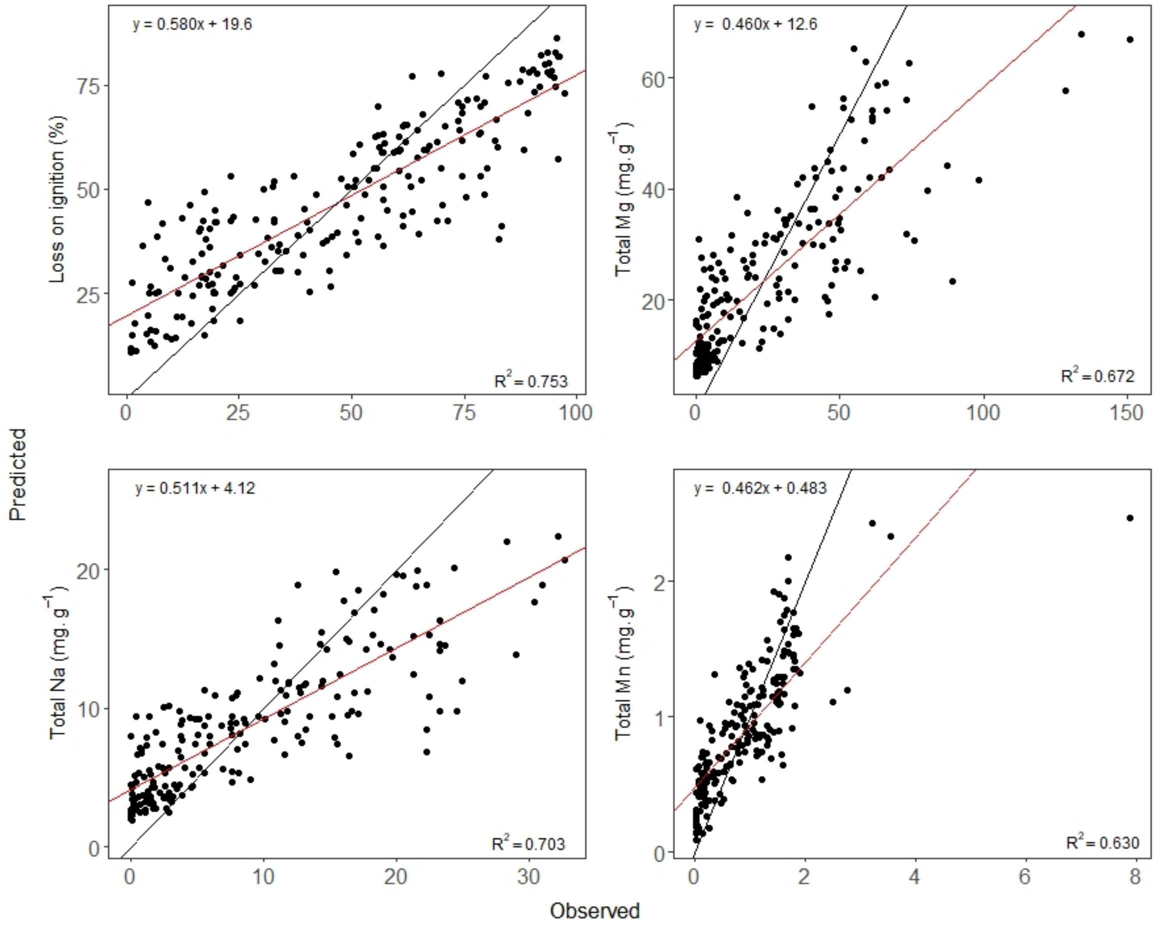


Figure C2. Observed sample points plotted against the predicted values estimated by the boosted regression tree models for soil properties. The red line indicates the linear regression of predicted over observed values with the equation for the line given and the black line indicates the 1:1 line. The R^2 of the linear models are indicated at the bottom right.

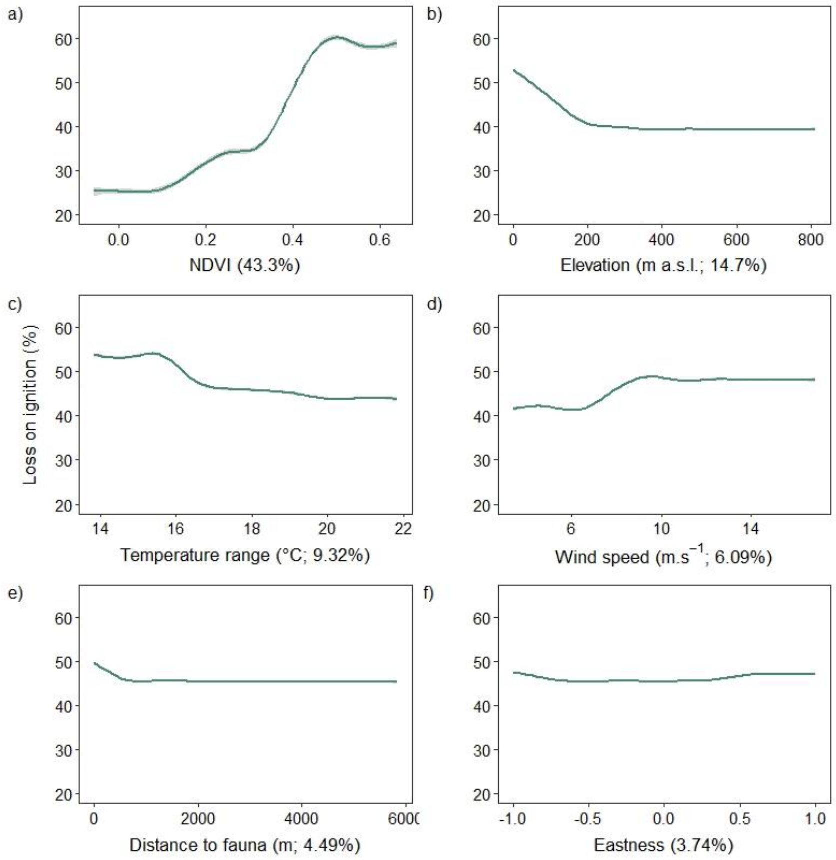


Figure C3. Partial dependence plots showing the relationship (± SE) between loss on ignition (LOI) and the six most important predictor variables a) NDVI, b) elevation, c) temperature range, d) wind speed, e) distance to fauna and f) eastness. The percentage relative importance of each variable in explaining LOI is shown in brackets on the x-axis.

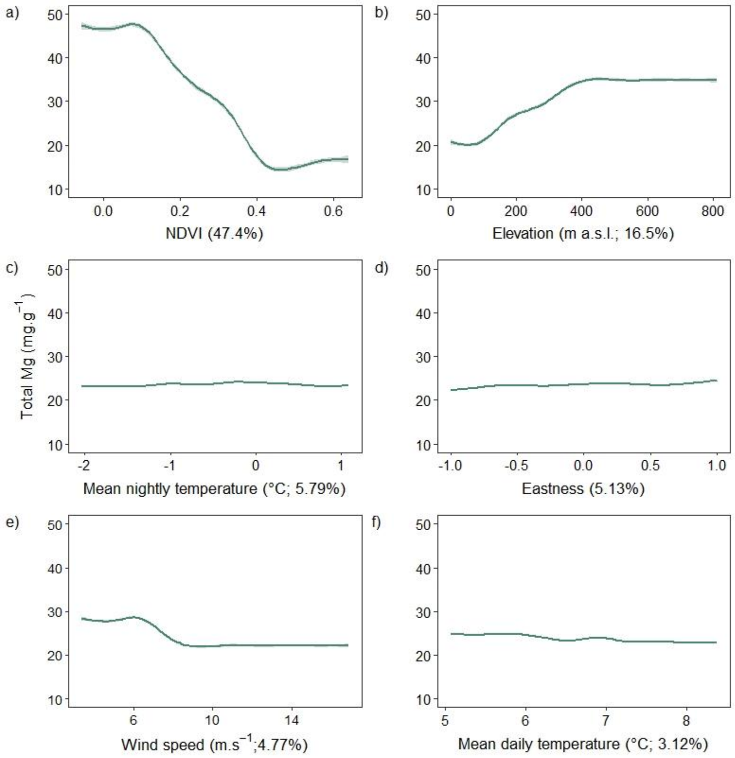


Figure C4. Partial dependence plots showing the relationship (± SE) between Mg and the six most important predictor variables a) NDVI, b) elevation, c) mean nightly temperature, d) eastness, e) wind speed and f) mean daily temperature. The percentage relative importance of each variable explaining Mg is shown in brackets on the x-axis.

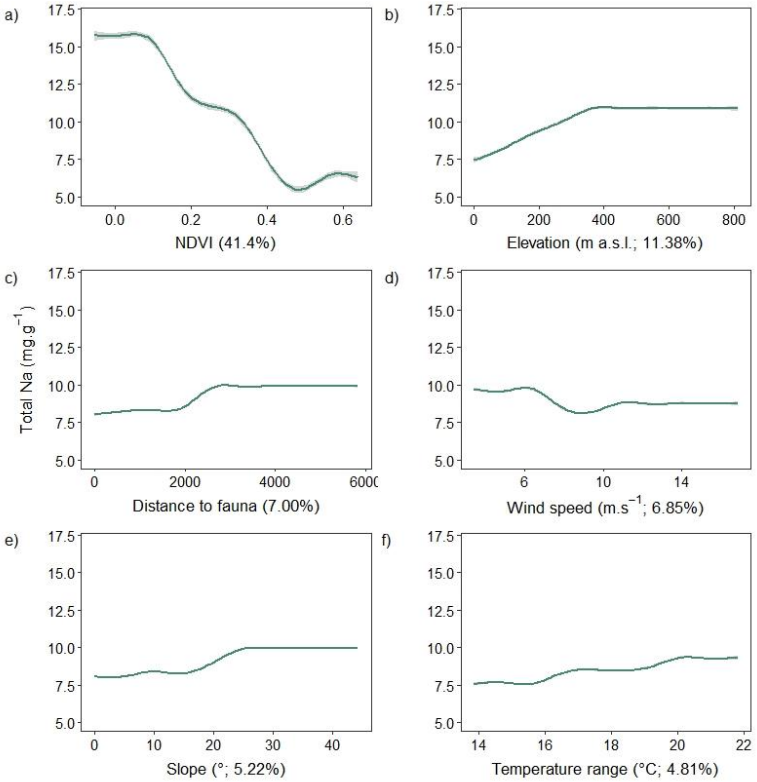


Figure C5. Partial dependence plots showing the relationship (± SE) between total Na and the six most important predictor variables a) NDVI, b) elevation, c) distance to fauna, d) wind speed, e) slope and f) temperature range. The percentage relative importance of each variable in explaining Na is shown in brackets on the x-axis.

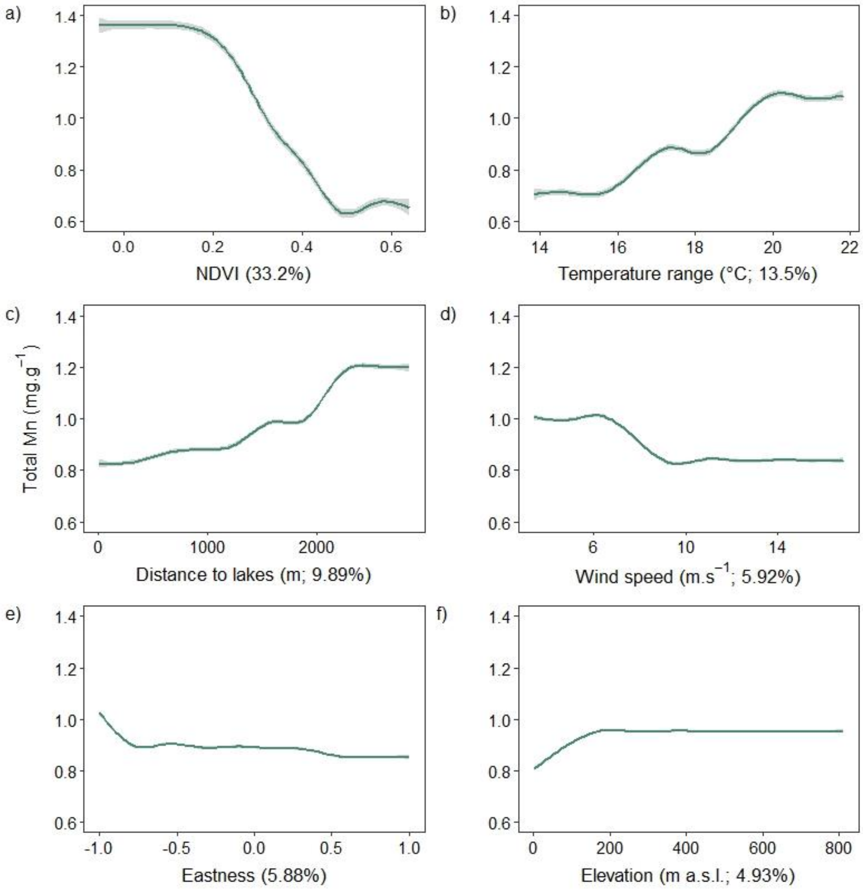


Figure C6. Partial dependence plots showing the relationship (± SE) between Mn and the six most important predictor variables a) NDVI, b) temperature range, c) distance to lakes, d) wind speed, e) eastness and f) elevation. The percentage relative importance of each variable explaining Mn is shown in brackets on the x-axis.

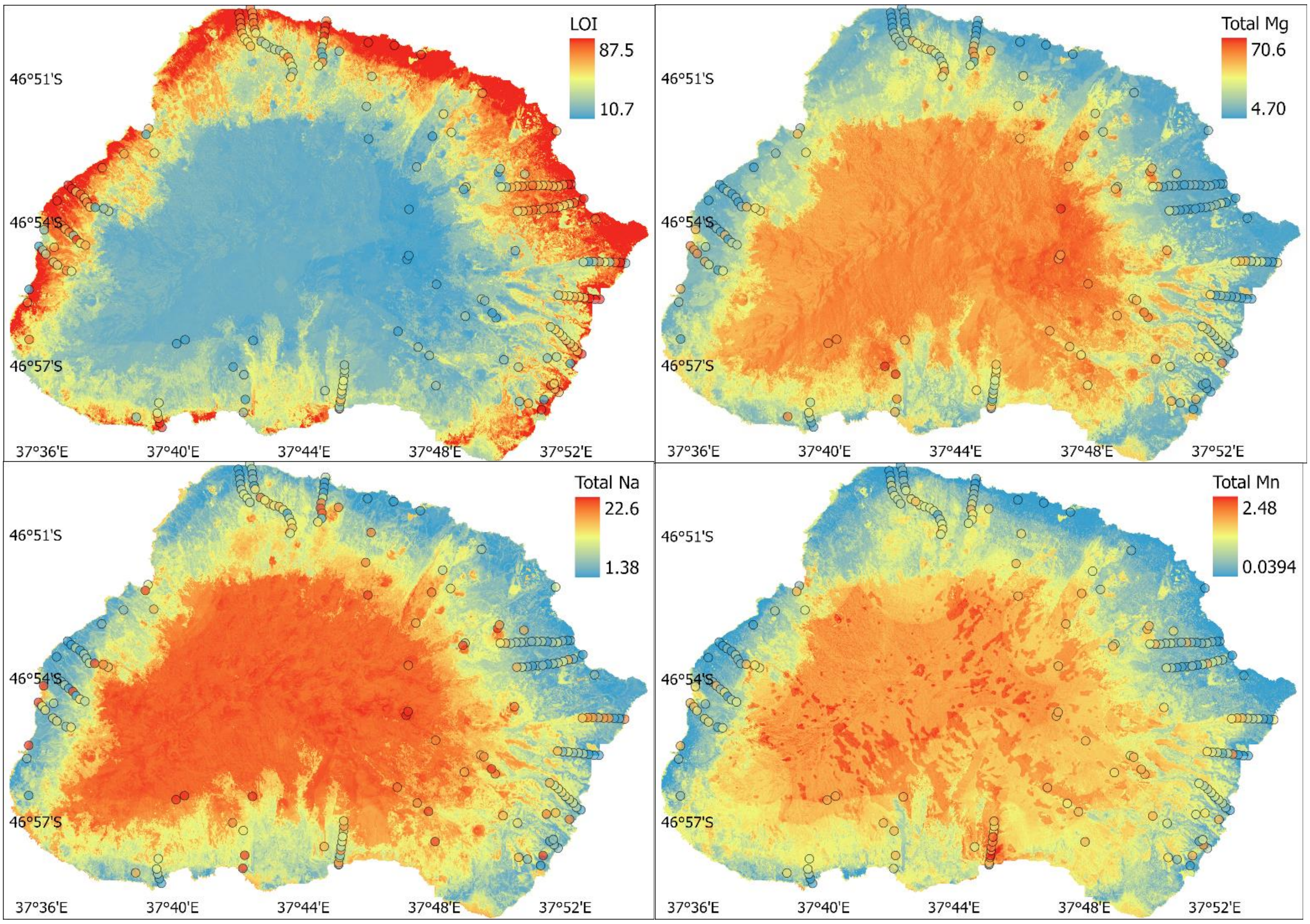


Figure C7. Spatial prediction maps of soil properties on MI. Observed values at each sampling location are indicated on the maps as points in the same colour gradient as the prediction maps. Where the colours of these points differ from the background the observed values differ from the modelled values. All soil properties, other than loss on ignition (LOI) are indicated as mg.g^{-1}.

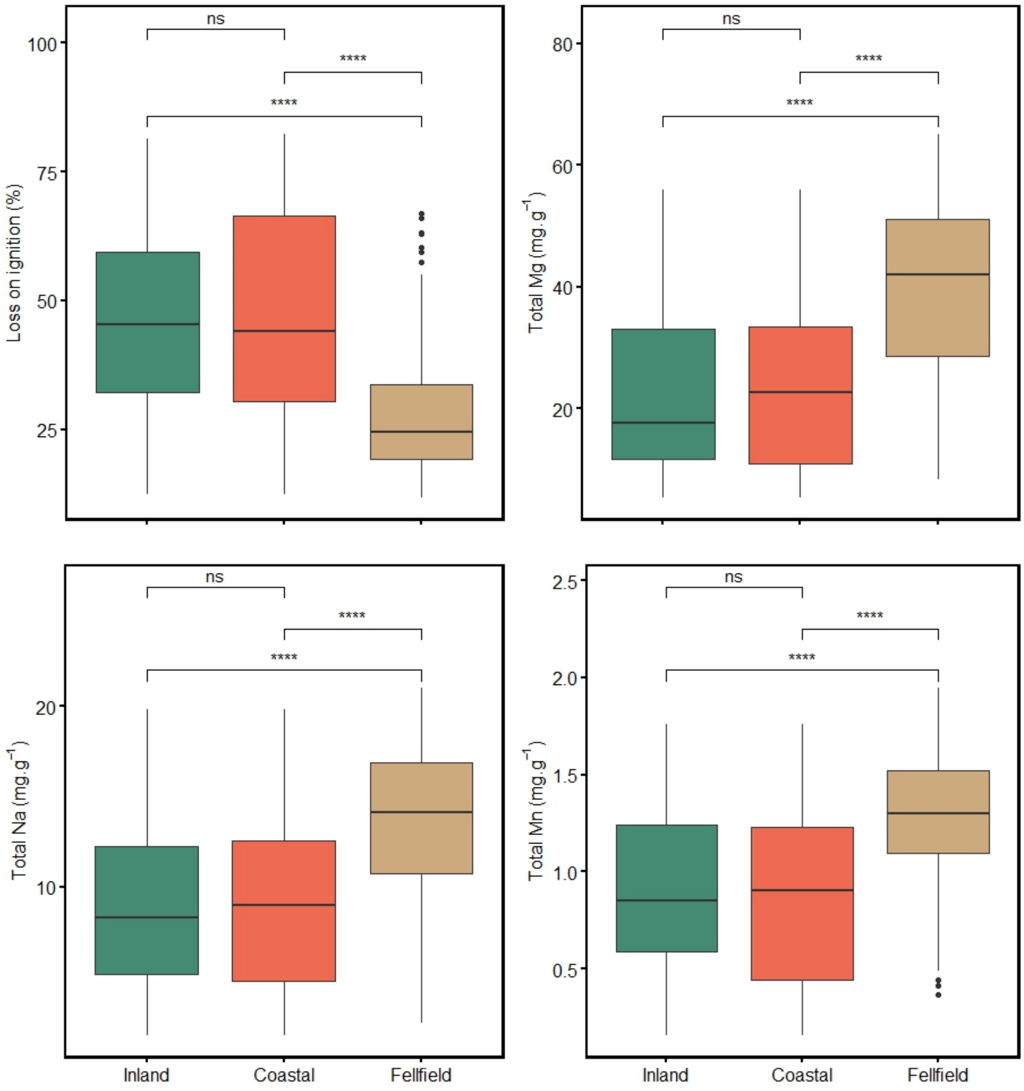


Figure C8. Comparison of soil properties between inland (n = 130), coastal (n = 140) and fellfield (n = 192) vegetation on MI. “ns”= not significant, “*” = $p < 0.05$, “****”= $p < 0.001$.

Chapter 5

Plant species respond individualistically to warming: Insights into specialists and generalists from species distribution modelling that include edaphic properties

Halophilous succulent specialist species *Crasssula moschata* (reddish green), interspersed by halophilous herb *Leptinella plumosa* in the fore- and midground where salt spray from the ocean is pronounced. Coprophilous specialist grass *Poa cookii* is also visible on the righthand slope where fauna occur.

Introduction

Global environmental change has led to extensive shifts in species distributions worldwide (Chen et al. 2011). Predicting the responses of plant species to environmental change has become a key research objective in ecological research (Elith & Leathwick 2009) to support proactive strategies that may reduce the negative impacts of environment change on biodiversity (Bellard et al. 2012). Among the drivers of plant species distributions, climate variables, especially temperature and precipitation, are commonly considered the key determinants (Austin & Van Niel 2011b; Gardner et al. 2019). However, in the absence of biophysiologically-relevant, non-climatic variables that may constrain distributions, the influence of climatic variables on species ranges may have been overestimated (Gardner et al. 2019), while non-climatic constraints to species ranges are often ignored (Cramer et al. 2022).

Appropriate selection of environmental variables determines the success of species distribution models (SDMs), the key tool used to understand the impact of environmental change on plant species distributions (Williams et al. 2012). While SDMs are used with the assumption that all biophysiologically-relevant variables are included, this is seldom possible due to data limitations, and thus selection of key variables is a critical step in the modelling process (Austin & Van Niel 2011b). However, many environmental variables that are ecologically critical to plant species, such as wind conditions (Momberg et al. 2021), biotic interactions (le Roux et al. 2013a) and soil properties (Roe et al. 2022), receive very little attention. The exclusion of edaphic properties in determining plant species distributions has been an oversight in many parts of the world, even though soil properties, together with climatic and topographic variables, may determine the suitability of a habitat to plant species (Hageer et al. 2017). Soil properties, such as pH and fertility, may have a significant (Cramer et al. 2019) or dominant (Walthert & Meier 2017) impact on the distribution of plant species. A consequence of the exclusion of soil properties in SDMs is that the importance of non-edaphic variables may be exaggerated in the models and species may be predicted to occur outside of their potential range. Soil properties may also vary markedly over short distances (Weil & Brady 2016), resulting in habitat fragmentation, which may not be correctly represented if soil properties are not included in the SDMs. Models that include edaphic characteristics as important predictors of species distributions are more likely to predict range shrinkage in response to climate change because the edaphic constraints restrict habitat suitability. Therefore, excluding soil variables limits the interpretation of species habitat requirements and the predictive power of SDMs, especially under climate change.

A key choice when studying vegetation distributions and changes therein is whether to use single SDMs or multiple species distributions simultaneously, also known as stacked or joint SDMs (Austin & Van Niel 2011b; Wilkinson et al. 2019). Joint or stacked SDMs model the distribution patterns of multiple species simultaneously, considering their potential interactions and co-occurrences (Zurell et al. 2020).

This approach may be appropriate when species interactions or co-dependencies are known or hypothesised to play a significant role in determining their distributions. The focus of stacked and joint SDMs is on understanding community-level dynamics, such as assessing the combined impacts of multiple species on ecosystem processes or predicting shifts in community composition (Wilkinson et al. 2021; Poggiato et al. 2021). Alternatively, in environments with low diversity, species interactions may not be as prevalent as those with high diversity (Schöb et al. 2018), and thus single SDMs may be more appropriate. The focus of single SDMs is rather to understand the specific habitat preferences, environmental tolerances, and potential changes for each species separately (Zurell et al. 2016). Consequently, single SDMs may be more appropriate in species-poor environments where species associations with the environment are expected to be more individualistic (Austin 2005; van der Merwe et al. 2023) and in younger environments where species may not have had time to develop strong biotic associations (i.e., low interaction environments).

Climate change has generally resulted in temperature increases worldwide, leading to species range shifts to the cooler parts of their ranges, often poleward and to higher elevations (Rubenstein et al. 2023). High latitudes have warmed particularly rapidly, with the sub-Antarctic warming at double the global average (Bergstrom & Chown 1999; Piao et al. 2020). A rapid change in air temperature and rainfall has been documented on several sub-Antarctic islands (le Roux & McGeoch 2008a; Lebouvier et al. 2011), and the range-restricted species on the islands have been predicted to be especially negatively impacted by climate change (Rogers et al. 2020). The few scattered islands in the sub-Antarctic have experienced pronounced impacts of climate change, often compounded by the impacts of invasive species (McClelland et al. 2018; Hoffmann et al. 2019). Plant species on islands have limited dispersal opportunities and thus upslope movement is often the only option to track climate change. The impact of warming and drying on the vegetation of Marion Island (MI) in the sub-Antarctic has not been well documented, but several species have extended their ranges upslope (le Roux & McGeoch 2008b). Here, temperatures have increased from *c.* 5.8°C to *c.* 6.3°C between 1949 and 2020 and rainfall has decreased from *c.* 2600 mm p.a. in 1960 to *c.* 1600 mm p.a. in 2020 (see Chapter 3). A temperature change of between 1°C and 2°C is considered to result in strong biologically-relevant impacts on vegetation, such as reduction in species richness (Nunez et al. 2019), with the probability of large compositional and structural change increasing with temperature increase (Nolan et al. 2018). The observed temperature changes alone have thus raised concerns about the potential impacts on plant species distributions and have highlighted the need to understand the constraints to species range shifts on MI.

Plant species have different environmental requirements that determine habitat suitability (Austin & Van Niel 2011b). Plant species that are considered habitat "generalists", may be able to tolerate and thrive in a wide range of environmental conditions and various habitats, and thus adapt more easily to changing conditions, compared to habitat “specialists” that are adapted to specific environmental conditions (Brouat et al. 2004; Denelle et al. 2020). Consequently, generalists are considered to be more resilient to environmental change than specialist species, as they may be able to dispersing to more suitable conditions or adapt to changing conditions by altering their physiology (Brouat et al. 2004). Specialist species on the other hand may not be able to survive or adapt if climate change alters the conditions they depend on (Cramer et al. 2022), and may risk extinction (Ainsworth & Drake 2020). Here, generalist species are viewed as those with a wide ecological amplitude, and thus occurring in multiple habitats. By contrast, specialist species are range restricted by specific environmental conditions, such as nutrient content or soil moisture. Generalist species are assumed to be more responsive to climate change, whereas specialist species that strongly depend on non-climatic factors, may not be able to respond to climate change and may restrict their geographic ranges under environmental change (Brouat et al. 2004; Denelle et al. 2020).

Researchers have warned that significant vegetation changes (Smith & Steenkamp 1990; Smith et al. 2001) and further species range shifts on MI (le Roux et al. 2008b) are probable under continued climate change. Likely consequences are that the suitability of current habitats to species that are adapted to the cooler and wetter environment may change, causing species to shift their distributions in order to track climate change. Dispersing to habitats within a species’ climatic envelope, such as to higher elevations, may be one of the only options for plant species on the sub-Antarctic islands if they are to track the rapid climatic changes, since there are no nearby land masses. However, upslope movement may be limited by the elevational severity gradient at MI, where environmental severity increases with elevation, including decreasing temperatures, increasing wind speeds and fewer biotic interactions as elevation increases (le Roux & McGeoch 2008c). Edaphic properties also change with elevation, likely further constraining species distributional shifts (Cramer et al. 2022), although this has not been tested. Climate change may also provide the opportunity for invasive species to thrive and expand their range (le Roux et al. 2013; McClelland et al. 2018), posing a threat to the impoverished native flora. As temperatures rise and habitats potentially shift, invasive species may find favorable conditions that facilitate their proliferation and may be able to outcompete native flora on MI (Gremmen et al. 1998; Mathakutha et al. 2019; Ripley et al. 2020), which may lead to detrimental impacts on the native biota.

By relating the occurrence of species with a combination of climatic and faunal (changing), as well as non-climatic environmental (fixed) predictors, the aim of this study was to determine the direction of and constraints to species distributional changes in response to climate change. I hypothesised that 1) the responses of plant species to climate change are individualistic, 2) generalist plant species have undergone and will continue to undergo range expansion, 3) specialist species have not undergone range expansion, 4) edaphic properties are a key constraint to and can predict the habitat suitability for some plant species. Studying the combined effects of climatic, topographic, biotic and edaphic variables in determining habitat suitability for individual plant species, may provide a more constrained and realistic view of species distributions and the impacts of climate change on distributional shifts on MI, than only considering climate variables.

Methods

Study site

Marion Island is a 290 km^2 peak of a shield volcano located in the sub-Antarctic (46°54′ S, 37°45′ E). The geology consists of older Pleistocene grey lavas overlain by younger Holocene black lavas (Rudolph et al. 2021), with similar chemical composition (le Roex et al. 2012). The climate is cool (mean annual temperature of *c.* 6.1°C), windy (mean 25 km h^{-1}), has high mean annual rainfall (*c.* 1600 mm) and is hyper-oceanic, resulting in little seasonal or diurnal temporal variation (le Roux & McGeoch 2008a). The soils on MI are shallow, acidic and high in organic matter, with nutrient content decreasing from the marine nutrient inputs at the coast towards the interior (Chapter 4), although soil properties may change over short distances due to the patchy and rugged terrain on MI (Huntley 1971). Topographically, the north and east coasts of the island slope gently from the coast to the high elevation interior, whereas the south coast is characterised by steep cliffs. The west coast has a *c.* 1 km coastal plain that abruptly slopes toward the interior of the island.

There are 21 indigenous vascular plant species and 17 alien plant species on the island, with vegetation concentrated on the coastal plains below 300 m a.s.l. and limited to *c.* 850 m a.s.l. Above this elevation vascular plants do not occur due to harsh climatic conditions and the lack of soils as the substrate is comprised of scoria and lava. Faunal influence occurs through trampling and nutrient-input by seals and seabirds, that mainly occur along the coast where animals have access to beaches (Smith & Steenkamp 2001). Feral domestic cats (*Felis catus*) were introduced to MI in 1949 to address the invasive house mouse (*Mus musculus*) infestation (Bester et al. 2002). The detrimental impact that the cats had on burrowing birds, and the associated allochthonous nutrient input by the birds, led to their eradication in 1991 (Bester et al. 2002). Consequently, mice increased rapidly in abundance and density, predating on birds (McClelland et al. 2018), reducing macroinvertebrate abundance and size (Smith et al. 2002) and burrowing and tunnelling through vegetation, causing die-back (Phiri et al. 2009). Therefore, since the eradication of cats, mice have likely further reduced allochthonous nutrient input to the island, especially at low elevations.

Data collection and study species

A comprehensive dataset of vascular plant species occurrence records was compiled from multiple field surveys that occurred between 2016 and 2020. Occurrence data were originally collected through various sampling methods including systematic randomised sampling of 3x3 m plots (see Chapter 2), random sampling and alien species monitoring. From these data, a total of 10 720 species presences were recorded across 23 vascular plant species. The dataset covered a wide range of environmental conditions across MI, at least for the widespread species. Only species with more than 30 observations were included in the analyses, as preliminary analyses revealed overfitting of models for species with fewer than 30 presence records. This resulted in 14 plant species, of which two are alien invasive species (*Poa annua* and *Sagina procumbens*). The nine species with fewer than 30 observation were highly restricted in their distribution. Of the retained species, habitat specialist species were considered to be those restricted to particular habitats, including coprophilous species (*Poa cookii* and *Montia fontana*) requiring nutrient-enriched soils such as around seal rookeries and seabird colonies, halophilous species (*Crassula moschata* and *Leptinella plumosa*) restricted to areas that receive regular wind-blown saltspray and hygrophilous species (*Carex dikei* and *Juncus scheuchzerioides*) restricted to high moisture habitats such as mires (Huntley 1971; le Roux & McGeoch 2008b). Cramer et al. (2022) found that more species may be classified as "specialist" when examining each species' niche breadth, but their study area was limited to 2 lava flows on MI, and may thus not include the entire range of each species. Therefore, I consider generalists (*Azorella selago, Polypogon magellanicus, Austroblechnum penna-marina, Acaena magellanica, Ranunculus biternatus* and *Phlegmariurus saururus*) to be widespread and thus with wider ecological amplitude (Huntley 1971), and specialist species to be range restricted, dependent more strongly on specific environmental (likely non-climatic) conditions.

Climate, satellite and topographic data

Climate variables consisted of temperature and wind layers (see Chapter 4 for more detailed methodology). Monthly temperature data (1 km resolution) were used, developed by Leihy et al. (2018). The mean daily and nightly temperatures were extracted, along with the temperature range, calculated as the difference between the maximum annual daily temperature and minimum annual nightly temperatures. A wind speed map was downloaded from Goddard et al. (2022) at 30 m resolution. No spatial precipitation data is available for MI, although precipitation is presumed to be relatively evenly distributed due to the hyper-oceanic nature of the climate and high rainfall experienced across the island. As a proxy for soil moisture, a TWI layer was generated in ArcGIS Pro 2.9 (Environmental Systems Research Institute, CA, USA) using "Slope" (converted to radians) and "Flow Accumulation" in the "Raster Calculator" to fit the TWI equation suggested by Beven & Kirkby (1979). Environmental variable selection was guided by Austin & Van Niel (2011b).

Topographic variables consisted of elevation, slope, aspect, distance to drainage lines, distance to lakes and distance to the coast. A digital surface model (DSM, 1 m resolution), developed by the National Geo-spatial Information Directorate of the South African Department of Rural Development and Land Reform, was used and resampled to 5 m resolution (Rudolph et al. 2022). In ArcGIS "slope" and "aspect" were extracted from the DSM. Aspect was converted to northness and eastness, by calculating the sine of the slope, multiplied by the cosine and sine of aspect, respectively, resulting in a circular variable that is transformed into a continuous variable from -1 to 1. A northness value of 1 represents a northern steep slope with high solar radiation and -1 a steep southern slope exposed to low solar radiation (Amatulli et al. 2018). The hydrology toolset in ArcGIS was used to generate drainage lines from the DSM, by first generating "Fill" (z-limit=unspecified), then "Flow Direction" (method = D8) and lastly "Flow Accumulation" using a >50 000 flow accumulation parameter. Furthermore, a "distance to coast" layer was created with the "Euclidean distance" tool in ArcGIS using a coastline digitised at a scale of 1:1000 using head-up digitising based on the RGB ESRI basemap imagery in ArcGIS. "Distance to lakes" was generated from a digitised lakes layer (Rudolph et al. 2022), also using the "Euclidean distance" tool. A geology map was obtained from Rudolph et al. (2021).

Copernicus Sentinel 2 2019 and 2020 satellite imagery, processed by the European Space Agency was downloaded using Google Earth Engine. A normalized difference vegetation index (NDVI) layer was created with the red (Sentinel band 4, 665 nm) and near infrared (Sentinel band 8, 842 nm) bands using the "raster" package (Hijmans 2023; see Chapter 4 for more detailed methodology).

All environmental layers were rasterised and resampled (using "nearest neighbour" for categorical data and "bilinear" for continuous data), to the same extent and resolution (5 m) as the DSM. All layers were "stacked" with the "raster" package in R.

Soil data

Little previous research has been conducted on the spatial distribution of soil properties on MI (although see Lubbe 2010), and consequently soil has not been considered in species distribution models. High resolution soil data for N, C, P, K, Ca, Mg and Na were used (see Chapter 4 for details). Because the soil properties were highly collinear, the soil layers were subjected to a principle component analysis (PCA) with the "rasterPCA" function in the "RStoolbox" package (Leutner et al. 2023), after which the first two principle components, that accounted for more than 99% of the variability in the data, were used in the analyses (Fig. D1 in Appendix D). Principal component 1 (PC1) represented an axis of soil fertility, with high values of PC1 indicating high N and C content and low values generally indicating higher values of cations (K, Ca, Mg and Ca). The second principal component (PC2) was negatively associated with P and positively associated with the other soil properties (Fig D1).

The “rasterPCA” function performs a PCA and creates a raster of each component by assigning values of the components to each cell in the raster.

Faunal distribution

A raster layer was created that represents faunal influence on MI (see Chapter 4 for more details). This was done by digitising the largest penguin colonies and the locations of seal rookeries and beaches in ArcGIS using the ESRI World Imagery at a scale of 1:1000. The census locations of southern elephant (*Mirounga leonina*), sub-Antarctic fur (*Arctocephalus tropicalis*) and Antarctic fur (*Arctocephalus gazella*) seals on MI were obtained from the Marion Marine Mammal Programme, published in Rudolph et al. (2022) and Wege et al. (2016). The penguin colonies that were mapped are mainly king (*Aptenodytes patagonicus*) and macaroni (*Eudyptes chrysolophus*) penguins which breed in dense colonies and cause severe erosion (Crawford et al. 2003).

Species distribution modelling: model training and evaluation

Species distribution modelling was conducted in R statistical software (R Core Team 2020) using the “SDMtune” package (Vignali et al. 2020), developed to facilitate training, tuning and evaluation of distribution models in a unified framework. Maximum entropy (“Maxent”; Phillips et al. 2006) is a machine learning algorithm and a robust method for presence-only species distribution modelling, especially in climate change studies (Qazi et al. 2022), and has been shown to perform as well or better than more traditional modelling methods (Merow et al. 2013) such as general additive models (Elith et al. 2006). The “maxnet” implementation of the Maxent method for model training was chosen that uses the “maxnet” package (Phillips 2021). Maxnet is the local R implementation of the Maxent algorithm (Phillips et al. 2006), thus not requiring the original java implementation of Maxent, increasing computational speed in R, as there is no need for external software (Vignali et al. 2020). All modelling decisions were guided by Phillips & Dudik (2008), Elith et al. (2011), Merow et al. (2013) and Vignali et al. (2020).

The dataset was divided into a training (80% of the data) and testing (20% of the data) subset to develop and validate the SDMs. The training dataset was used to relate the selected environmental variables to the occurrence of species. Ten thousand background points (pseudo-absences) were generated with the “randomPoints” function in the “dismo” package (Hijmans et al. 2022). Species-specific tuning increases the robustness of models (Anderson & Gonzalez Jr. 2011), and thus hyperparameters were optimised for each species using the function “optimiseModel” that iteratively compares different combinations of feature classes (linear, quadratic, product and hinge) and regularisation multipliers (0.2 to 4), while monitoring the evaluation metrics with the test dataset, to produce the optimal model parameters. A smaller regularisation multiplier results in a closer fit to the known presences and thus a more localised output distribution. Therefore, for species with occurrence records of over 800, smaller regularisation multipliers were particularly considered, while avoiding model overfitting, judged through the evaluation metrics on the test dataset. Conversely, for species with fewer occurrence records and thus whose presences may not include their entire niche, a higher regularisation multiplier was considered, to allow more generalisation in the model output.

Model performance was assessed using the area under the receiver operating characteristic curve (AUC), the true skill statistic (TSS) and the model's ability to capture known species distributions. Both AUC (Bradley 1997; Phillips & Dudik 2008) and TSS (Allouche et al. 2006) are well established model evaluation measures that have become the standard for model evaluation in ecological research. The AUC represents the probability that a randomly selected presence site (true positive) will be ranked higher than a randomly chosen absence site (false positive), ranked from 0 to 1, with 1 indicating that the model can perfectly distinguish between positive and negative values. An AUC of 0.75 and above is considered a useful model (Phillips & Dudik 2008). The TSS essentially calculates sensitivity + specificity - 1. It ranges from -1 to +1, where values less than 0 indicate model performance is not better than random, values closer to +1 indicates perfect agreement (Allouche et al. 2006) and a value above 0.4 may indicate good model performance. Model hyperparameters that produced models with both the highest AUC and TSS values were chosen.

Species distribution modelling: variable selection

Multicollinearity of environmental variables were initially determined from the full set of variables by plotting a correlation matrix and calculating variable inflation factors (threshold = 10) for all environmental variables with the "usdm" package (Naimi et al. 2014), after which elevation and NDVI were removed, because of high collinearity with numerous variables (see Figure D2 in Appendix D). The shape of the island, given its volcanic origin, naturally results in elevation being closely associated with climatic conditions, with temperature decreasing, and wind speed and snow cover increasing with elevation. There could thus be an argument for elevation being a good predictor of multiple abiotic conditions. However, elevation in itself is not a biologically-relevant variable and has been shown to be redundant in SDMs (Hof et al. 2012), especially when the conditions that change with elevation are already included in the SDMs. The environmental conditions that change with elevation are better represented by the topographic and climatic variables included in this study. Elevation was also an important predictor of soil properties (see Chapter 4), thus elevation was excluded.

For each species, data-driven variable selection was performed using the function "varSel" in the "maxnet" package, with the following parameters chosen to select variables: metric = AUC, method = Spearman, correlation threshold= 0.7, permutation = 1. This function iteratively calculates variable importance and finally removes those that are highly correlated (above the 0.7 correlation threshold). If there are highly correlated variables, a leave-one-out Jackknife test is performed with the full model, after which the correlated variables that decrease model performance on the training data set the least, are removed (Vignali et al. 2020). This is done until all variables fall below the correlation threshold, resulting in a parsimonious model trained by the most important variables that explain the occurrence of the species. Only distance to coast, distance to fauna, soil PC1 and pH were above the 0.7 correlation threshold (Figure D2). A key consideration when selecting variables was that soil properties change with distance to the coast and distance to fauna. Soil nutrients (represented by soil PC1) are higher around faunal influence, which in turn is higher in close proximity to the coast where seals and penguins have access to the island. Although dependent on individual species, in models where one of these three variables were particularly important and perhaps the two collinear variables dropped, all three variables may actually influence habitat suitability and I considered this in the interpretation of habitat suitability based on the autecological characteristics of each species.

Species distribution modelling: past, present and future predictions

Once model evaluation and calibration was completed, the current distribution of species were predicted at 5 m resolution for the entire island using the “predict” function in the “dismo” package. To evaluate the potential impact of warming that has occurred on the island, species distributions were projected to the maximum mean annual temperature increase since 1949, which was an increase of 1.4°C that occurred between 1965 (*c.* 5.3°C) and 1999 (*c.* 6.7°C; see Chapter 3). The vegetation has experienced this rapid increase in temperature in the past, and thus 1.4°C was considered a realistic climate projection for the future. Consequently, I subtracted 1.4°C from the temperature variables (day and night temperature) to retrodict past species distributions and added 1.4°C to the temperature variables to predict future species distributions, assuming that climate change will continue its current trend.

The resulting spatial predictions were analysed to identify areas of potential expansion, contraction, or stability for each plant species. This was done by first converting the habitat suitability maps to presence-absence maps using a presence threshold value. Four threshold methods that have been demonstrated to perform well in reducing errors for presence-only prediction (Liu et al. 2005; Vale et al. 2014; Liu et al. 2016; Scherrer et al. 2018) were considered for each species: equal sensitivity and specificity (for both training and test data) and maximum sensitivity plus specificity (for both training and test data). Because the number of occurrence records differed between species, some species with few occurrences may have been overfitted whereas those with numerous occurrences may have been underfitted, requiring different threshold values. Each species may thus have had a different threshold, as specificity and sensitivity differ for each model. These methods aimed to minimise false positives (i.e., where the model missed suitable habitats) and minimise true negatives (i.e., where the model erroneously predicted presences in unsuitable habitats; Liu et al. 2005). Range size was estimated by summing all 5x5 m grid cells of the prediction maps where a species was present in the prediction maps (i.e., above the threshold). Elevational limits were estimated by extracting the elevation for every cell where a species was predicted to occur in the past, present and future. Because elevation was not included in the models due to multicollinearity (Fig. D2), some presence predictions may fall within the high elevation polar desert of the island, where habitat is actually unsuitable to most vascular plants, even though habitat suitability may be predicted to increase with temperature amelioration.

Documented vegetation change assessed between 1965 and 2020 using repeat photography (Chapter 3) was used as a benchmark to compare to the model results of both the past and present distributions.

Results

Species distribution modelling: model training and evaluation

The SDMs performed well, with AUC values for all species being above 0.80 and all TSS values being above 0.42 (Table 1). The hyperparameters selected after model optimisation are presented in Table 1. Models for the specialist and invasive species performed the best (Table 1).

Table 4. Model evaluation results and hyperparameter settings selected after model optimisation for the Maxent species distributional models. Alien species are identified by "*". Feature class includes "l" = linear, "q" = quadratic, "h" = hinge, "p" = product. "Regularisation multiplier" is a parameter that imposes a penalty to the models in Maxent with smaller values indicating a closer fit to known presences.

Species	Number of occurrence records	AUC	TSS	Feature class	Regularisation multiplier
Acaena magellanica	862	0.848	0.560	lqh	2
Austroblechnum penna-marina	1832	0.865	0.577	lqph	1
Azorella selago	1999	0.790	0.416	lqph	1
Carex dikei	755	0.909	0.659	lqh	2
Crassula moschata	54	0.994	0.951	lqph	1
Juncus scheuchzerioides	164	0.935	0.727	lqph	1.2
Leptinella plumosa	194	0.968	0.870	lq	3.2
Montia fontana	32	0.918	0.747	lqph	1
Phlegmariururus saururus	67	0.918	0.682	lqh	0.8
**Poa annua*	68	0.976	0.870	lqh	2
Poa cookii	483	0.892	0.622	lq	0.7
Polypogon magellanicus	2348	0.830	0.495	lqph	0.3
Ranunculus biternatus	126	0.927	0.714	lqp	0.8
**Sagina procumbens*	230	0.917	0.724	lq	0.8

Species distribution modelling: variable importance

Following model simplification, the most important predictors explaining species occurrence were retained in each model (Table 2). The SDMs consistently identified the temperature variables as important predictors. Mean nightly temperature was retained in the SDMs for all species and was strongly associated with six species, being the most important predictor of *A. selago* and *P. magellanicus* (Table 2). Mean daily temperature was retained in 12 of the models but was not as important as mean nightly temperature (Table 2). The probability of occurrence of all species generally increased with warmer mean nightly and daily temperatures (see Fig. D3:16 for the response curves), although *J. scheuchzerioides* (Fig. D8), *L. plumosa* (Fig. D9), *P. annua* (Fig. D10), *P. cookii* (Fig. D11), *R. biternatus* (Fig. D15) and *S. procumbens* (Fig. D16) were more likely to occur at lower (5 – 7°C) mean daily temperatures. Soil PC1 was the most influential predictor for four species, *A. magellanica, A. penna-marina, J. scheuchzerioides* and *P. cookii,* with the probability of occurrence increasing with soil PC1, i.e., with higher N and C content. Soil PC2 was retained in all models but did not have high influence in any model (Table 2). Soil pH was retained in the models of four species and was the most important variable that predicted the occurrence of the sedge *C. dikei,* with the probability of occurrence increasing at lower pH values.

The distance to fauna was important in predicting the occurrence of five species, with *P. annua* (Fig. D12)*, R. biternatus* (Fig. D13) and *S. procumbens* (Fig. D14) being more likely to occur in close proximity to fauna. *Azorella selago* and *P. magellanica* were equally likely to occur within *c.* 2000 m of fauna, with the probability of occurrence decreasing further away. The distance to coast was important for three species (Table 2), with *C. moschata* and *L. plumosa* only occurring in close proximity to the coast and *P. saururus* occurrence increasing in likelihood up to *c.* 1000 m from the coast and then decreasing. The distance to lakes was also retained in all models, being the most important predictor of *M. fontana* (Table 2), with the probability of occurrence increasing with proximity to lakes. Northness was only strongly associated with *M. fontana*, while geology was only associated with *P. saururus, which* occurs only on black and grey lava and not on scoria*.* No other variables had high predictive power in determining species distributions.

Species distribution modelling: past, present and future predictions

Comparing the past to the present, the habitat suitability of eight species increased, whereas for seven species habitat suitability decreased (Table 3). In particular, the ranges of *A. magellanica, A. selago, A. penna-marina, P. magellanicus, P. saururus,* all generalists, as well as of *M. fontana, C. dikei* and *J. scheuchzerioides* were predicted to have increased (Table 3). On the other hand, the habitat suitability for *C. moschata, L. plumosa, P. cookii* (all specialist species) and *R. biternatus* decreased (Table 3)*.* The habitat suitability for the two invasive species, *P. annua* and *S. procumbens*, was also predicted to have decreased from the past to the present (Table 3). In terms of upper elevational boundaries, all species, other than *L. plumosa* and *S. procumbens*, were predicted to have expanded to higher mean elevations, to have increased their upper elevational boundaries (Table 3) and to have become more abundant on the west of the island (Fig. 1).

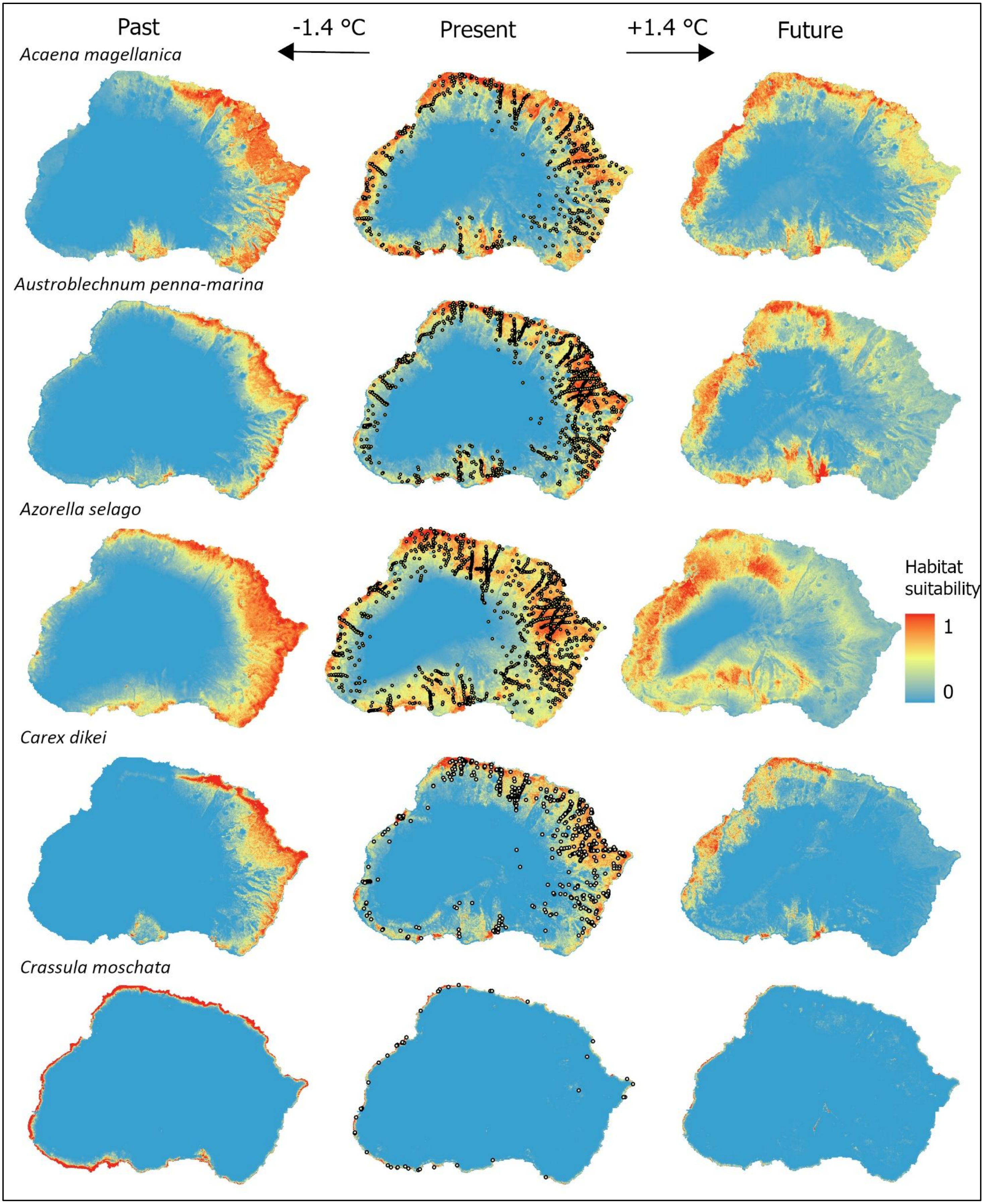
Under warmer temperatures in the future, nine species, *A. magellanica, A. penna-marina, A. selago, C. dikei, C. moschata, L. plumosa, P. cookii, P. magellanicus, P. saururus* and *S. procumbens* were predicted to decrease their ranges (Table 3). The ranges of *J. scheuchzerioides, M. fontana, R. biternatus* and *P. annua* and were predicted to increase in the future. An increase in mean elevation and upper elevational boundaries were predicted for all species in future other than *L. plumosa, S. procumbens, P. annua* and *P. cookii* (Table 3)*.* Further expansion towards the interior of the island and to the west with a concurrent contraction from the east of the island were predicted for *A. magellanica, A. penna-marina, A. selago, C. dikei, M. fontana, P. saururus* and *P. magellanicus* (Fig. 1)*.*

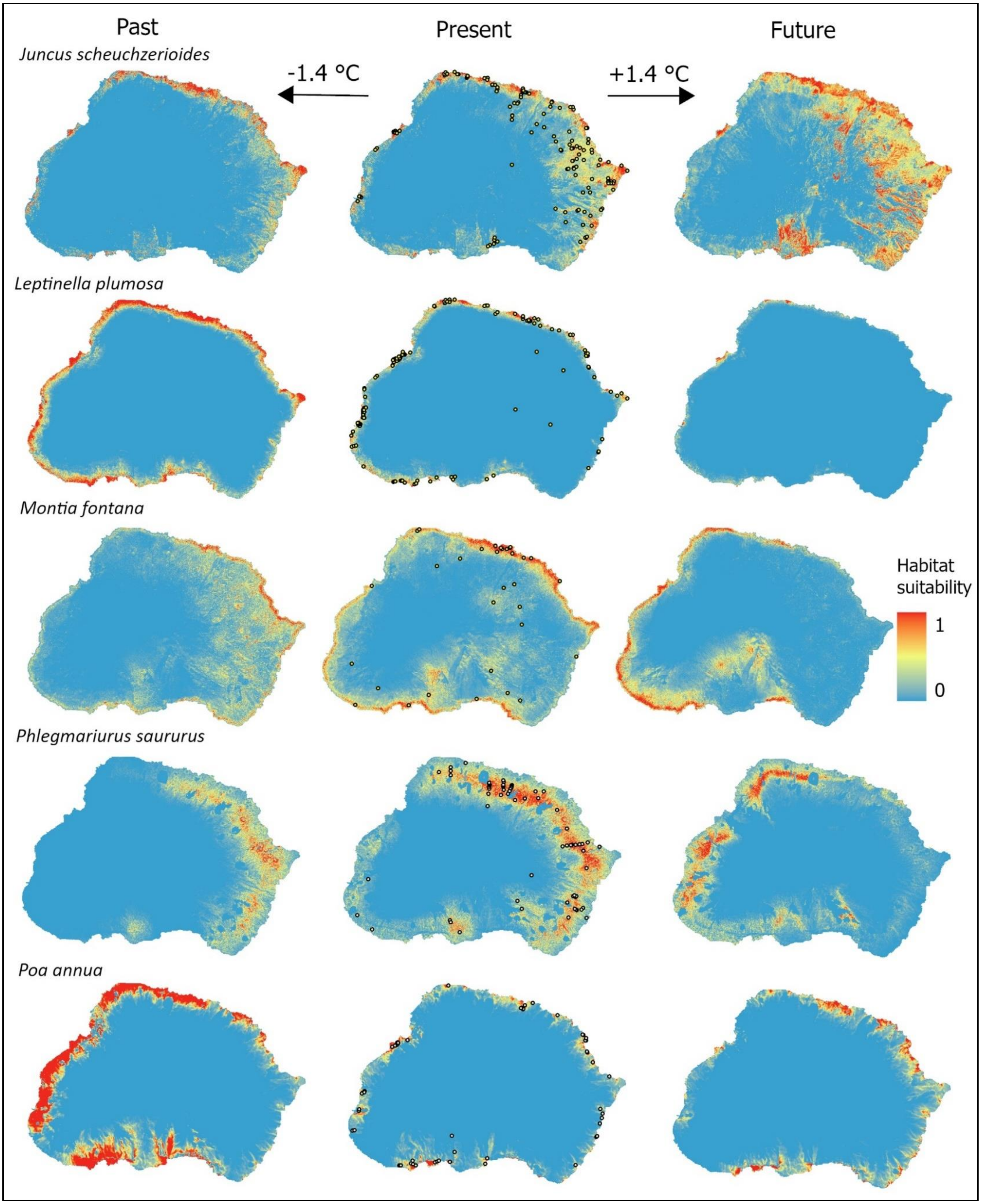
Table 5. Variable permutation importance (%) for each predictor of the species distribution models, representing the most important habitat conditions in determining the distribution of each vascular plant species on MI. Variable importance >20% is shown in bold. Alien species are identified by "*". Cells with no value indicate that the variable was dropped during the variable selection process. See Fig. D1:A14 in the Appendix for variable response curves of each species.

Species	Temp nightly mean	Temp daily mean	Temp range	Soil PC1	Soil PC2	pH	Distance to fauna	Distance to coast	Distance to lakes	East-ness	North-ness	Geology	Slope	Wind speed	Distance to drainage	TWI
Acaena magellanica	17.3	3.3	-	**73.0**	0.1	-	-	-	0.2	0.5	0.4	0.4	0.6	4.1	-	0.2
Austroblechnum penna-marina	**23.2**	-	-	**65.0**	0.5	-	-	-	6.5	0.9	0.5	0.2	0.2	2.0	1.0	0.2
Azorella selago	**44.9**	-	-	-	0.5	14.7	**25.5**	-	1.6	1.1	0.8	0.5	6.8	0.5	2.4	0.5
Carex dikei	**31.6**	6.2	-	-	0.1	**50.5**	-	0.7	2.4	0.1	0.8	-	4.5	1.8	0.9	0.3
Crassula moschata	9.6	10.0	-	-	0.1	0.6	-	**73.0**	0.4	0.2	0.5	3.5	0.8	0.3	0.6	0.4
Juncus scheuchzerioides	**35.6**	6.6	-	**36.3**	4.2	-	-	-	3.0	1.0	2.8	0.7	4.7	2.7	2.4	0.1
Leptinella plumosa	8.1	18.5	-	-	4.3	-	-	**66.1**	0.2	0.5	0.3	0.1	1.0	0.1	0.8	
Montia fontana	18.7	19.3	**-**	-	9.8	-	-	10.4	14.9	10.8	6.7	-	1.7	2.0	0.9	2.8
**Poa annua*	1.3	8.4	-	-	0.1	-	**71.0**	-	2.7	-	0.1	4.8	2.6	8.6	0.2	0.2
Poa cookii	4.2	10.0	-	**80.6**	1.3	-	-	-	1.7	-	0.1	0.7	0.1	0.7	0.3	0.3
Phlegmariurus saururus	10.9	9.5	-	-	1.3	0.900	-	**27.8**	14.2	0.1	5.9	15.9	5.9	1.6	2.0	4.1
Polypogon magellanicus	**36.2**	10.7	-	-	0.8	6.30	**24.7**	-	7.9	2.2	0.5	0.3	6.6	1.7	1.6	0.5
Ranunculus biternatus	19.7	16.1	-	-	2.9	-	**23.6**	-	8.4	2.6	1.2	1.2	11.2	8.9	2.1	1.9
**Sagina procumbens*	4.2	11.0	-	-	0.6	-	**71.5**	-	4.2	-	0.4	-	5.9	0.3	1.7	-

Table 6. Plant species range estimates, extracted from predicted habitat suitability maps after applying thresholds for the "past", where temperatures were predicted to have been lower by 1.4°C, "present" under current temperatures and "future" where temperatures were predicted to increase by a further 1.4°C. Elevational boundary estimates are presented as the 5th and 95th percentile, as well as the mean elevation. "Range" and "Area" are the possible sizes of the habitats a species may occupy in terms of the habitat suitability predictions. Alien species are identified by "*". "g" indicates generalist and "s" indicates a specialist species.

Species	Time period	Range (km^2)	Area of the island (%)	Elevation: 5th percentile	Elevation: mean ± SD	Elevation: 95th percentile
Acaena magellanica (g)	Past	57	20	16	85 ± 61	212
	Present	85	29	17	93 ± 73	242
	Future	67	23	17	96 ± 88	303
Austroblechnum penna-marina (g)	Past	43	15	15	59 ± 35	131
	Present	82	28	20	99 ± 74	246
	Future	75	26	23	177± 131	145
Azorella selago (g)	Past	70	24	16	85 ± 60	200
	Present	121	42	21	150 ± 116	377
	Future	84	29	30	274 ± 174	560
Carex dikei (s)	Past	33	11	14	62 ± 43	156
	Present	49	17	17	79 ± 65	215
	Future	22	8	22	124 ± 120	388
Crassula moschata (s)	Past	17	6	7	50 ± 70	203
	Present	7	2	5	28 ± 40	56
	Future	3	1	7	68 ± 157	395
Juncus scheuchzerioides (s)	Past	19	6	11	44 ± 36	97
	Present	32	11	13	65 ± 58	190
	Future	74	26	18	144 ± 147	418
Leptinella plumosa (s)	Past	44	15	11	74 ± 87	286
	Present	24	8	9	62 ± 81	272
	Future	2	1	5	31 ± 30	61
Montia fontana (s)	Past	28	10	13	102 ± 99	302
	Present	39	13	13	116 ± 143	462
	Future	29	10	16	201 ± 219	667
Phlegmariururus saururus (g)	Past	15	5	32	85 ± 42	164
	Present	39	14	33	129 ± 88	312
	Future	20	7	27	168 ± 124	423
**Poa annua*	Past	53	18	13	121 ± 119	378
	Present	17	6	7	55 ± 77	256
	Future	24	8	9	43 ± 34	108
Poa cookii (s)	Past	79	27	16	95 ± 90	312
	Present	53	18	14	72 ± 73	235
	Future	45	16	14	59 ± 49	137
Polypogon magellanicus (g)	Past	42	15	15	72 ± 49	175
	Present	93	32	21	132 ± 106	350
	Future	79	27	30	321 ± 205	669
Ranunculus biternatus (g)	Past	61	21	15	149 ± 174	542
	Present	45	16	13	107 ± 144	429
	Future	109	38	19	212 ± 207	675
**Sagina procumbens*	Past	63	22	14	101 ± 113	369
	Present	34	11	11	70 ± 89	286
	Future	18	6	9	46 ± 55	116


Past
-1.4 °C
Present
+1.4 °C
Future
Acaena magellanica
Austroblechnum penna-marina
Azorella selago
Carex dikei
Crassula moschata
Habitat suitability
1
0


Past
Present
Future
Juncus scheuchzerioides
-1.4 °C
+1.4 °C
Leptinella plumosa
Montia fontana
Habitat suitability
1
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Phlegmariurus saururus
Poa annua

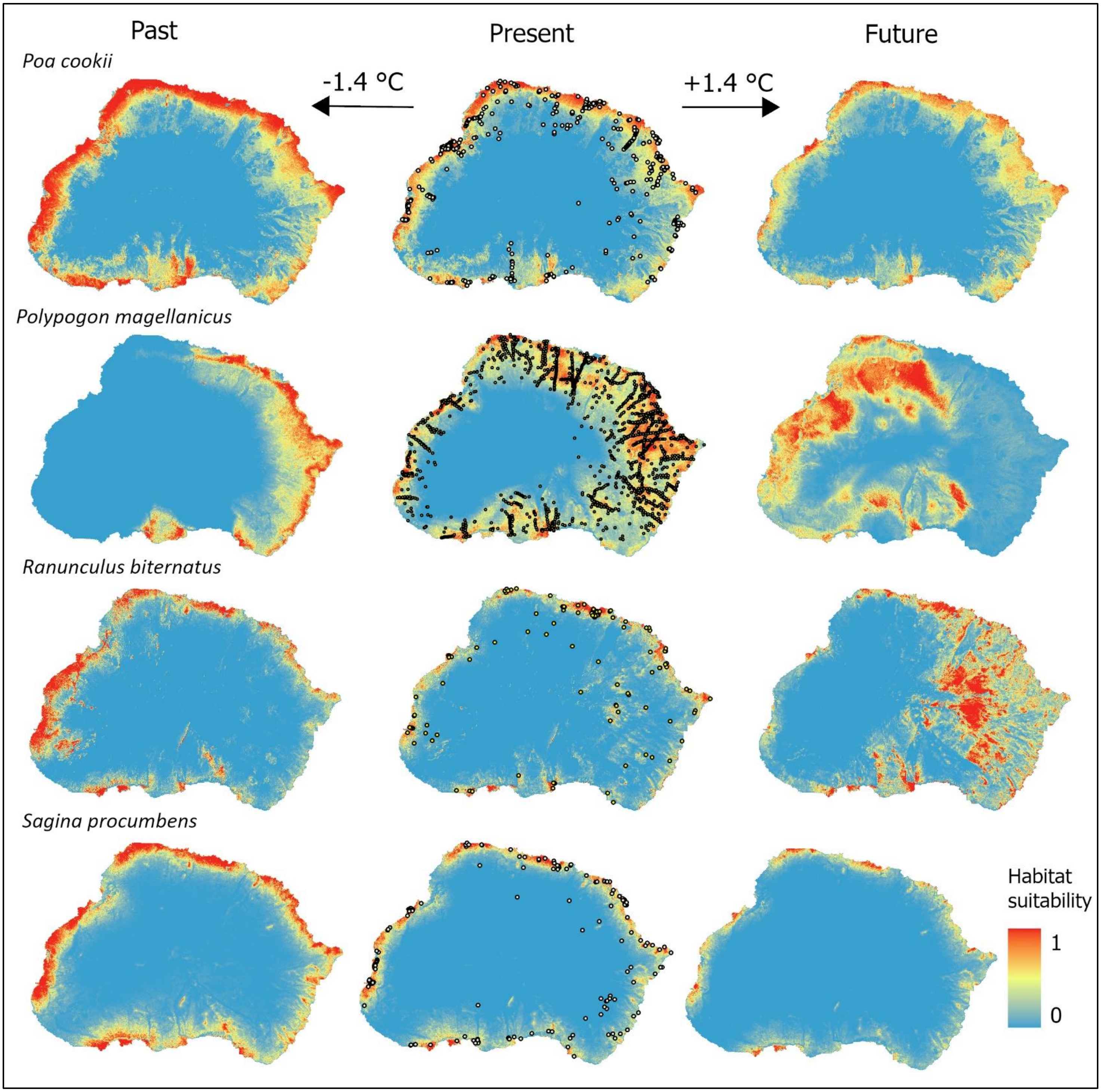

Figure 2. Habitat suitability models for 14 vascular plant species on MI. Habitat suitability values indicate the probability of occurrence of each species, predicted by the SDMs for each cell of the raster. "Past" represents a climate scenario where temperatures were 1.4°C cooler, which occurred on the island between 1965 and 1999 and "Future" represents a 1.4°C warmer climate if climate change were to continue. Occurrence records used to develop the SDMs are indicated as points on the "Present" maps.

Discussion

The most important determinants of habitat suitability and responses to changes in temperature were species-specific, supporting the hypothesis that responses of plant species to climate change are individualistic. For instance, of the generalist species whose habitat suitability increased from the past to the present, *A. selago* and *P. magellanicus* were primarily associated with mean nightly temperature, *P. saururus* with distance to the coast and *A. magellanica* and *A. penna-marina* with soil properties. Therefore, both the habitat requirements and the responses of species to changes in temperature occur at the species-level on MI. Consequently, the individual responses may not be detected if the average of all species distributional changes is considered. le Roux et al. (2008b) found that there was an average upslope range expansion of the entire vascular flora on MI, but that this broad response to climate change was dominated by only a few highly responsive species. Therefore, studying vegetation change at the species-level provides a deeper understanding of distributional shifts, echoing the view of van der Merwe et al. (2023) that vegetation should be considered at the species-level and not as an assemblage in species-poor environments.

While the main faunal influence on MI was included in the SDMs, a key biotic factor not included and that has become an important research topic in SDMs in recent years, was plant-plant interactions (Wisz et al. 2013; Poggiato et al. 2021). Facilitation may be important at the upper limits of some species ranges on MI (Raath-Krüger et al. 2019), although generally the importance of facilitative interactions increase with diversity (Schöb et al. 2018), while MI is species-poor. For instance, a key facilitative interaction found on MI involves *A. selago* cushion plants that act as a growth medium for other plants (Phiri et al. 2015). This is especially important at the rocky, higher elevations where abiotic conditions become harsher and the surrounding substrate is unsuitable for germination and thus where species reach their elevational range limits. However, the facilitative effect of *A. selago* is species-specific as only some species are affected by the interaction (Raath-Krüger et al. 2019). In terms of competition, *A. penna-marina* seems to shade other plants, especially where it reaches dominance on slopes. This may lead to *A. penna-marina* outcompeting other plants for light, and ultimately their exclusion in some areas, but only less competitive species, such as the slow growing cushion plants appear to be affected (see Chapter 3; Smith et al. 2001). Furthermore, young environments may not have had sufficient time for strong plant-plant species interactions to develop (van der Merwe et al. 2023), especially in terms of facilitative interactions. Climate change is also expected to alter these species interactions, as a result of such individualistic responses. Consequently, complex future changes in species interactions will lead to erroneous predictions if using the current web of interactions in predictions (Pearson & Dawson 2003). Furthermore, somewhat unique when compared to more temperate and diverse environments where biotic interactions are important (Schöb et al. 2018), plant species are closely coupled to the harsh abiotic conditions on MI (Smith & Steenkamp 2001). Plant-plant interactions were thus not included here due to the highly dynamic nature of plant-plant interactions, together with presumably lower importance of plant-plant interactions in low diversity environments, making their inclusion in SDMs challenging.

In support of the second hypothesis, the habitat suitability was predicted to have increased for all native generalist species on MI. While predicted distributional changes varied with species-specific habitat requirements, the habitat suitability models indicate that most generalists have expanded toward the interior, i.e., to higher elevations, and westward, thus toward the cooler parts of their ranges. This may be because of the amelioration of cooler temperatures at the extreme ends of species ranges and a likely increase in habitat suitability. Mean nightly and daily temperatures are cooler on the island's west coast compared to the east coast and also decrease with elevation toward the island's interior polar desert (Huntley 1971). Habitat generalists have a wide ecological amplitude and are able to adapt to a wide range of environmental conditions (Denelle et al. 2020). They are thus more likely to either persist in their current distribution and/or expand their ranges with changing conditions (Pandit et al. 2009). Conversely, specialist plant species are more strongly associated with an explicit environmental condition, for example nutrient enriched soils, and are thus constrained from range shifts in response to temperature amelioration (Cramer et al. 2022). Such specific habitat requirements suggests that specialists may respond more to localised conditions, whereas generalists may rather respond to broader scale processes (Pandit et al. 2009).

Most specialist species, except those that are considered hygrophilous, were predicted to have shrunk their ranges, regardless of specialisation, providing some support for the third hypothesis. Coprophilous species occur in soils enriched by the manuring of seals and seabirds (Huntley 1971) and thus their distribution is constrained by their proximity to fauna. Indeed, the coprophilous *P. cookii* was predicted to occur only near fauna where soils had high nutrient content. Changes in the distribution of *P. cookii* have also occurred rapidly in the past (Smith et al. 2001), due to this close coupling of *P. cookii* with faunal distribution. In areas where cats diminished the abundance of burrow-nesting birds, and thus also the associated localised nutrient enrichment, *P. cookii* has decreased considerably (Smith & Mucina 2006). After cats were eradicated in 1991, mice continued to predate on burrowing seabirds, resulting in the seabird numbers not increasing as expected (Dilley et al. 2017). Until mice are also eradicated, the habitat suitability of *P. cookii* is likely to continue decreasing, as predicted here under continued warming alone, regardless of mouse predation. Therefore, distributional changes in coprophilous species will be highly influenced by faunal population dynamics, rather than temperature changes.

The two halophytes, *C. moschata* and *L. plumosa*, only occur in close proximity to the coast in areas that receive regular wind-blown saltspray. Such conditions are especially common on the west coast where saltspray can reach further inland with the strong westerly winds (Huntley 1971; Gremmen 1981). Their habitat suitability can only expand if the saltspray reaches further inland, which is an unlikely scenario, since the mean wind speed has not increased on MI (see Chapter 3). Because it is a small, succulent species with a tolerance for high salinity (Zeng et al. 2018), *C. moschata* is one of only two species that can tolerate the high saltspray on MI (Huntley 1971) and does not occur in any other habitat, likely because it can not compete with the taller species elsewhere. Saltspray and competition with taller species thus likely restricts *C. moschata* to within meters of the coast. However, if saltspray will not reach as far inland in the future, if wind speed decreases for instance, generalist species could possibly expand toward such previously unsuitable habitats. Therefore, if the predictions for halophytes are for range contraction under temperature increase alone, as predicted here, a decrease in mean wind speed, which has occurred in the past on MI (Chapter 3) may further reduce habitat suitability for the halophytes and increase suitability for generalists.

Not all the specialist species were predicted to retract their ranges. Particularly, the habitat suitability for the two hygrophilous species, *J. scheuchzerioides* and *C. dikei*, was predicted to increase even though the evidence suggests that this is unlikely to occur. While the upslope expansion of the hygrophilous species was also documented by le Roux & McGeoch (2008b) at a rate similar to the generalist species, a key environmental change not represented in the change predictions, is the drying of the island (Chapter 3; le Roux & McGeoch 2008a). Precipitation decreased from by *c.* 1000 mm p.a. between 1960 and 2020 with a linearly deceasing trend that seems likely to continue (Chapter 3). The mires where the hygrophilous species occur are thus likely drying out, increasing habitat suitability for species that cannot tolerate the waterlogged soils. Indeed, *A. penna-marina*, that prefers well-drained soils (Huntley 1971), has expanded into mires (Chapter 3). Furthermore, mice eat the flowering heads of *C. dikei*, reducing their reproductive output (Smith et al. 2002). Because of this herbivory, *C. dikei* has more rapidly decreased than can be expected under drier conditions alone. Therefore, while habitat suitability was erroneously predicted to have increased for hygrophilous species by the SDMs, this is unlikely to occur due to the continued decrease in precipitation and herbivory by mice.

The two invasive species studied here are the most widespread invasive plant species on MI (le Roux et al. 2013a). Their habitat suitability changes followed a similar trend to the coprophilous species, decreasing with warming, although *P. annua* was predicted to expand from the present to the future scenario. Since warming temperatures in climatically-harsh conditions are associated with climate amelioration, the range contraction of the two invasive species is contrary to what might be expected of invasive species which usually increase under more favourable conditions (Richardson & van Wilgen 2004; Lee et al. 2017; Ripley et al. 2020). This is likely because rate of spread could not be included in the SDMs. The invasive plant species on MI have likely not reached equilibrium, as they are still rapidly spreading across the island (le Roux et al. 2013b; Chapter 3), and thus range contraction is unlikely to occur. Furthermore, since their habitat suitability overlaps with coprophilous species, *P. annua* and *S. procumbens* may compete with the coprophilous species in particular. Similarly, on Possession Island in the sub-Antarctic, the SDMs for *P. annua* and *S. procumbens s*howed that their occurrence was weakly affected by anthropogenic factors, such as distance to hiking paths or buildings, and concluded thar their dispersal is likely not human-induced after establishment (Bazzichetto et al. 2021). Indeed, they suggested that factors other than anthropogenic and topographic conditions must be responsible for the occurrence of *P. annua* and *S. procumbens* due to the low predictive performance of the SDMs when only including anthropogenic, topographic, precipitation and temperature variables. Both these species spread and persist in biotically-influenced areas on MI, although *S. procumbens* occurs in most habitats (pers. Obs). Their spread is facilitated by the rising fur seal populations that trample previously extensive *P. 162ecogn* tussock grasslands, creating the opportunity and suitable habitats for invasive species (Ryan et al. 2003; Haussmann et al. 2013). Since coprophilous species are range restricted, *P. annua* and *S. procumbens* may negatively affect the coprophilous species on MI in particular.

The distribution of 10 of the 14 species was predicted to expand into higher mean elevations with increased temperatures. However, vascular plant species are constrained from rapid upslope movement toward the interior by the limited availability of suitable substrate above *c.* 300 m a.s.l., which results in soil nutrient limitations. They are also constrained from upslope movement by the increasingly harsher climatic conditions which occur with increasing elevation (le Roux & McGeoch 2010). This is evident by the observation that vegetation does not currently exceed 850 m a.s.l. (le Roux & McGeoch 2008b). Since soil development will lag the more rapid impacts of temperature increase (Cramer et al. 2022) and precipitation decrease, upslope movement of vascular plants may be slow. This is because species are constrained at the their upper elevational ranges to the distribution of suitable microsites, particularly cushion-forming plants and bryophytes that accumulate organic matter and facilitate the germination of vascular plant species (le Roux & McGeoch 2008b). Because of this, the distribution of vascular plant species into the interior polar desert is unlikely. Therefore, the predictions of the SDMs of vascular species expanding toward the harsh interior of the island, should not be considered an eventuality, as rock cover and/or soil depth could not be included as a potential constraint in the SDMs. Vascular plants may thus reach their range limits on the island in the near future if climate change continues its current trajectory.

Soil properties were included to determine whether plant species distributions can indeed be predicted by soils and because I believed that soil properties are a key constraint to species on MI, as soil nutrients reduce with elevation and increase with proximity to dense vegetation and fauna (Chapter 4; see also Huntley 1971; Smith & Steenkamp 2001). Soil properties contributed to the habitat suitability models of all species, for six of which soil fertility (represented by soil PC1) was the most important predictor. Consequently, there is support for the hypothesis that soil properties are important in predicting habitat suitability of plant species. Soil properties are mostly ignored in SDMs, due to data limitations, and this is considered a key gap in SDM and climate change research (Hageer et al. 2017; Cramer et al. 2019; Roe et al. 2022). Soil properties will lag the more rapid changes in temperature associated with climate change, and thus species that are adapted to specific edaphic conditions, such as coprophilous species, will be constrained by their edaphic requirements, limiting distributional changes (Cramer et al. 2022). However, soil maps were spatially predicted using boosted regression trees and likely have inaccuracies, particularly overprediction of the extreme values (see Chapter 4), and may have also influenced the habitat suitability prediction of plant species. Reducing the uncertainty of the soil maps with additional soil samples to increase the number of observations for each soil model, would improve the accuracy of the plant SDMs.

A consequence of excluding soil properties and fixed variables from species distribution models (SDMs) is that models may overemphasise the importance of changing variables, particularly climatic factors, with species being predicted to occur outside of their potential ranges (Austin & Van Niel 2011a). However, together with changing climate and biotic variables, here I also included “fixed” environmental variables, such as the topographic variables suggested to be included by other sub-Antarctic researchers (Bricher 2012; Fitzgerald et al. 2022), and soils which change much slower than vegetation and expands upon previous sub-Antarctic methods to include environmental variables in SDMs (Bricher 2012), and still temperature change was predicted to impact plant species ranges. This indicates that temperature, although considered as the only climatic variable to change in these models, influences plant species ranges significantly in tundra vegetation. The less pronounced distributional changes predicted for specialist species were likely revealed partially due to the inclusion of fixed variables and soils, leading to more realistic species-environment relationships. Specialists are highly dependent on particular environmental conditions (Brouat et al. 2004), and thus range shifts in response to temperature change is dependent on the environmental or biotic conditions that a specialist species relies on. If these conditions do not shift along with climate, specialists may be limited in their ability to track climate change (Cramer et al. 2022).

Even though every step in the modelling process was carefully considered and hyperparameters were finely tuned for each species (Elith et al. 2011; Merow et al. 2013), the somewhat dramatic habitat suitability changes predicted for some species by the models are likely overestimated. This may be due to the delicate balance between finding the best model performance and overfitting or underfitting (Elith et al. 2006; Pichler & Hartig 2023). This is why species distribution modelling is considered an ”art” (Elith et al. 2010). SDMs, especially in climate change studies, are not always realistic reflections of species ranges or changes therein (Carneiro et al. 2016; Dearborn et al. 2022). Because not all constraints to plant species can be included in modelling attempts, the readily available and most important determinants of habitat suitability are usually selected (Williams et al. 2012; Hageer et al. 2017). However, these shortcomings may rather be overcome by including a biophysiological-relevant combination of fixed variables, such as topographic or slowly changing edaphic properties, that may potentially constrain species distributions from movement, together with the changing climate variables. I acknowledge that some constraints to plant species distributions, such as soil depth or plant-plant interactions (le Roux et al. 2013a), may be important in determining some species habitat requirements but were not included here. The estimates for species ranges and elevational limits should thus be cautiously interpreted. Uncertainty is inherent in any prediction model (Wiens et al. 2009), but the general trends are still clear, even if range sizes and upper elevational boundaries may be dependent on the modelling parameters chosen. Somewhat unusually for SDM development, an independent check on past vegetation change was available (Chapter 4) that gives confidence in some of the patterns revealed by the SDMs for the past to present scenario.

Conclusion

While the habitat requirements of the vascular plant species on MI were species-specific, with the distribution of species being predicted by differential variables, the responses of generalists were similar, whereas responses for specialist species to warming were similar. With the warming that has occurred on MI, the habitat suitability of generalist plant species was predicted to have increased, within the physical constraints imposed by the environment, and toward the west coast, whereas the habitat suitability of most specialist species was predicted to have decreased with warming. With the exponential increase in remotely-sensed data availability, it has become possible to include the diverse aspects that plant species encounter in their environment, both abiotic and biotic, in spatial modelling. Researchers have called for the inclusion of a broad set of environmental variables in SDMs in recent decades (Austin & Van Niel 2011b; Williams et al. 2012; Guisan et al. 2013; Zurell, Franklin et al. 2020) to incorporate more constraints to species range shifts and this is now a possibility, even in remote regions such as the sub-Antarctic, as shown in this study.

References

Ainsworth, A., & Drake, D.R. 2020. Classifying Hawaiian plant species along a habitat generalist-specialist continuum: Implications for species conservation under climate change. *PLOS ONE 15:* e0228573.

Allouche, O., Tsoar, A., & Kadmon, R. 2006. Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). *Journal of Applied Ecology* 43: 1223–1232.

Amatulli, G., Domisch, S., Tuanmu, M.-N., Parmentier, B., Ranipeta, A., Malczyk, J., & Jetz, W. 2018. A suite of global, cross-scale topographic variables for environmental and biodiversity modeling. *Scientific Data* 5: 180040.

Anderson, R.P., & Gonzalez Jr., I. 2011. Species-specific tuning increases robustness to sampling bias in models of species distributions: An implementation with Maxent. *Ecological Modelling* 222: 2796–2811.

Austin, M.P. 2005. Vegetation and environment: discontinuities and continuities. In van der Maarel, E. (ed.), *Vegetation Ecology*, Blackwell Publishing, Oxford, UK.

Austin, M.P., & Van Niel, K.P. 2011a. Impact of landscape predictors on climate change modelling of species distributions: a case study with *Eucalyptus fastigata* in southern New South Wales, Australia. *Journal of Biogeography* 38: 9–19.

Austin, M.P., & Van Niel, K.P. 2011b. Improving species distribution models for climate change studies: variable selection and scale. *Journal of Biogeography* 38: 1–8.

Bazzichetto, M., Massol, F., Carboni, M., Lenoir, J., Lembrechts, J.J., Joly, R., Renault, D. 2021. Once upon a time in the far south: Influence of local drivers and functional traits on plant invasion in the harsh sub-Antarctic islands. *Journal of Vegetation Science* 32, e13057.

Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W., & Courchamp, F. 2012. Impacts of climate change on the future of biodiversity. *Ecology Letters* 15: 365–377.

Bergstrom, D.M., & Chown, S.L. 1999. Life at the front: history, ecology and change on southern ocean islands. *Trends in Ecology & Evolution* 14: 472–477.

Bester, M.N., Bloomer, J.P., Van Aarde, R.J., Erasmus, B.H., Van Rensburg, P.J.J., Skinner, J.D., Howell, P.G., & Naude, T.W. 2002. A review of the successful eradication of feral cats from sub-Antarctic Marion Island, Southern Indian Ocean. *South African Journal of Wildlife Research* 32: 65-73.

Beven, K.J., & Kirkby, M.J. 1979. A physically based, variable contributing area model of basin hydrology. *Hydrological Sciences Journal* 24: 43-69.

Bradley, A.P. 1997. The use of the area under the roc curve in the evaluation of machine learning algorithms. *Pattern Recognition* 30: 1145–1159.

Bricher, P. 2012. Methods for mapping the tundra vegetation of sub-Antarctic Macquarie Island. PhD thesis, University of Tasmania, Tasmania.

Brouat, C., Chevallier, H., Meusnier, S., Noblecourt, T., & Rasplus, J.Y. 2004. Specialization and habitat: Spatial and environmental effects on abundance and genetic diversity of forest generalist and specialist Carabus species. *Molecular Ecology* 13: 1815–1826.

Carneiro, L.R. de A., Lima, A.P., Machado, R.B., & Magnusson, W.E. 2016. Limitations to the use of species-distribution models for environmental-impact assessments in the Amazon. *PLOS ONE* 11: e0146543.

Chen, I.-C., Hill, J.K., Ohlemueller, R., Roy, D.B., & Thomas, C.D. 2011. Rapid range shifts of species associated with high levels of climate warming. *Science* 333: 1024–1026.

Cramer, M.D., Hedding, D., Greve, M., Midgley, G.F., & Ripley, B.S. 2022. Plant specialisation may limit climate-induced vegetation change to within topographic and edaphic niches on a sub-Antarctic island. *Functional Ecology* 36: 2636–2648.

Cramer, M.D., Wootton, L.M., van Mazijk, R., & Verboom, G.A. 2019. New regionally modelled soil layers improve prediction of vegetation type relative to that based on global soil models. *Diversity and Distributions* 25: 1736–1750.

Crawford, R.J.M., Cooper, J., Dyer, B.M., Greyling, M.D., Klages, N.T.W., Ryan, P.G., Petersen, S.L., Underhill, L.G., Upfold, L., Wilkinson, W., De Villiers, M.S., Du Plessis, S., Du Toit, M., Leshoro, T.M., Makhado, A.B., Mason, M.S., Merkle, D., Tshingana, D., Ward, V.L., & Whittington, P.A. 2003. Populations of surface-nesting seabirds at Marion Island, 1994/95-2002/03. *African Journal of Marine Science* 25: 427–440.

Dearborn, K.D., Murray, C., & Westwood, R. 2022. Ground validation reveals limited applicability of species distribution models for dakota skipper (*Hesperia dacotae*, Lepidoptera: Hesperiidae) recovery efforts in Canada. *Environmental EntomologY* 51: 1249–1261.

Denelle, P., Violle, C., Munoz, F., & Consortium, D. 2020. Generalist plants are more competitive and more functionally similar to each other than specialist plants: insights from network analyses. *Journal of Biogeography* 47: 1922–1933.

Dilley, B.J., Schramm, M., & Ryan, P.G. 2017. Modest increases in densities of burrow-nesting petrels following the removal of cats (*Felis catus*) from Marion Island. *Polar Biology* 40: 625–637.

Elith, J., Graham, C.H., Anderson, R.P., Dudik, M., Ferrier, S., Guisan, A., Hijmans, R.J., Huettmann, F., Leathwick, J.R., Lehmann, A., Li, J., Lohmann, L.G., Loiselle, B.A., Manion, G., Moritz, C., Nakamura, M., Nakazawa, Y., Overton, J.M., Peterson, A.T., Phillips, S.J., Richardson, K., Scachetti-Pereira, R., Schapire, R.E., Soberon, J., Williams, S., Wisz, M.S., & Zimmermann, N.E. 2006. Novel methods improve prediction of species' distributions from occurrence data. *Ecography* 29: 129–151.

Elith, J., Kearney, M., & Phillips, S. 2010. The art of modelling range-shifting species. *Methods in Ecology and Evolution* 1: 330–342.

Elith, J., & Leathwick, J.R. 2009. Species distribution models: Ecological explanation and prediction across space and time. *Annual Review of Ecology, Evolution and Systematics* 40: 677–697.

Elith, J., Phillips, S.J., Hastie, T., Dudik, M., Chee, Y.E., & Yates, C.J. 2011. A statistical explanation of MaxEnt for ecologists. *Diversity and Distributions* 17: 43–57.

Fitzgerald, N.B., Kirkpatrick, J.B., Dickson, C.R., Williams, L.K., Fergus, A.J., & Whinam, J. 2022. Determining the distributions of plant communities in subantarctic vegetation using species distribution models. Australian Journal of Botany 70: 311–322.

Gardner, A.S., Maclean, I.M.D., & Gaston, K.J. 2019. Climatic predictors of species distributions neglect biophysiologically meaningful variables. *Diversity and Distributions* 25: 1318–1333.

Goddard, K.A., Craig, K.J., Schoombie, J., & le Roux, P.C. 2022. Investigation of ecologically relevant wind patterns on Marion Island using computational fluid dynamics and measured data. *Ecological Modelling* 464: 464: 109827.

Gremmen, N.J.M. 1981. *The vegetation of the Subantarctic islands Marion and Prince Edward*. Dr W. Junk Publishers, The Hague, Netherlands.

Gremmen, N.J.M., Chown, S.L., & Marshall, D.J. 1998. Impact of the introduced grass *Agrostis stolonifera* on vegetation and soil fauna communities at Marion Island, sub-Antarctic. *Biological Conservation* 85: 223-231.

Guisan, A., Tingley, R., Baumgartner, J.B., Naujokaitis-Lewis, I., Sutcliffe, P.R., Tulloch, A.I.T., Regan, T.J., Brotons, L., McDonald-Madden, E., Mantyka-Pringle, C., Martin, T.G., Rhodes, J.R., Maggini, R., Setterfield, S.A., Elith, J., Schwartz, M.W., Wintle, B.A., Broennimann, O., Austin, M., Ferrier, S., Kearney, M.R., Possingham, H.P., & Buckley, Y.M. 2013. Predicting species distributions for conservation decisions. *Ecology Letters* 16: 1424–1435.

Hageer, Y., Esperon-Rodriguez, M., Baumgartner, J.B., & Beaumont, L.J. 2017. Climate, soil or both? Which variables are better predictors of the distributions of Australian shrub species? *Peerj* 5: e3446.

Haussmann, N.S., Rudolph, E.M., Kalwij, J.M., & McIntyre, T. 2013. Fur seal populations facilitate establishment of exotic vascular plants. *Biological Conservation* 162: 33–40.

Hijmans, R. 2023. raster: Geographic data analysis and modeling. Available at https://CRAN.R-project.org/package=raster [Accessed 17 May 2023].

Hijmans, R.J., Phillips, S.J., Leathwick, J., & Elith, J. 2022. dismo: Species distribution modeling. Available at https://CRAN.R-project.org/package=dismo [Accessed 11 May 2023].

Hof, A.R., Jansson, R., & Nilsson, C. 2012. The usefulness of elevation as a predictor variable in species distribution modelling. *Ecological Modelling* 246: 86–90.

Hoffmann, A.A., Rymer, P.D., Byrne, M., Ruthrof, K.X., Whinam, J., McGeoch, M., Bergstrom, D.M., Guerin, G.R., Sparrow, B., Joseph, L., Hill, S.J., Andrew, N.R., Camac, J., Bell, N., Riegler, M., Gardner, J.L., & Williams, S.E. 2019. Impacts of recent climate change on terrestrial flora and fauna: Some emerging Australian examples. *Austral Ecology* 44: 3–27.

Huntley, B. 1971. Vegetation. In E. M. Van Zinderen Bakker (Ed.), Marion and Prince Edward Islands, pp. 98-160, A.A. Balkema, Cape Town, South Africa.

Lebouvier, M., Laparie, M., Hulle, M., Marais, A., Cozic, Y., Lalouette, L., Vernon, P., Candresse, T., Frenot, Y., & Renault, D. 2011. The significance of the sub-Antarctic Kerguelen Islands for the assessment of the vulnerability of native communities to climate change, alien insect invasions and plant viruses. *Biological Invasions* 13: 1195–1208.

Lee, J.R., Raymond, B., Bracegirdle, T.J., Chades, I., Fuller, R.A., Shaw, J.D., & Terauds, A. 2017. Climate change drives expansion of Antarctic ice-free habitat. *Nature* 547: pages49–54.

Leihy, R.I., Duffy, G.A., Nortje, E., & Chown, S.L. 2018. High resolution temperature data for ecological research and management on the Southern Ocean Islands. *Scientific Data* 5: 180177.

Leutner, B., Horning, N., & Schwalb-Willmann, J. 2023. RStoolbox: Tools for remote sensing data analysis. Available at https://bleutner.github.io/RStoolbox [Accessed 17 June 2023].

Liu, C.R., Berry, P.M., Dawson, T.P., & Pearson, R.G. 2005. Selecting thresholds of occurrence in the prediction of species distributions. *Ecography* 28: 385–393.

Liu, C., Newell, G., & White, M. 2016. On the selection of thresholds for predicting species occurrence with presence-only data. *Ecology and Evolution* 6: 337–348.

Lubbe, N.R. 2010. Soil characteristics and pedogenesis on sub-Antarctic Marion Island. PhD thesis, University of Pretoria, Pretoria, South Africa.

McClelland, G.T.W., Altwegg, R., Van Aarde, R.J., Ferreira, S., Burger, A.E., & Chown, S.L. 2018b. Climate change leads to increasing population density and impacts of a key island invader: *Ecological Applications* 28: 212–224.

Merow, C., Smith, M.J., & Silander Jr., J.A. 2013. A practical guide to MaxEnt for modeling species' distributions: what it does, and why inputs and settings matter. *Ecography* 36: 1058–1069.

van der Merwe, S., Greve, M., Skowno, A.L., Hoffman, M.T., & Cramer, M.D. 2023. Can vegetation be discretely classified in species-poor environments? Testing plant community concepts for vegetation monitoring on sub-Antarctic Marion Island. *Ecology and Evolution* 13: e9681.

Mathakutha, R., Steyn, C., le Roux, P.C., Blom, I.J., Chown, S.L., Daru, B.H., Ripley, B.S., Louw, A., & Greve, M. 2019. Invasive species differ in key functional traits from native and non-invasive alien plant species. *Journal of Vegetation Science* 30: 994–1006.

Momberg, M., Hedding, D.W., Luoto, M., & le Roux, P.C. 2021. Species differ in their responses to wind: the underexplored link between species fine-scale occurrences and variation in wind stress. *Journal of Vegetation Science* 32: e13093.

Naimi, B., Hamm, N.A., Groen, T.A., Skidmore, A.K., & Toxopeus, A.G. 2014. Where is positional uncertainty a problem for species distribution modelling. *Ecography* 37: 191-203.

Nolan, C., Overpeck, J.T., Allen, J.R.M., Anderson, P.M., Betancourt, J.L., Binney, H.A., Brewer, S., Bush, M.B., Chase, B.M., Cheddadi, R., Djamali, M., Dodson, J., Edwards, M.E., Gosling, W.D., Haberle, S., Hotchkiss, S.C., Huntley, B., Ivory, S.J., Kershaw, A.P., Kim, S.-H., Latorre, C., Leydet, M., Lezine, A.-M., Liu, K.-B., Liu, Y., Lozhkin, A. V, McGlone, M.S., Marchant, R.A., Momohara, A., Moreno, P.I., Mueller, S., Otto-Bliesner, B.L., Shen, C., Stevenson, J., Takahara, H., Tarasov, P.E., Tipton, J., Vincens, A., Weng, C., Xu, Q., Zheng, Z., & Jackson, S.T. 2018. Past and future global transformation of terrestrial ecosystems under climate change. *Science* 361: 920–923.

Nunez, S., Arets, E., Alkemade, R., Verwer, C., & Leemans, R. 2019. Assessing the impacts of climate change on biodiversity: is below 2 degrees C enough? *Climatic Change* 154: 351–365.

Pandit, S.N., Kolasa, J., & Cottenie, K. 2009. Contrasts between habitat generalists and specialists: an empirical extension to the basic metacommunity framework. *Ecology* 90: 2253–2262.

Pearson, R., & Dawson, T. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global Ecology and Biogeography* 12: 361-371.

Phillips, S. 2021. maxnet: Fitting “Maxent” species distribution models with “glmnet.” Available at https://CRAN.R-project.org/package=maxnet [Accessed 17 May 2023].

Phillips, S.J., Anderson, R.P., & Schapire, R.E. 2006. Maximum entropy modeling of species geographic distributions. *Ecological Modelling* 190: 231–259.

Phillips, S.J., & Dudik, M. 2008. Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. *Ecography* 31: 161–175.

Phiri, E.E., Mcgeoch, M.A., & Chown, S.L. 2009. Spatial variation in structural damage to a keystone plant species in the sub-Antarctic: interactions between *Azorella selago* and invasive house mice. *Antarctic Science* 21: 189–196.

Phiri, E.E., McGeoch, M.A., & Chown, S.L. 2015. The abundance structure of *Azorella selago* Hook. f. on sub-Antarctic Marion Island: testing the peak and tail hypothesis. *Polar Biology* 38: 1881–1890.

Piao, S., Wang, X., Park, T., Chen, C., Lian, X., He, Y., Bjerke, J.W., Chen, A., Ciais, P., Tommervik, H., Nemani, R.R., & Myneni, R.B. 2020. Characteristics, drivers and feedbacks of global greening. *Nature Reviews Earth & Environment* 1: 14–27.

Pichler, M., & Hartig, F. 2023. Machine learning and deep learning-A review for ecologists. *Methods in Ecology and Evolution* 14: 994–1016.

Poggiato, G., Munkemuller, T., Bystrova, D., Arbel, J., Clark, J.S., & Thuiller, W. 2021. On the interpretations of joint modeling in community ecology. *Trends in Ecology and Evolution* 36: 391–401.

Qazi, A.W., Saqib, Z., & Zaman-ul-Haq, M. 2022. Trends in species distribution modelling in context of rare and endemic plants: a systematic review. *Ecological Processes* 11: 40.

R Core Team. 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing.

Raath-Krüger, M.J., McGeoch, M.A., Schöb, C., Greve, M., & le Roux, P.C. 2019. Positive plant-plant interactions expand the upper distributional limits of some vascular plant species. *Ecosphere* 10: e02820.

Richardson, D.M., & van Wilgen, B.W. 2004. Invasive alien plants in South Africa: how well do we understand the ecological impacts? *South African Journal of Science* 100: 45–52.

Ripley, B.S., Edwardes, A., Rossouw, M.W., Smith, V.R., & Midgley, G.F. 2020. Invasive grasses of sub-Antarctic Marion Island respond to increasing temperatures at the expense of chilling tolerance. *Annals of Botany* 125: 765–773.

Roe, N.A., Ducey, M.J., Lee, T.D., Fraser, O.L., Colter, R.A., & Hallett, R.A. 2022. Soil chemical variables improve models of understorey plant species distributions. *Journal of Biogeography* 49: 753–766.

le Roex, A.P., Chevallier, L., Verwoerd, W.J., & Barends, R. 2012. Petrology and geochemistry of Marion and Prince Edward Islands, Southern Ocean: Magma chamber processes and source region characteristics. *Journal of Volcanology and Geothermal Research* 223: 11–28.

Rogers, A.D., Frinault, B.A. V, Barnes, D.K.A., Bindoff, N.L., Downie, R., Ducklow, H.W., Friedlaender, A.S., Hart, T., Hill, S.L., Hofmann, E.E., Linse, K., McMahon, C.R., Murphy, E.J., Pakhomov, E.A., Reygondeau, G., Staniland, I.J., Wolf-Gladrow, D.A., & Wright, R.M. 2020. *Antarctic Futures: An Assessment of Climate-Driven Changes in Ecosystem Structure, Function, and Service Provisioning in the Southern Ocean*. In Carlson, C.A. & Giovannoni, S.J. (Eds.), Annual Review of Marine Science. Annual Reviews, CA, USA.

le Roux, P.C., Lenoir, J., Pellissier, L., Wisz, M.S., & Luoto, M. 2013b. Horizontal, but not vertical, biotic interactions affect fine-scale plant distribution patterns in a low-energy system. *Ecology* 94: 671–682.

le Roux, P.C., & McGeoch, M.A. 2008a. Changes in climate extremes, variability and signature on sub-Antarctic Marion Island. *Climatic Change* 86: 309–329.

le Roux, P.C., & McGeoch, M.A. 2010. Interaction intensity and importance along two stress gradients: adding shape to the stress-gradient hypothesis. *Oecologia* 162: 733–745.

le Roux, P.C., & McGeoch, M.A. 2008b. Rapid range expansion and community reorganization in response to warming. *Global Change Biology* 14: 2950-2962.

le Roux, P.C., & McGeoch, M.A. 2008c. Spatial variation in plant interactions across a severity gradient in the sub-Antarctic. *Oecologia* 155: 831–844.

le Roux, P.C., Ramaswiela, T., Kalwij, J.M., Shaw, J.D., Ryan, P.G., Treasure, A.M., McClelland, G.T.W., McGeoch, M.A., & Chown, S.L. 2013a. Human activities, propagule pressure and alien plants in the sub-Antarctic: Tests of generalities and evidence in support of management. *Biological Conservation* 161: 18–

27.

Rubenstein, M.A., Weiskopf, S.R., Bertrand, R., Carter, S.L., Comte, L., Eaton, M.J., Johnson, C.G., Lenoir, J., Lynch, A.J., Miller, B.W., Morelli, T.L., Rodriguez, M.A., Terando, A., & Thompson, L.M. 2023. Climate change and the global redistribution of biodiversity: substantial variation in empirical support for expected range shifts. *Environmental Evidence* 12: 7.

Rudolph, E.M., Hedding, D.W., De Bruyn, P.J.N., & Nel, W. 2022. An open access geospatial database for the sub-Antarctic Prince Edward Islands. *South African Journal of Science* 118: 12302.

Rudolph, E.M., Hedding, D.W., & Nel, W. 2021. The surface geology of the Prince Edward Islands: refined spatial data and call for geoconservation. *South African Journal of Geology* 124: 627–638.

Ryan, P.G., Smith, V.R., & Gremmen, N.J.M. 2003. The distribution and spread of alien vascular plants on Prince Edward Island. *African Journal of Marine Science* 25: 555–562.

Scherrer, D., D'Amen, M., Fernandes, R.F., Mateo, R.G., & Guisan, A. 2018. How to best threshold and validate stacked species assemblages? Community optimisation might hold the answer. *Methods in Ecology and Evolution* 9: 2155–2166.

Schöb, C., Brooker, R.W., & Zuppinger-Dingley, D. 2018. Evolution of facilitation requires diverse communities. *Nature Ecology & Evolution* 2: 1381–1385.

Smith, V.R., Avenant, N., & Chown, S.L. 2002. The diet and impact of house mice on a sub-Antarctic island. *Polar Biology* 25: 703–715.

Smith, V.R., & Mucina, L. 2006. Vegetation of sub-Antarctic Marion and Prince Edward Islands. In Mucina, L., Rutherford, M.C., & Powrie, L.W. (Eds.), *Vegetation of South Africa, Lesotho and Swaziland*, pp. 699–723. South African National Biodiversity Institute, Pretoria, South Africa.

Smith, V.R., & Steenkamp, M. 2001. Classification of the terrestrial habitats on Marion Island based on vegetation and soil chemistry. *Journal of Vegetation Science* 12: 181–198.

Smith, V.R., & Steenkamp, M. 1990. *Climatic change and its ecological implications at a subantarctic island*. Oecologia 85: 14-24.

Smith, V.R., Steenkamp, M., & Gremmen, N.J.M. 2001. Terrestrial habitats on sub-Antarctic Marion Island: Their vegetation, edaphic attributes, distribution and response to climate change. *South African Journal of Botany* 67: 641–654.

Vale, C.G., Tarroso, P., & Brito, J.C. 2014. Predicting species distribution at range margins: Testing the effects of study area extent, resolution and threshold selection in the Sahara-Sahel transition zone. *Diversity and Distributions* 20: 20–33.

Vignali, S., Barras, A.G., Arlettaz, R., & Braunisch, V. 2020. SDMtune: An R package to tune and evaluate species distribution models. *Ecology and Evolution* 10: 11488–11506.

Walthert, L., & Meier, E.S. 2017. Tree species distribution in temperate forests is more influenced by soil than by climate. *Ecology and Evolution* 7: 9473–9484.

Wege, M., Etienne, M.-P., Oosthuizen, W.C., Reisinger, R.R., Bester, M.N., & de Bruyn, P.J.N. 2016. Trend changes in sympatric Subantarctic and Antarctic fur seal pup populations at Marion Island, Southern Ocean. *Marine Mammal Science* 32: 960–982.

Weil, R.R., & Brady, N.C. 2016. *The nature and properties of soils*. Pearson, London, UK.

Wiens, J.A., Stralberg, D., Jongsomjit, D., Howell, C.A., & Snyder, M.A. 2009. Niches, models, and climate change: Assessing the assumptions and uncertainties. *Proceedings of the National Academy of Sciences of the United States of America* 106: 19729–19736.

Wilkinson, D.P., Golding, N., Guillera-Arroita, G., Tingley, R., & McCarthy, M.A. 2019. A comparison of joint species distribution models for presence-absence data. *Methods in Ecology and Evolution* 10: 198–211.

Wilkinson, D.P., Golding, N., Guillera-Arroita, G., Tingley, R., & McCarthy, M.A. 2021. Defining and evaluating predictions of joint species distribution models. *Methods in Ecology and Evolution* 12: 394–404.

Williams, K.J., Belbin, L., Austin, M.P., Stein, J.L., & Ferrier, S. 2012. Which environmental variables should I use in my biodiversity model? *International Journal of Geographical Information Science* 26: 2009–2047.

Wisz, M.S., Pottier, J., Kissling, W.D., Pellissier, L., Lenoir, J., Damgaard, C.F., Dormann, C.F., Forchhammer, M.C., Grytnes, J.-A., Guisan, A., Heikkinen, R.K., Hoye, T.T., Kuehn, I., Luoto, M., Maiorano, L., Nilsson, M.-C., Normand, S., Ockinger, E., Schmidt, N.M., Termansen, M., Timmermann, A., Wardle, D.A., Aastrup, P., & Svenning, J.-C. 2013. The role of biotic interactions in shaping distributions and realised assemblages of species: implications for species distribution modelling. *Biological Reviews* 88: 15–30.

Zeng, F., Shabala, S., Maksimovic, J.D., Maksimovic, V., Bonales-Alatorre, E., Shabala, L., Yu, M., Zhang, G., & Zivanovic, B.D. 2018. Revealing mechanisms of salinity tissue tolerance in succulent halophytes: A case study for *Carpobrotus rossi*. *Plant Cell and Environment* 41: 2654–2667.

Zurell, D., Franklin, J., Koenig, C., Bouchet, P.J., Dormann, C.F., Elith, J., Fandos, G., Feng, X., Guillera-Arroita, G., Guisan, A., Lahoz-Monfort, J.J., Leitao, P.J., Park, D.S., Peterson, A.T., Rapacciuolo, G., Schmatz, D.R., Schroeder, B., Serra-Diaz, J.M., Thuiller, W., Yates, K.L., Zimmermann, N.E., & Merow, C. 2020. A standard protocol for reporting species distribution models. *Ecography* 43: 1261–1277.

Zurell, D., Thuiller, W., Pagel, J., Cabral, J.S., Munkemuller, T., Gravel, D., Dullinger, S., Normand, S., Schiffers, K.H., Moore, K.A., & Zimmermann, N.E. 2016. Benchmarking novel approaches for modelling species range dynamics. *Global Change Biology* 22: 2651–2664.

Zurell, D., Zimmermann, N.E., Gross, H., Baltensweiler, A., Sattler, T., & Wuest, R.O. 2020. Testing species assemblage predictions from stacked and joint species distribution models. *Journal of Biogeography* 47: 101–113.

Appendix D

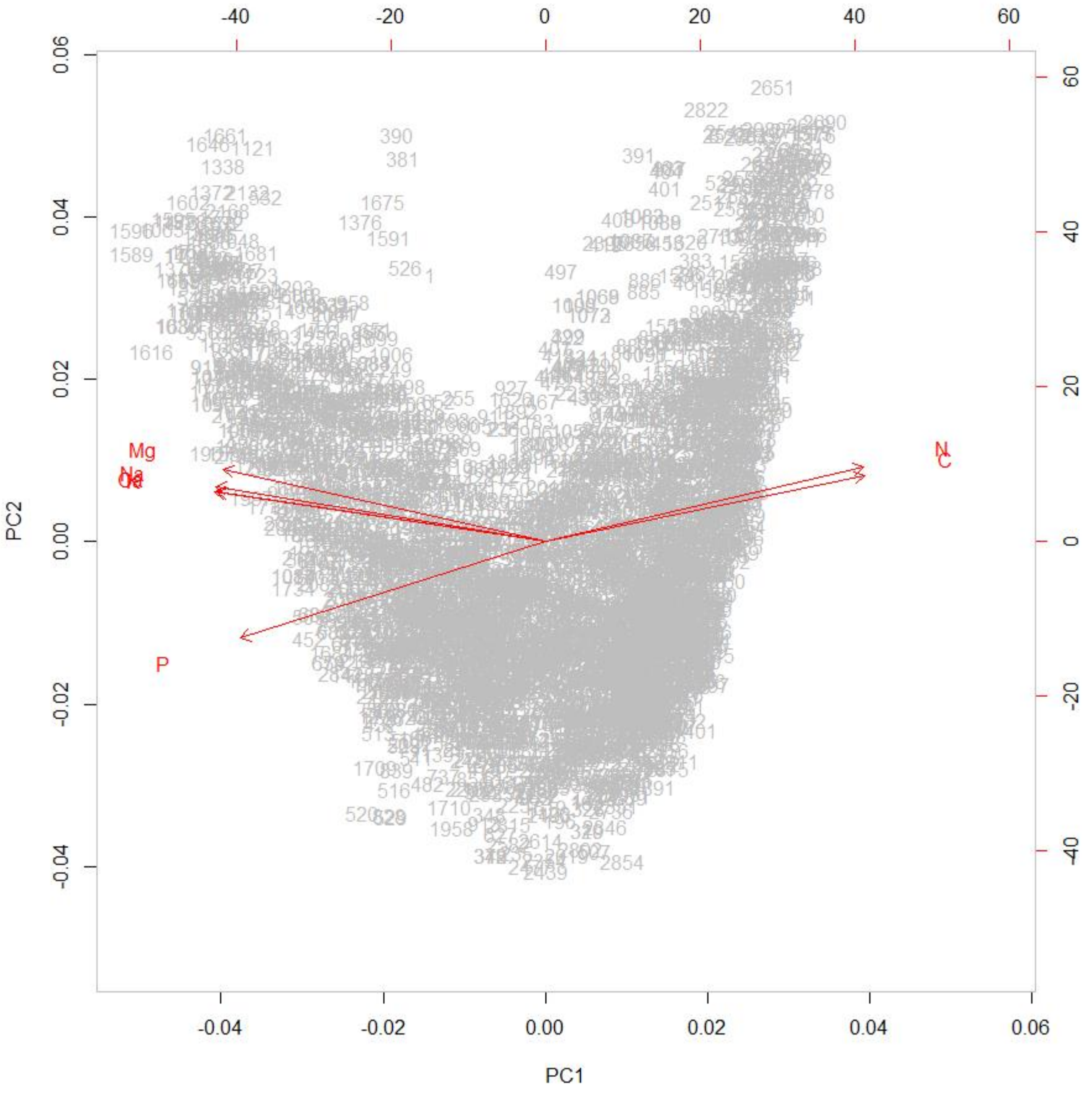

Figure D1. Principle component analysis (PCA) of soil properties. Values of each soil property were extracted from the soil raster layers (N, P, K, C, Ca, Mg, Na) for each species location and subjected to a PCA.

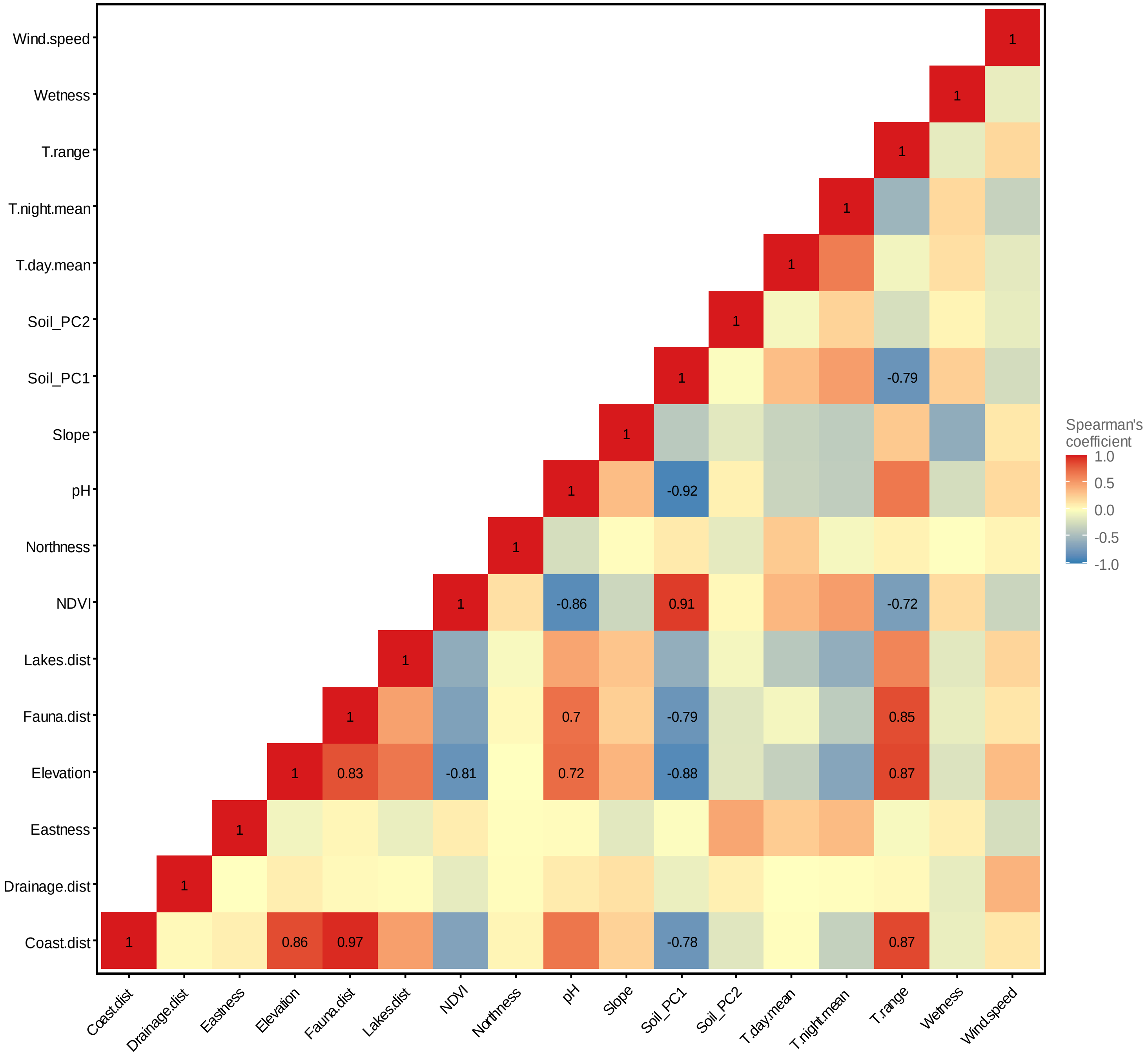

Figure D2. Correlation matrix of the full set of environmental variables considered for the SDMs. Only values above the 0.7 Spearman's correlation, which was used as the correlation threshold in this study, are shown.

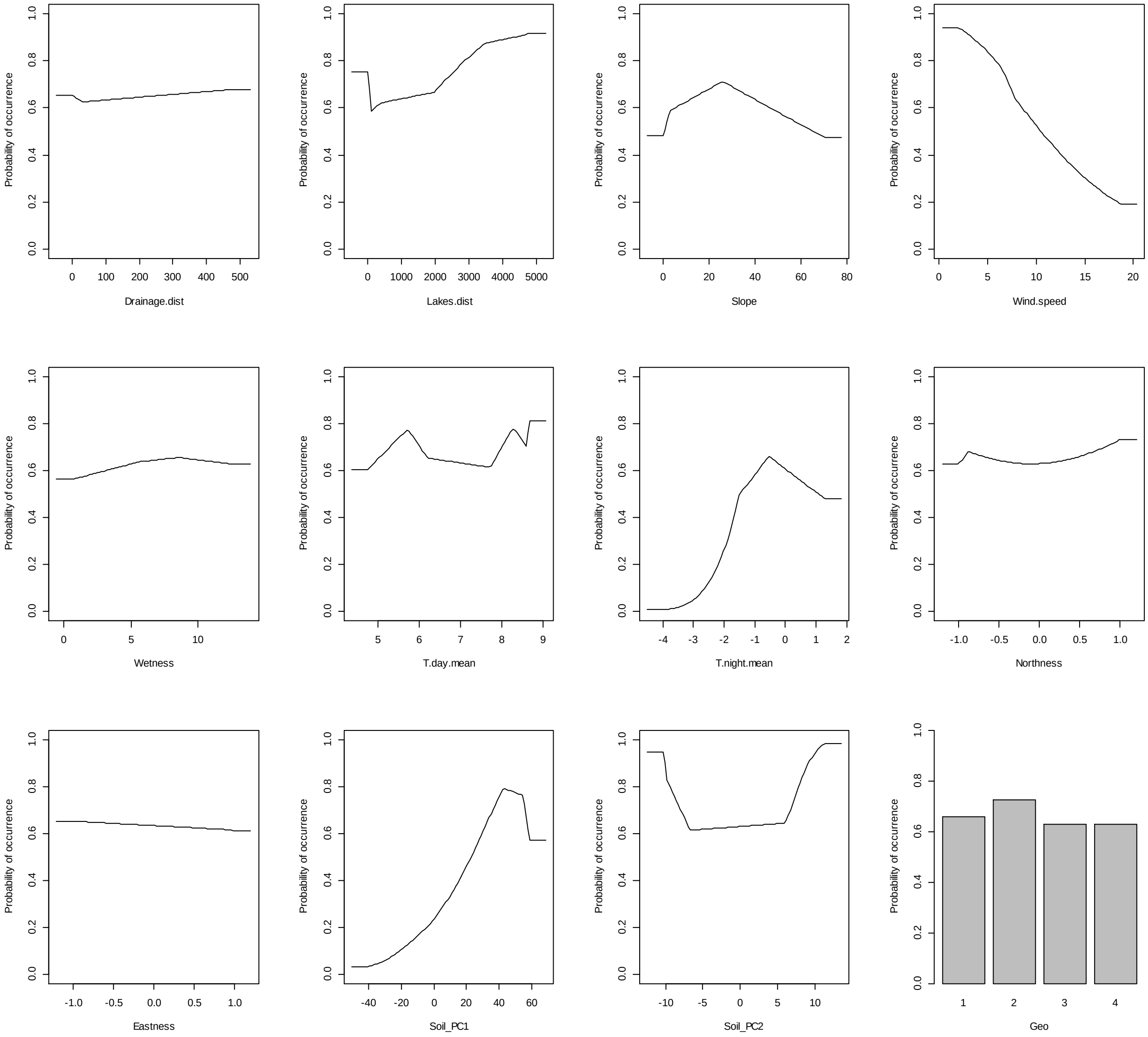

Figure D3 Response curves showing the relationship between the probability of occurrence of *Acaena magellanica* and the predictor variables retained in the SDMs. “Coast.dist” = distance to coast, “Drainage.dist” = distance to drainage lines, “Fauna.dist” = distance to fauna, “Lakes.dist” = distance to lakes, “T.range” = Temperature range, “T.day.mean” = mean daily temperature, “T.night.mean” = mean nightly temperature, “Wetness” = topographic wetness index, “Geo” = geology. “Northness” and “Eastness” are continuous measures of aspect. “Soil_PC1” = first principal component and “Soil_PC2” = second principal of the soil variables.

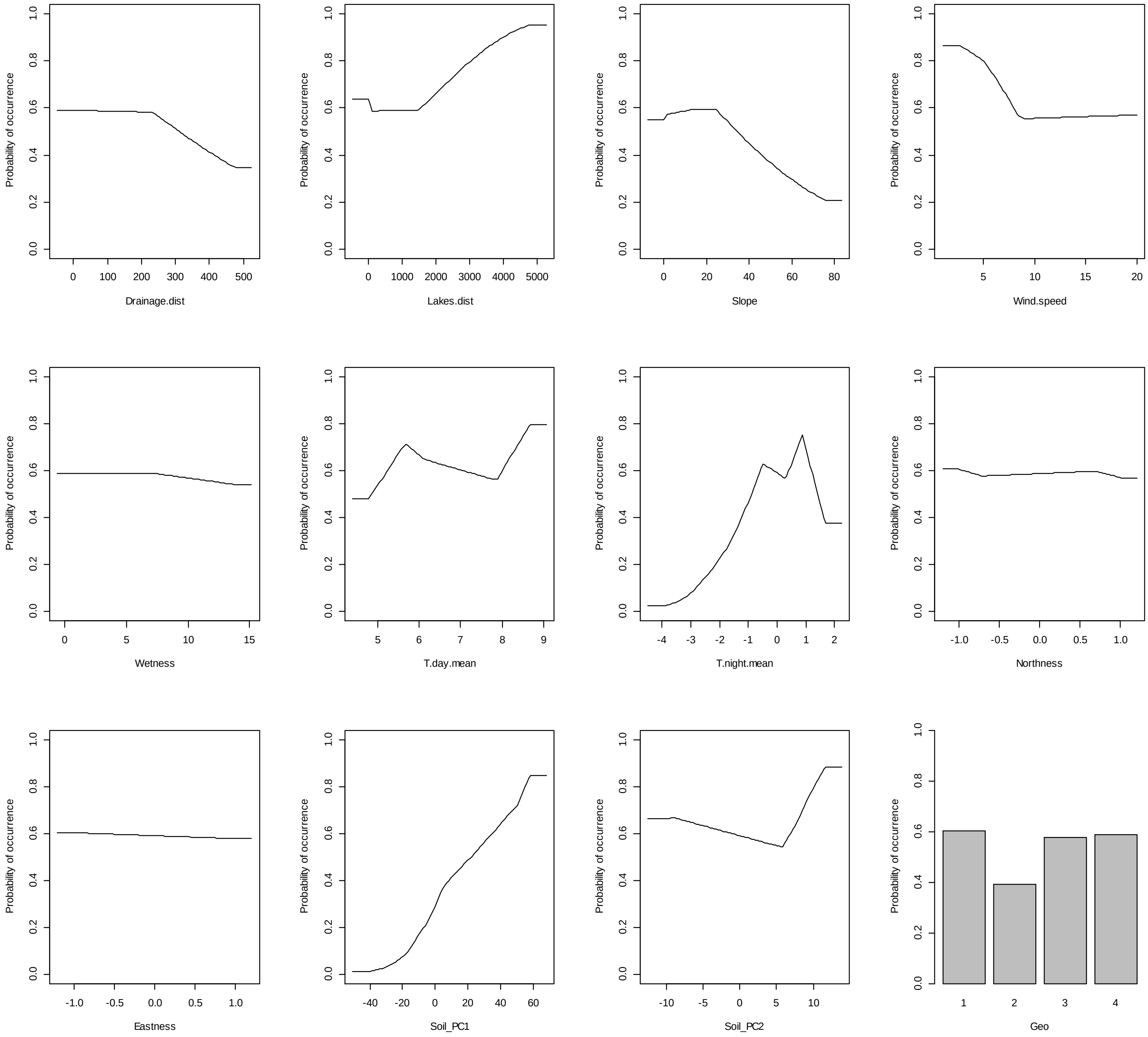

Figure D4. Response curves showing the relationship between the probability of occurrence of *Austroblechnum penna-marina* and the predictor variables retained in the SDMs. “Coast.dist” = distance to coast, “Drainage.dist” = distance to drainage lines, “Fauna.dist” = distance to fauna, “Lakes.dist” = distance to lakes, “T.range” = Temperature range, “T.day.mean” = mean daily temperature, “T.night.mean” = mean nightly temperature, “Wetness” = topographic wetness index, “Geo” = geology. “Northness” and “Eastness” are continuous measures of aspect. “Soil_PC1” = first principal component and “Soil_PC2” = second principal of the soil variables.

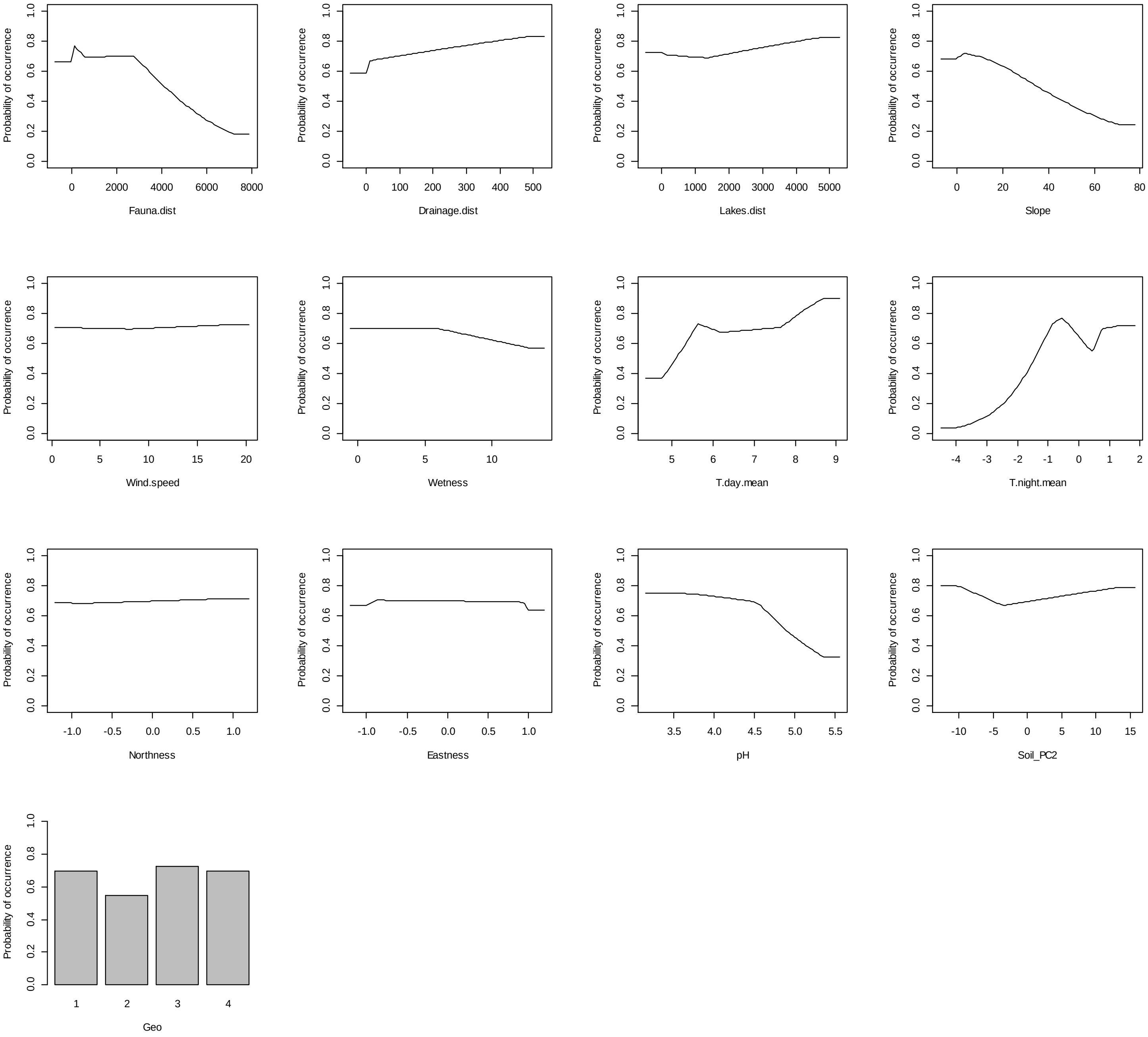

Figure D5. Response curves showing the relationship between the probability of occurrence of *Azorella selago* and the predictor variables retained in the SDMs. "Coast.dist" = distance to coast, "Drainage.dist" = distance to drainage lines, "Fauna.dist" = distance to fauna, "Lakes.dist" = distance to lakes, "T.range" = Temperature range, "T.day.mean" = mean daily temperature, "T.night.mean" = mean nightly temperature, "Wetness" = topographic wetness index, "Geo" = geology. "Northness" and "Eastness" are continuous measures of aspect. "Soil_PC1" = first principal component and "Soil_PC2" = second principal of the soil variables.

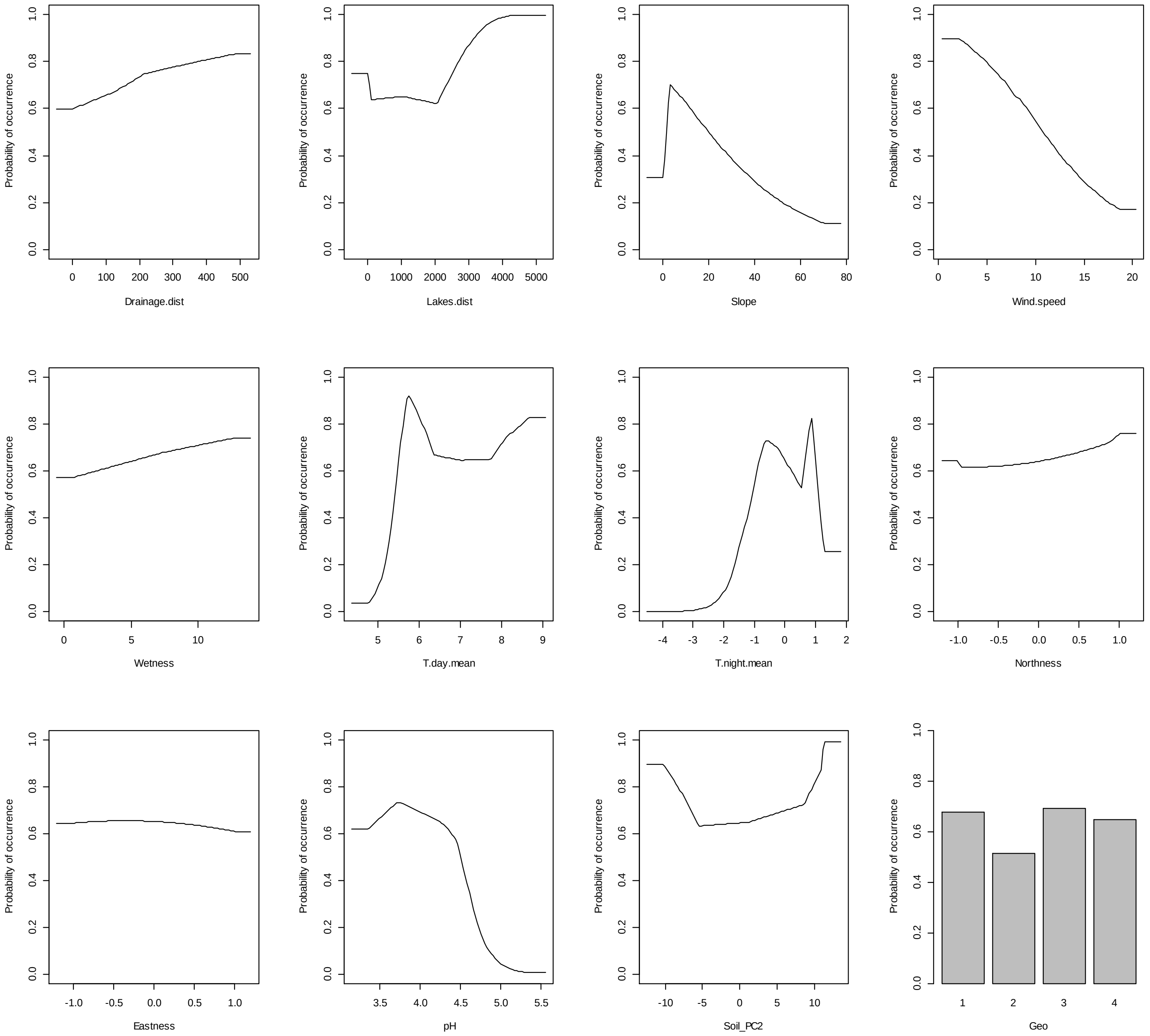

Figure D6. Response curves showing the relationship between the probability of occurrence of *Carex dikei* and the predictor variables retained in the SDMs. "Coast.dist" = distance to coast, "Drainage.dist" = distance to drainage lines, "Fauna.dist" = distance to fauna, "Lakes.dist" = distance to lakes, "T.range" = Temperature range, "T.day.mean" = mean daily temperature, "T.night.mean" = mean nightly temperature, "Wetness" = topographic wetness index*, "Geo" = geology*. "Northness" and "Eastness" are continuous measures of aspect. "Soil_PC1" = first principal component and "Soil_PC2" = second principal of the soil variables.

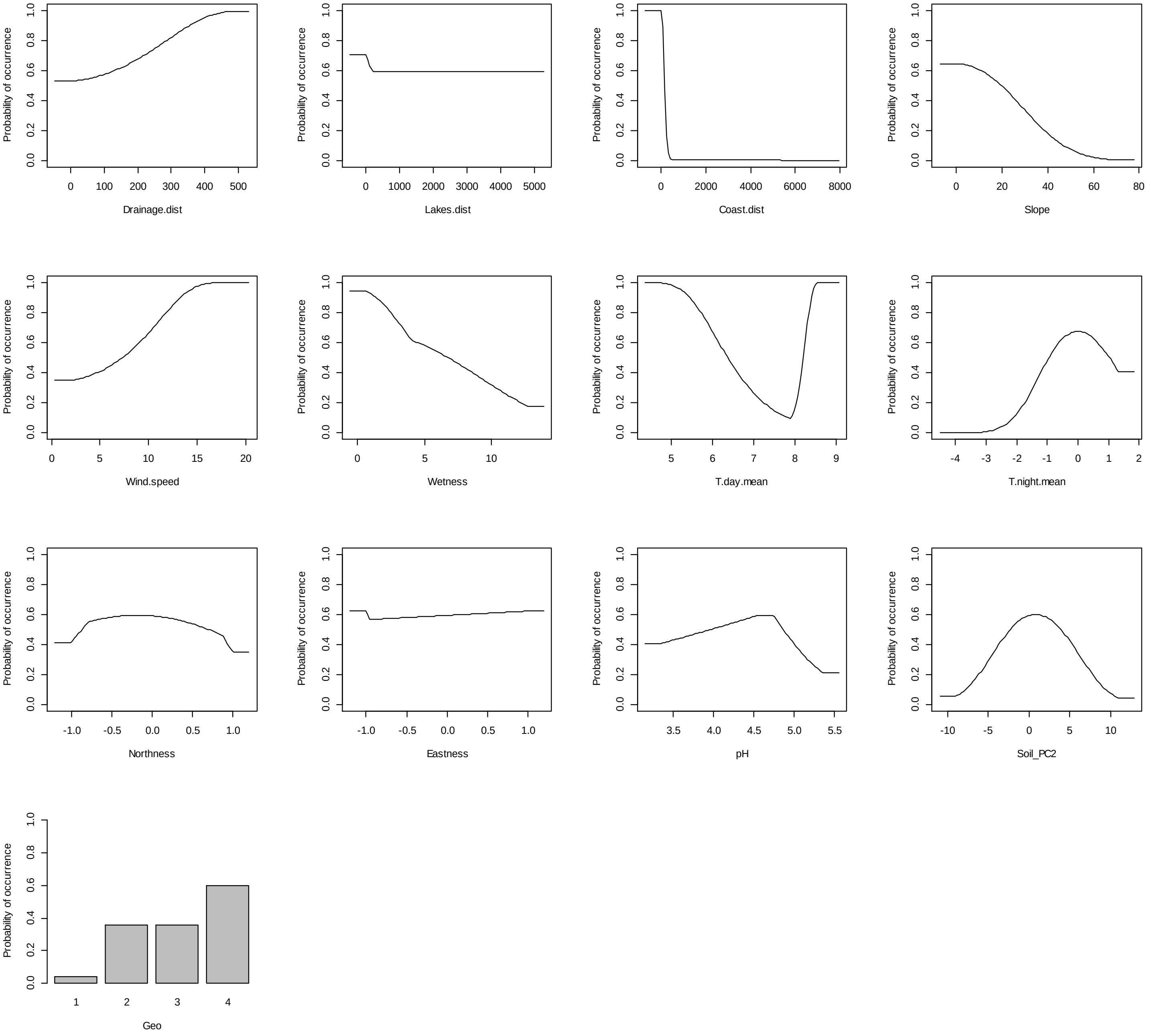

Figure D7. Response curves showing the relationship between the probability of occurrence of *Crassula moschata* and the predictor variables retained in the SDMs. “Coast.dist” = distance to coast, “Drainage.dist” = distance to drainage lines, “Fauna.dist” = distance to fauna, “Lakes.dist” = distance to lakes, “T.range” = Temperature range, “T.day.mean” = mean daily temperature, “T.night.mean” = mean nightly temperature, “Wetness” = topographic wetness index*, “Geo” = geology*. “Northness” and “Eastness” are continuous measures of aspect. “Soil_PC1” = first principal component and “Soil_PC2” = second principal of the soil variables.

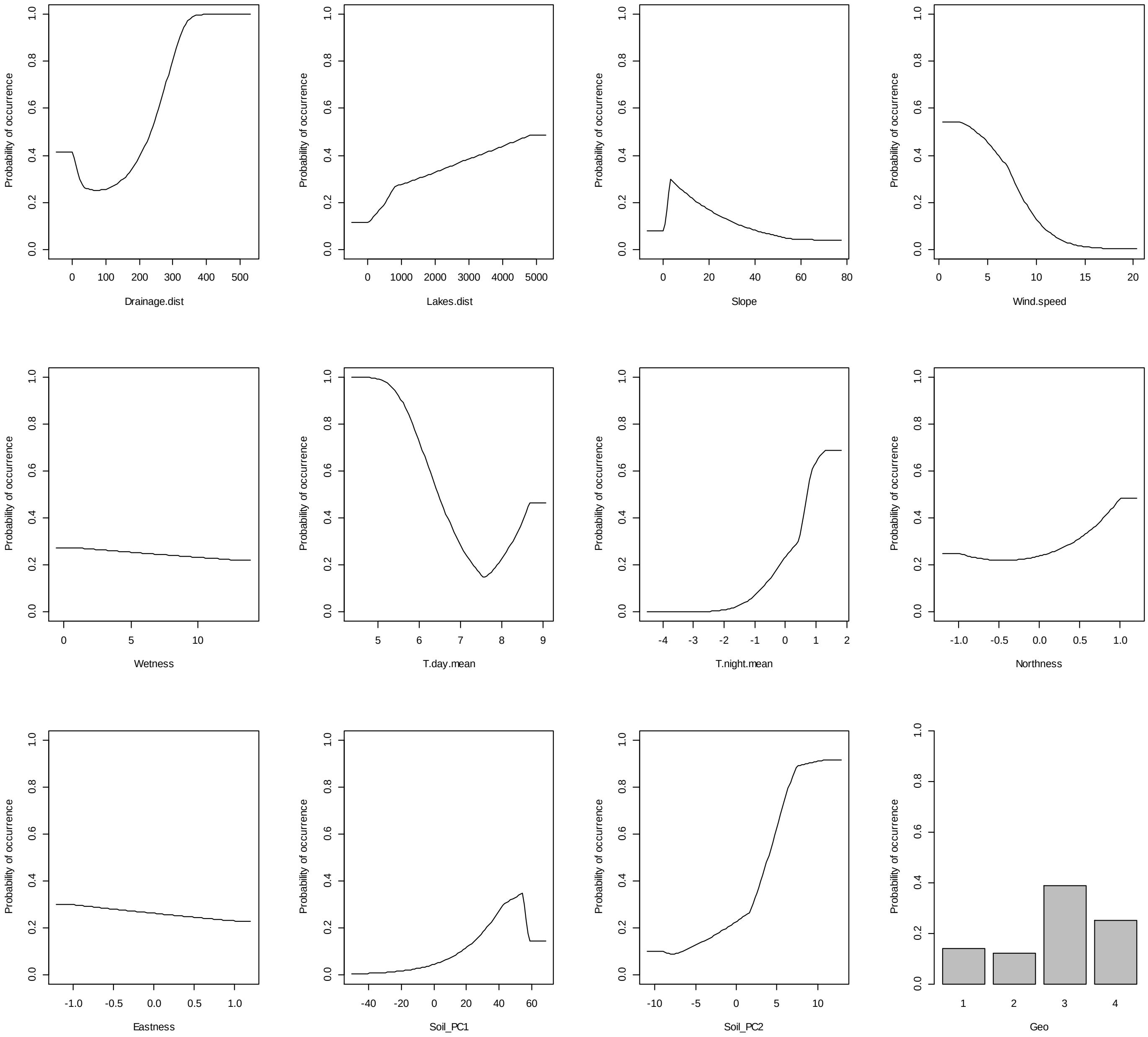

Figure D8. Response curves showing the relationship between the probability of occurrence of *Juncus scheuchzerioides* and the predictor variables retained in the SDMs. “Coast.dist” = distance to coast, “Drainage.dist” = distance to drainage lines, “Fauna.dist” = distance to fauna, “Lakes.dist” = distance to lakes, “T.range” = Temperature range, “T.day.mean” = mean daily temperature, “T.night.mean” = mean nightly temperature, “Wetness” = topographic wetness index*, “Geo” = geology*. “Northness” and “Eastness” are continuous measures of aspect. “Soil_PC1” = first principal component and “Soil_PC2” = second principal of the soil variables.

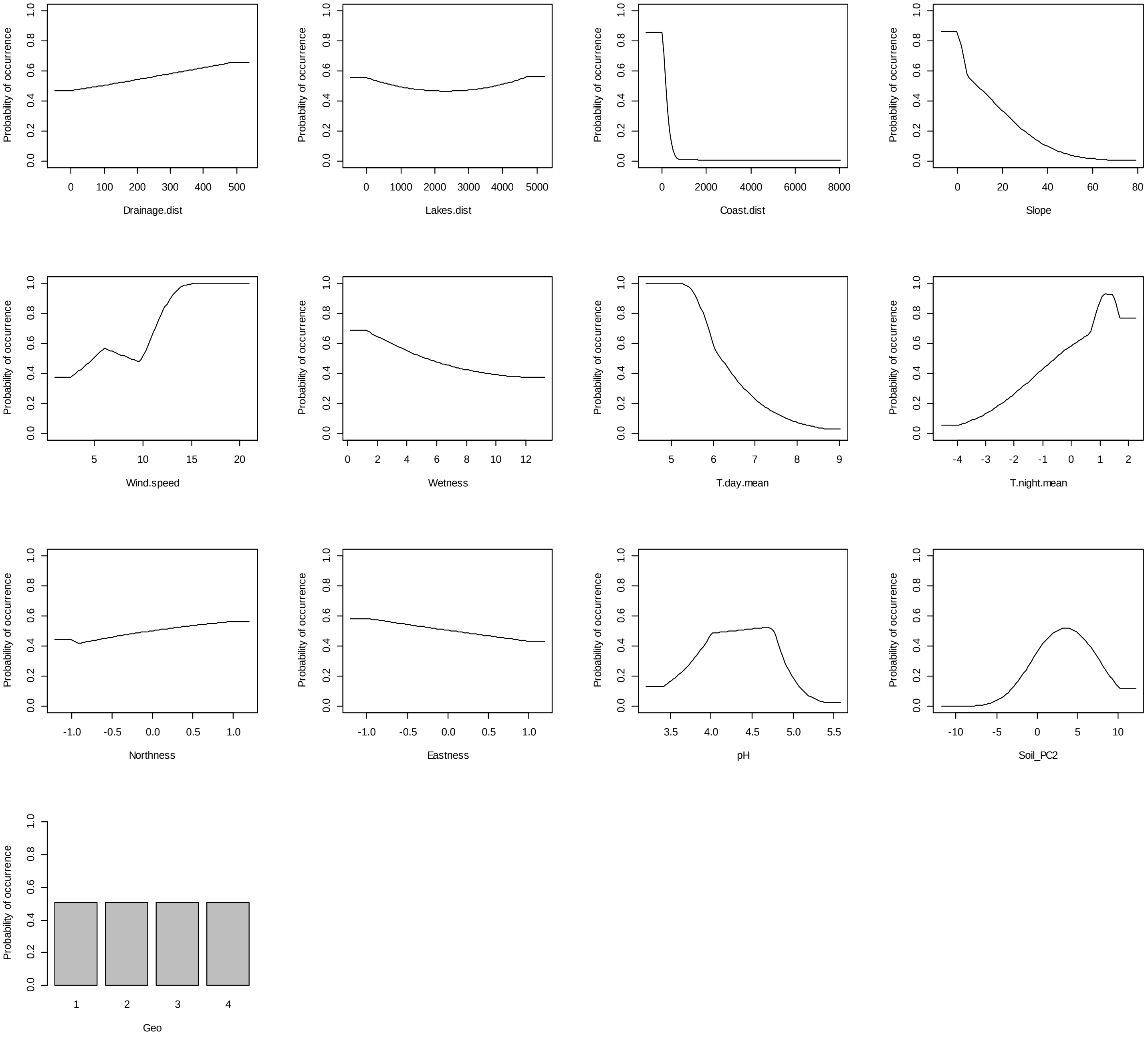

Figure D9. Response curves showing the relationship between the probability of occurrence of *Leptinella plumosa* and the predictor variables retained in the SDMs. "Coast.dist" = distance to coast, "Drainage.dist" = distance to drainage lines, "Fauna.dist" = distance to fauna, "Lakes.dist" = distance to lakes, "T.range" = Temperature range, "T.day.mean" = mean daily temperature, "T.night.mean" = mean nightly temperature, "Wetness" = topographic wetness index*, "Geo" = geology*. "Northness" and "Eastness" are continuous measures of aspect. "Soil_PC1" = first principal component and "Soil_PC2" = second principal of the soil variables.

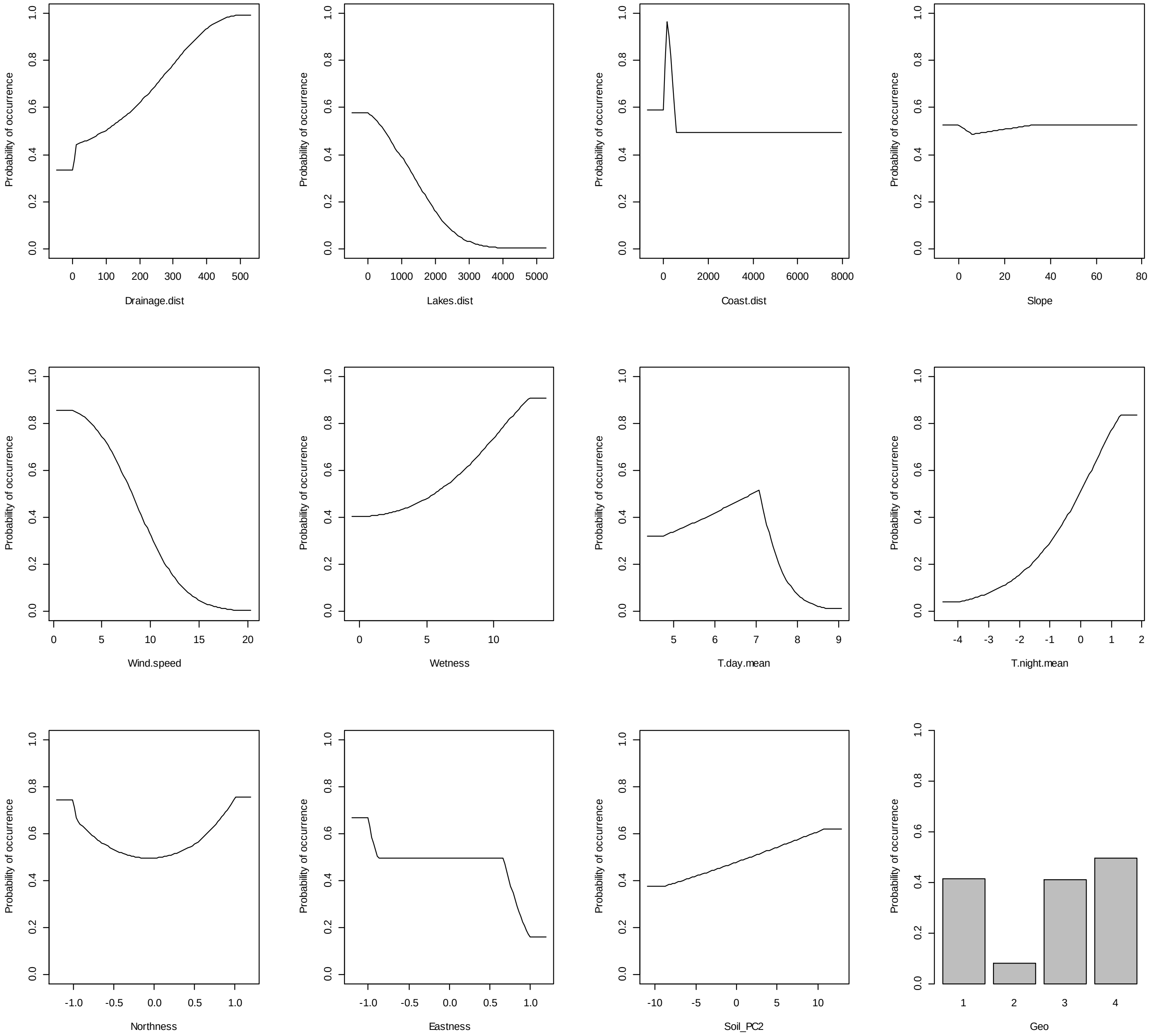

Figure D10. Response curves showing the relationship between the probability of occurrence of *Montia fontana* and the predictor variables retained in the SDMs. “Coast.dist” = distance to coast, “Drainage.dist” = distance to drainage lines, “Fauna.dist” = distance to fauna, “Lakes.dist” = distance to lakes, “T.range” = Temperature range, “T.day.mean” = mean daily temperature, “T.night.mean” = mean nightly temperature, “Wetness” = topographic wetness index, *“Geo” = geology*. “Northness” and “Eastness” are continuous measures of aspect. “Soil_PC1” = first principal component and “Soil_PC2” = second principal of the soil variables.

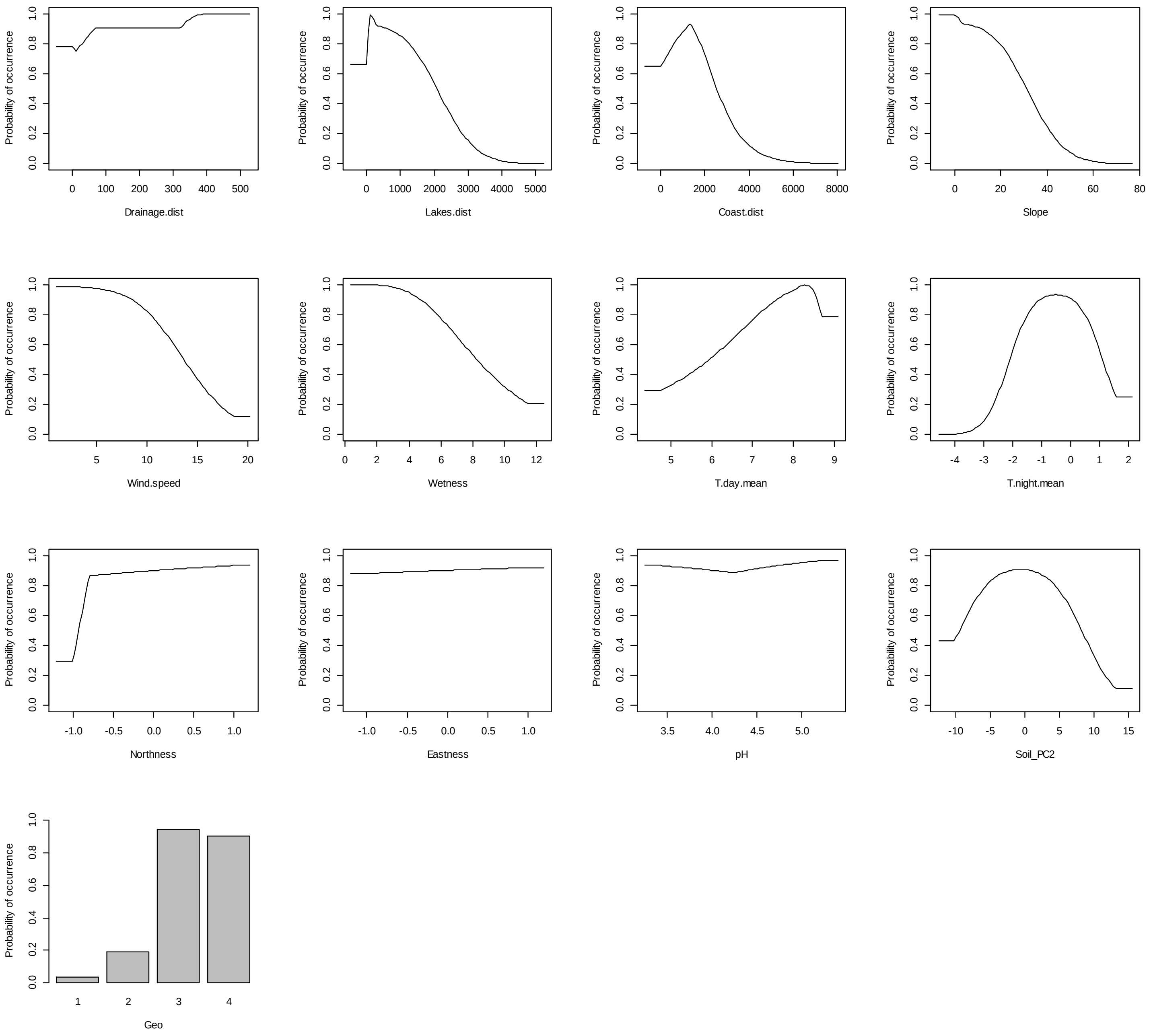

Figure D11. Response curves showing the relationship between the probability of occurrence of *Phlegmariurus 184ecogniz* and the predictor variables retained in the SDMs. "Coast.dist" = distance to coast, "Drainage.dist" = distance to drainage lines, "Fauna.dist" = distance to fauna, "Lakes.dist" = distance to lakes, "T.range" = Temperature range, "T.day.mean" = mean daily temperature, "T.night.mean" = mean nightly temperature, "Wetness" = topographic wetness index*, "Geo" = geology*. "Northness" and "Eastness" are continuous measures of aspect. "Soil_PC1" = first principal component and "Soil_PC2" = second principal of the soil variables.

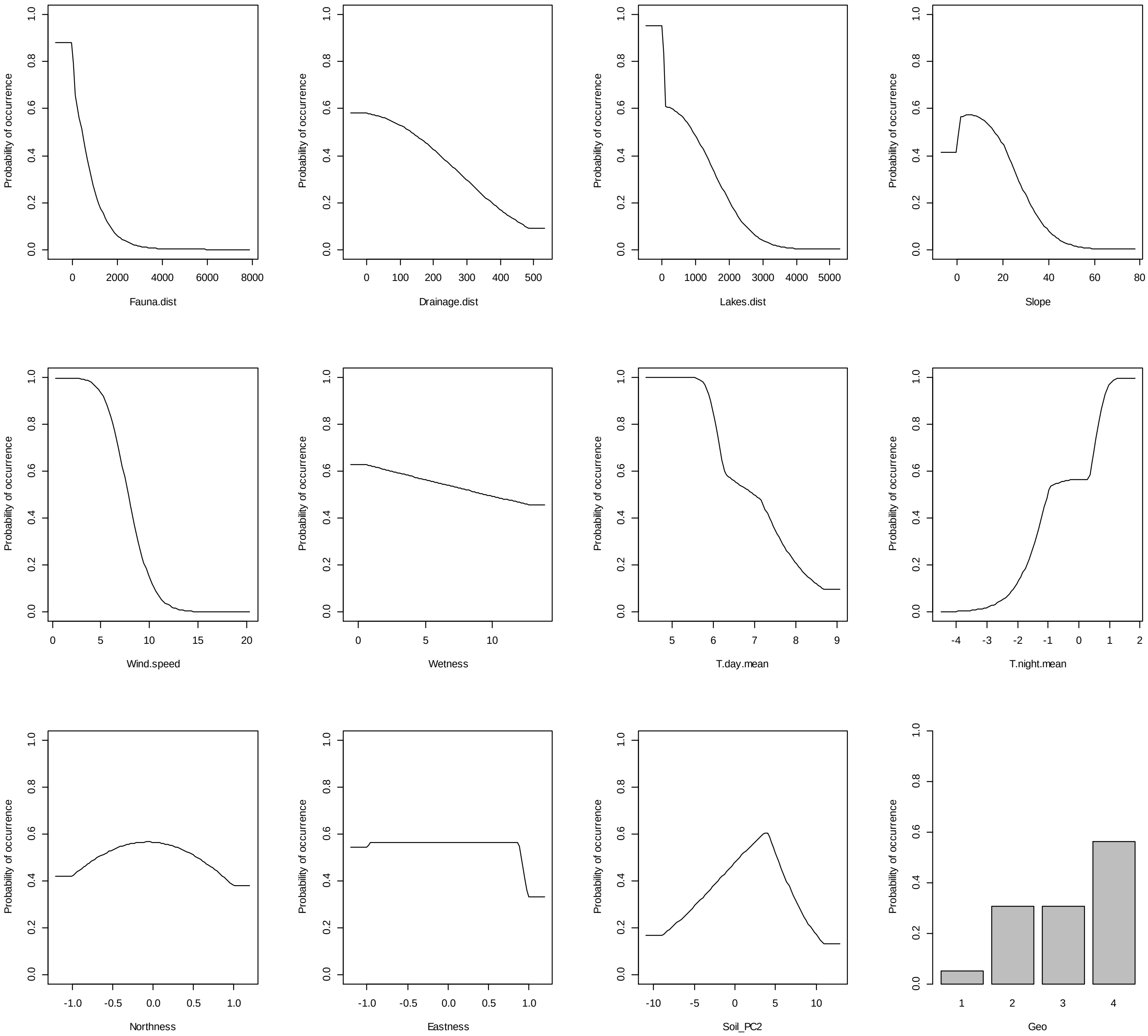

Figure D12. Response curves showing the relationship between the probability of occurrence of *Poa annua* and the predictor variables retained in the SDMs. “Coast.dist” = distance to coast, “Drainage.dist” = distance to drainage lines, “Fauna.dist” = distance to fauna, “Lakes.dist” = distance to lakes, “T.range” = Temperature range, “T.day.mean” = mean daily temperature, “T.night.mean” = mean nightly temperature, “Wetness” = topographic wetness index*, “Geo” = geology*. “Northness” and “Eastness” are continuous measures of aspect. “Soil_PC1” = first principal component and “Soil_PC2” = second principal of the soil variables.

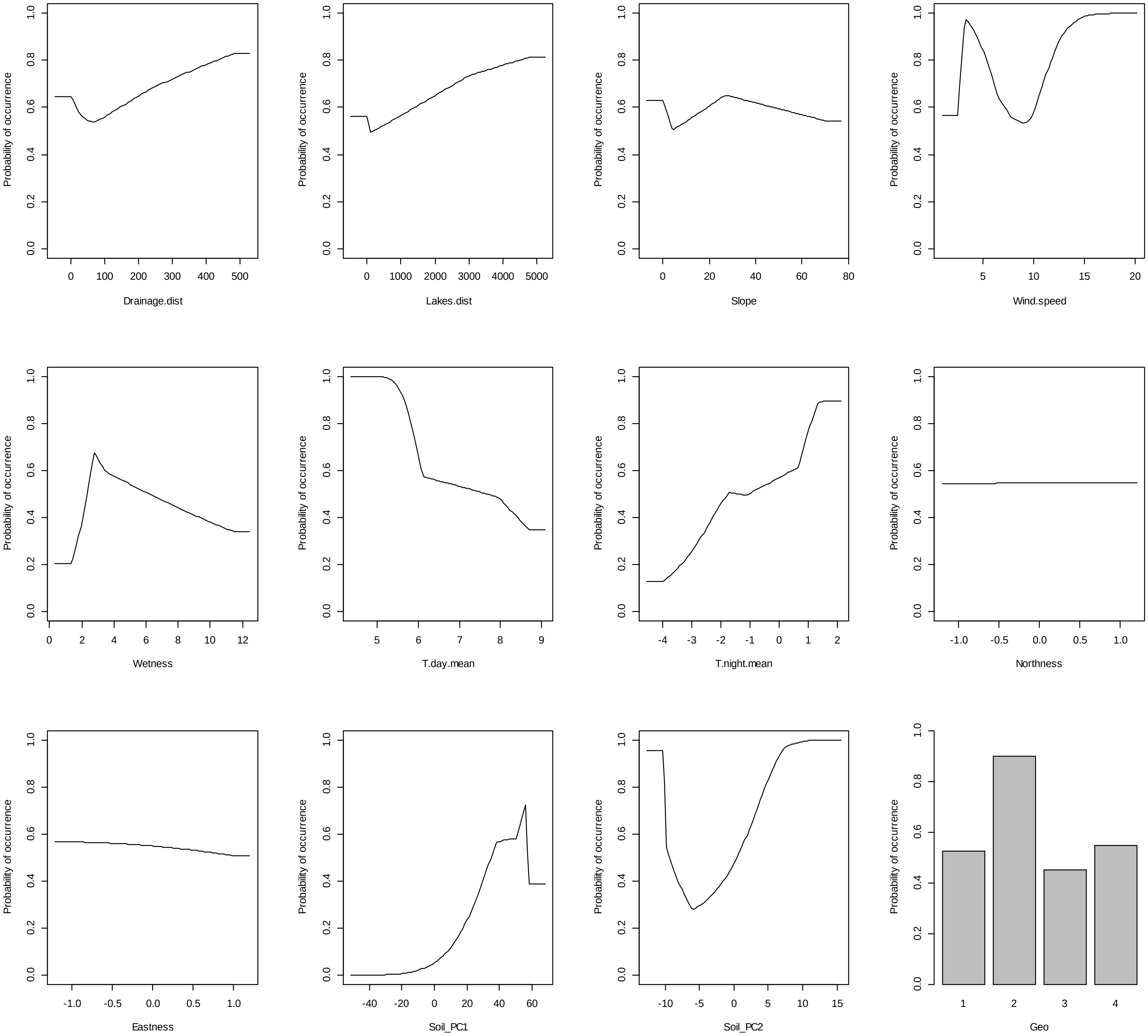

Figure D13. Response curves showing the relationship between the probability of occurrence of *Poa 186ecogn* and the predictor variables retained in the SDMs. “Coast.dist” = distance to coast, “Drainage.dist” = distance to drainage lines, “Fauna.dist” = distance to fauna, “Lakes.dist” = distance to lakes, “T.range” = Temperature range, “T.day.mean” = mean daily temperature, “T.night.mean” = mean nightly temperature, “Wetness” = topographic wetness index, *“Geo” = geology*. “Northness” and “Eastness” are continuous measures of aspect. “Soil_PC1” = first principal component and “Soil_PC2” = second principal of the soil variables.

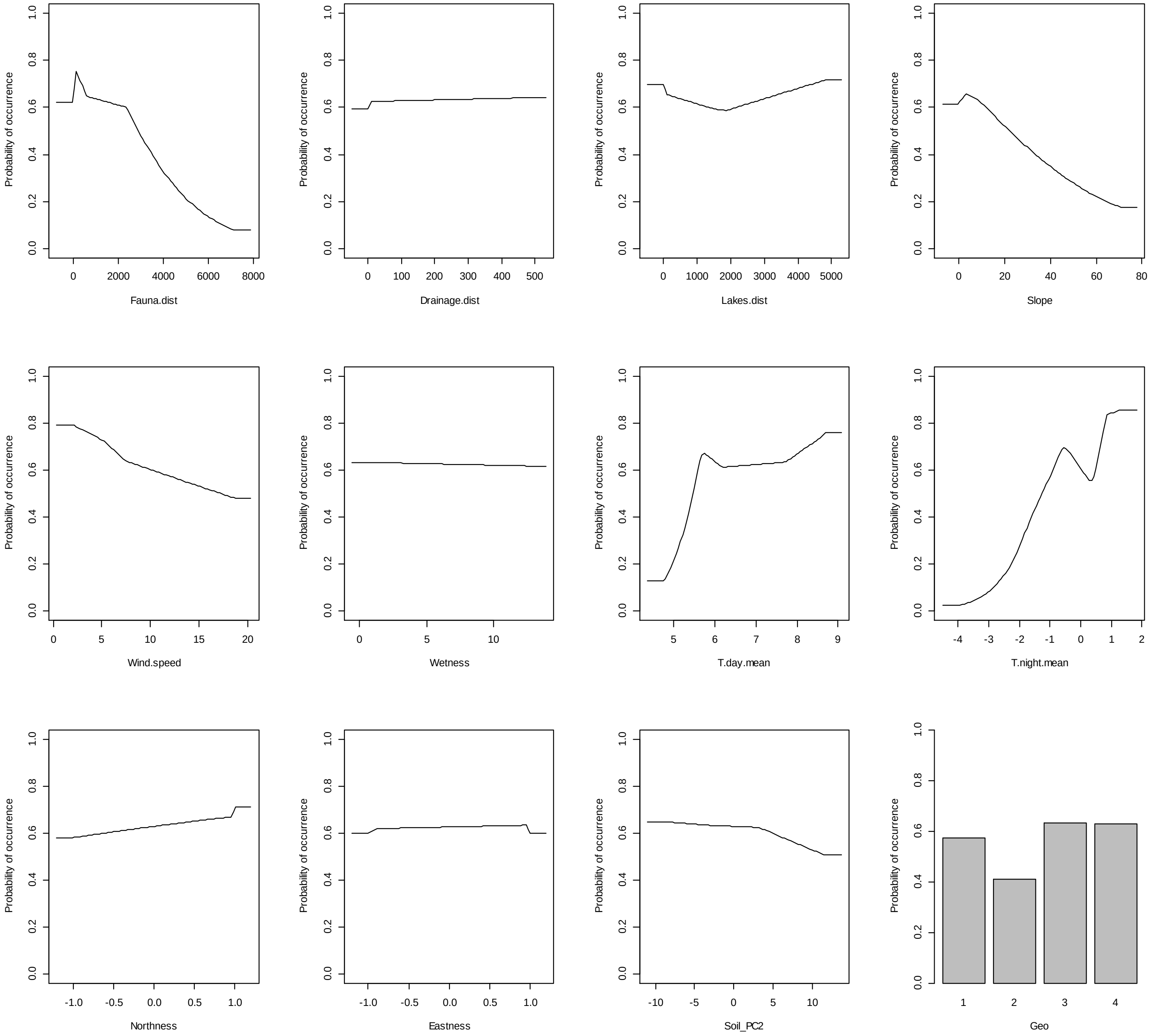

Figure D14. Response curves showing the relationship between the probability of occurrence of *Polypogon magellanicus* and the predictor variables retained in the SDMs. "Coast.dist" = distance to coast, "Drainage.dist" = distance to drainage lines, "Fauna.dist" = distance to fauna, "Lakes.dist" = distance to lakes, "T.range" = Temperature range, "T.day.mean" = mean daily temperature, "T.night.mean" = mean nightly temperature, "Wetness" = topographic wetness index*, "Geo" = geology*. "Northness" and "Eastness" are continuous measures of aspect. "Soil_PC1" = first principal component and "Soil_PC2" = second principal of the soil variables.

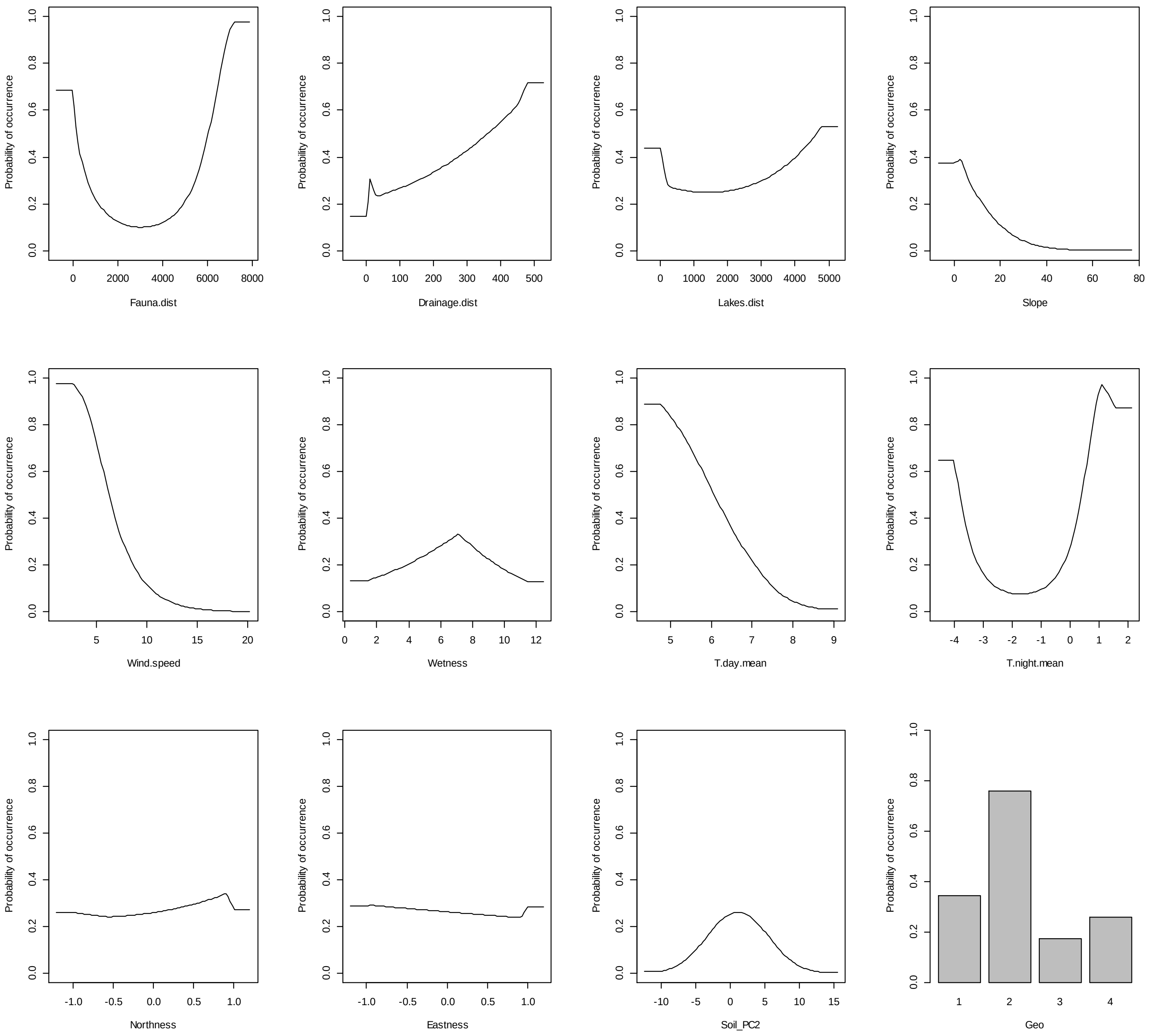

Figure D15. Response curves showing the relationship between the probability of occurrence of *Ranunculus biternatus* and the predictor variables retained in the SDMs. “Coast.dist” = distance to coast, “Drainage.dist” = distance to drainage lines, “Fauna.dist” = distance to fauna, “Lakes.dist” = distance to lakes, “T.range” = Temperature range, “T.day.mean” = mean daily temperature, “T.night.mean” = mean nightly temperature, “Wetness” = topographic wetness index*, “Geo” = geology*. “Northness” and “Eastness” are continuous measures of aspect. “Soil_PC1” = first principal component and “Soil_PC2” = second principal of the soil variables.

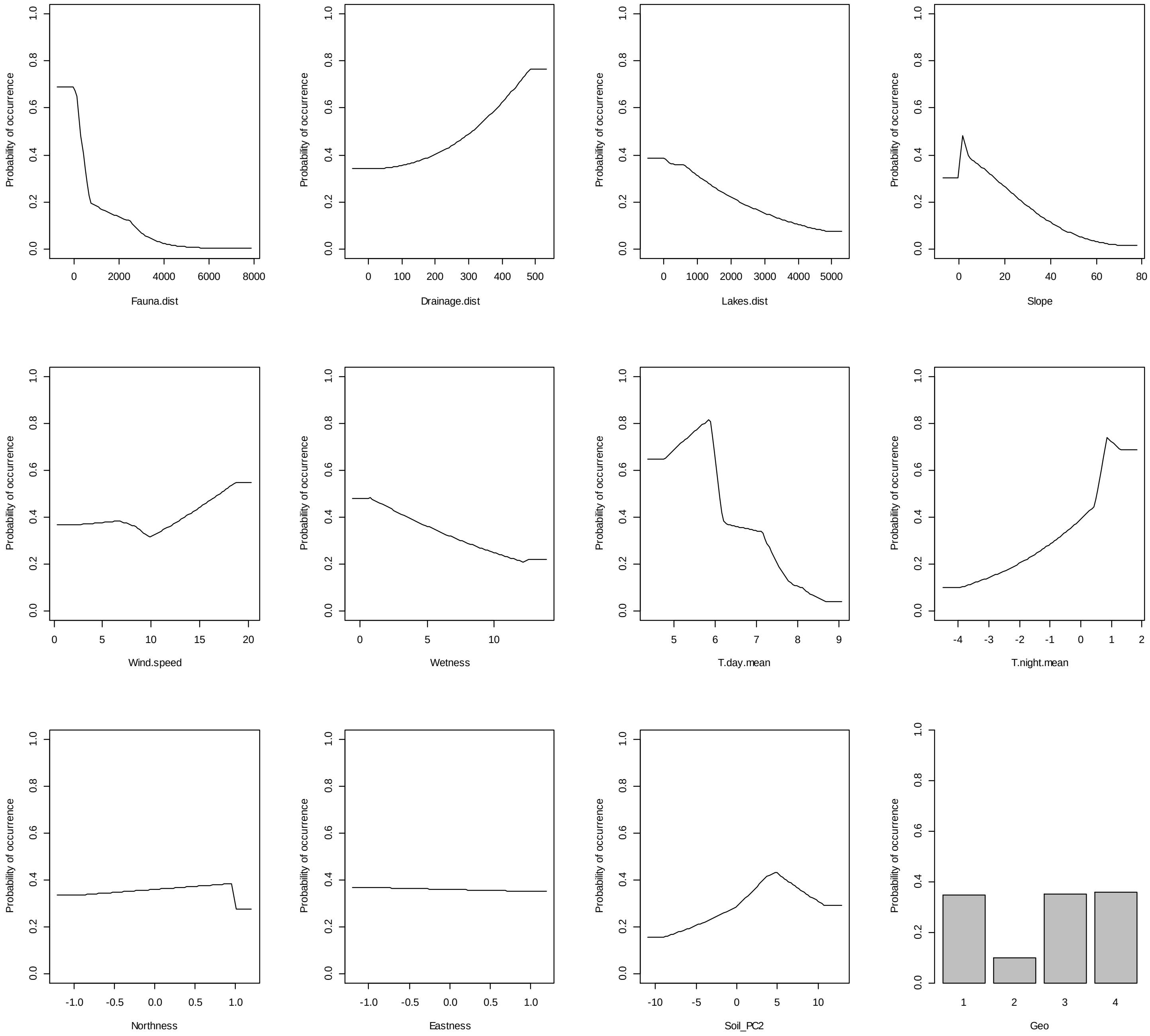

Figure D16. Response curves showing the relationship between the probability of occurrence of *Sagina procumbens* and the predictor variables retained in the SDMs. “Coast.dist” = distance to coast, “Drainage.dist” = distance to drainage lines, “Fauna.dist” = distance to fauna, “Lakes.dist” = distance to lakes, “T.range” = Temperature range, “T.day.mean” = mean daily temperature, “T.night.mean” = mean nightly temperature, “Wetness” = topographic wetness index*, “Geo” = geology*. “Northness” and “Eastness” are continuous measures of aspect. “Soil_PC1” = first principal component and “Soil_PC2” = second principal of the soil variables.

Chapter 6

Synthesis

Damage to and die-off of *Azorella selago* cushion plants due to invasive house mice burrowing and tunnelling.

6.1. Drivers of vegetation change: climate change and invasive species

Despite the fact that MI is a geographically isolated and a relatively simple system (i.e., 21 native vascular plant species), attributing vegetation change to specific drivers has proven challenging. Indeed, understanding the processes that have led to the development and changes in vegetation patterns has always challenged ecologists (Oepik et al. 2014). Therefore, attributing vegetation change to a specific driver non-experimentally, is complicated by the noisy nature of species abundance and climate data, along with the complexities of biotic interactions, resulting in difficulty recognising clear patterns. Nevertheless, the climate has changed significantly on MI during the study period, accompanied by an increase in cover of invasive plant species (Chapter 3; le Roux et al. 2013), as well as an increase in the abundance and density of invasive mice (*Mus musculus*; McClelland et al. 2018). In the absence of other well-known vegetation change drivers, including land clearing, land-use change, fire, herbivory (other than the invasive mice), and drought, the evidence suggests that the vegetation changes observed and predicted in this research have thus likely been predominantly driven by climate change and the impacts of invasive species (Chapters 3 & 5). Similarly, vegetation change has been attributed to climate change (Bergstrom et al. 2015; Hoffmann et al. 2019) and invasives species (Frenot et al. 2005; Shaw 2013) on other islands in the sub-Antarctic. For example, on Macquarie Island the combination of negative direct and indirect impacts of climate change (and possibly invasive species) on the native vegetation, caused large-scale dieback of the foundation species and subsequent rapid collapse of fellfield ecosystems (Bergstrom et al. 2015 Dickson et al. 2021). Therefore, the results, consistent with those from other sub-Antarctic islands, support the overarching hypothesis that vegetation change on MI occurred as a consequence of the interaction of factors, key among them being climate change and invasive species.

Climate change and invasive species are well known for having synergistic effects on biodiversity, exacerbating the risks to the native biodiversity that each driver would pose alone (Treasure & Chown 2014; Ricciardi et al. 2021; Kappes et al. 2021; Yang et al. 2022; Gonzalez-Orenga et al. 2022). The rapid range expansion of alien species on MI has been suggested to be driven largely by warmer temperatures (Chown et al. 2008; Chown et al. 2013; le Roux et al. 2013). The residence time of each invasive species is also an important factor to consider, since most invasive plant species are likely still expanding from their sites of introduction (le Roux et al. 2013). However, the evidence does indicate that warmer temperatures may have accelerated their expansion, as the cover of invasive plant species increased between 1965 and 2020 (Chapter 3), and the modelled distribution of the three most widespread invasive species was strongly influenced by temperature, with habitat suitability having increased with warmer temperatures (Chapter 5). Similarly, on Possession Island in the sub-Antarctic, the occurrence of many invasive plant species were strongly associated with temperature, and the occurrence of *P. annua* and *S. procumbens* studied here, were weakly related to anthropogenic and topographic factors (Bazzichetto et al. 2021). Furthermore, invasive grasses on MI, two of which were included in this study, have been shown experimentally to respond to warming by increasing photosynthetic rates (Ripley et al. 2020). Since the number of visitors to the island is limited to *c.* 80 per annual four week visit and only *c.* 24 people overwinter on the island, the spread of vascular plant invasive species is likely not only facilitated by human dispersal. Rather, invasive plant species have been spreading as a result of a combination of factors, including the residence time (most non-native plant species were only recorded for the first time in 1965 (Greve et al. 2017), changes in climate (le Roux et al. 2013), and non-human vectors such as seals (Haussmann et al. 2013) and birds (Ryan et al. 2003). Research from Possession Island also suggested that non-human factors are likely responsible for the dispersal of *Cerastium fontanum, P. annua* and *S. procumbens* which also all also occur on MI (Bazzichetto et al. 2021). The global rise in atmospheric CO_2 may further provide a growth advantage to invasive plant species in the sub-Antarctic (Frenot et al. 2005), because invasives plant species have been shown to enhance their photosynthetic rates in more favourable conditions compared to native plant species (Ripley et al. 2020). However, the impacts of invasive plants on the native flora, other than the displacement of native species by *Agrostis stolonifera* (Gremmen et al. 1998), are poorly studied (Greve et al. 2017). Further research should investigate the potential impacts of invasive plant species on native flora, given the predicted expansion of invasive species on MI with warming (Chapter 5).

Mice have been recorded on the island since seals were exploited for their blubber at the PEIs in the early 1800's (Cooper 2008), presumably having been introduced from ships. Therefore, mice have influenced the island's biota far longer than the duration of this study, with cats (*Felis catus*) being introduced to the island in 1949 to control mouse populations (Bester et al. 2002). In 1965, when the historical photographs of this study were taken (Chapter 3), cats were still present on the island and thus mouse abundance was already lower than before cats arrived. After cats were eradicated in 1991, there were no control agents for mice, thus the density of mice increased considerably (McClelland et al. 2018). Their rapid increase since the eradication of cats was also attributed to climate change, as the thermal constraints to mice have been reduced by warmer temperatures at night and longer periods without rain provide longer foraging opportunities (McClelland et al. 2018). The increased foraging opportunity combined with the depletion of macroinvertebrates, the mice's main protein source (Smith et al. 2002), have likely lead to increased reliance on plant matter (Angel et al. 2009) and structural damage to the native flora (Phiri et al. 2009). The plant species targeted by mice may be disproportionally vulnerable, with three species being of particular concern. Firstly, mice can reduce the reproductive output of the sedge *Carex dikei,*, reducing their populations considerably and leading to its rapid decline (Chown & Smith 1993). The substantial increase in density of mice in mires specifically, may indicate that mice are relying more on the mire graminoids for food. Secondly, *Acaena magellanica* may also be targeted for the large seed heads (Angel et al. 2009), since *C. dikei* has already declined considerably, and is no longer abundant in mires (Chapter 3). The reduction in *A. magellanica* observed in this study may also be partly due to mice predation (Chapter 3), although *A. magellanica* is the only deciduous plant species, and thus the cover may have been underestimated in the repeat photography. Lastly, the cushion plant *Azorella selago* is sensitive to mechanical disturbance due to its hemispherical shape and slow growth rate, thus tunnelling by mice causes severe structural damage (Phiri et al. 2009). The planned mouse eradication on MI (Preston et al. 2019) will provide a key opportunity to monitor the recovery of the vegetation from disturbance by mice.

6.2. Generalist *vs.* specialist plant species responses

While the classification of species as either habitat "generalists" or "specialists" may be debatable (discussed later), there were commonalities in patterns for what has previously been defined as habitat generalists (see Huntley 1971 and le Roux & McGeoch 2008). Generalist species, particularly the fern *Austroblechnum penna-marina* and grass *Polypogon magellanicus*, have increased in cover (Chapter 3) and were predicted to increase in distribution with warming (Chapter 5). Similarly, habitat specialists had comparable modeled responses as a group to the predicted temperature change (Chapter 5). For all these species, habitat suitability was not predicted to increase with warmer temperatures, with the exception of hygrophilous species, which may have been erroneously predicted to expand because rainfall could not be included in the SDMs. Habitat generalist species are predicted to benefit from environmental change, as such species may adapt to changing conditions by altering their physiology or distributing to more suitable conditions (Brouat et al. 2004). Furthermore, generalists respond more to regional processes, such as climate change, whereas specialist species may respond more to localised conditions, being adapted to more specific conditions (Pandit et al. 2009). Therefore, generalist species on MI are likely to expand their ranges, up to the topographic and climatic constraints imposed by the harsh, high elevation interior of the island. Specialist species are more restricted to specific habitats and may not be able to expand or shift their ranges as the climate changes. Indeed, the cover of specialist species, in particular the halophytes, did not change significantly over the last few decades (Chapter 3), suggesting that specialists did not undergo range expansion with climate change as did generalists. Specialist species may thus be more vulnerable to climate change than generalists (le Roux & McGeoch 2008).

A challenge when trying to identify general trends in habitat suitability of generalist *vs.* specialist species is the differentiation between which species were indeed generalist or specialist. The term “generalist” is often used interchangeably with “widespread”. However, there is a possibility that a species could be a habitat specialist and also widespread as a result of the habitat being widespread (Pandit et al. 2009). For instance, Cramer et al. (2022) suggested that species accepted as generalist species previously, may in fact be habitat specialists when quantifying species’ realised niches. Echoing the Gleasonian view of vegetation organization as a continuum of individualistic responses, the classification of plant species as generalist or specialist should perhaps also rather be viewed as a continuum of specialisation to environmental and biotic conditions. Quantifying the vascular plant species’ realised niches across the island may thus shed light on their particular habitat specialisations.

6.3. Community *vs.* continuum theory in species-poor environments

The continuing global debate regarding species responses to environmental variation in space, whether gradual or occurring as discrete communities with sharp boundaries, remains unresolved partially due to lack of empirical evidence (Liautaud et al. 2019). The two contrasting views are particularly evident when examining environmental gradients, as they produce different predictions regarding species distributions or community patterns along environmental gradients. The individualistic “Gleasonian” view suggests that vegetation components (i.e., species) are gradually replaced by new species as the environment changes steadily (Gleason 1927). In contrast, the “Clementian” view considers communities as organismic entities with distinct boundaries that can shift between different community types with minor changes in environmental conditions (Weaver & Clements 1929; Mucina 1997; Cushman et al. 2010; Moncrieff et al. 2016). Numerous studies have investigated species distributions along environmental gradients (Austin 1985; Austin & Smith 1989; Scott 1995; le Roux & McGeoch 2010; Mod et al. 2016; Liautaud et al. 2019), leading to divergent conclusions on whether vegetation exhibits continuous (i.e., individualistic) or discontinuous (i.e., organismic) patterns. While studies increasingly show species-specific responses of vegetation to environmental gradients (Penuelas et al. 2007; Raath-Krüger et al. 2019; van der Merwe et al. 2021), supporting the Gleasonian view, there is also substantial support for the Clementian view that examine community-level responses (Mucina et al. 2016; Brown & Bredenkamp 2018; Gellie et al. 2018; Wiser & De Cáceres 2018). While neither view is wholly right or wrong, identifying ecological or environmental conditions that result in observed vegetation patterns can help researchers determine when vegetation is best represented as individuals or assemblages (Austin 2005; Cushman et al. 2010; Liautaud et al. 2019). If vegetation patterns in certain environments primarily arise from the individualistic responses of species to combinations of constraints imposed by gradual multivariate environmental gradients, do categorical discrete vegetation types really exist?

To my knowledge, this research was one of the first attempts at explicitly identifying whether species-poor environments can be viewed as individualistic or as assemblages (although see Liautaud et al. 2019). None of the modern classification techniques used in this study provided a reliable classification of species assemblages on MI (Chapter 2). Soil properties also did not differentiate the vegetation, other than fellfield. The low clusterability of plot data can be attributed, in part, to the absence of distinct "indicator" species, as generalist species are abundant throughout the island. Additionally, the relatively minor role of plant-plant interactions on sub-Antarctic islands, compared to older and more species-rich continental or temperate systems, may have contributed to this lack of robust classification. Most plant-plant interactions on MI that have been tested so far were not significant (Raath-Krüger et al. 2019; van der Merwe et al. 2021), suggesting that the islands in the sub-Antarctic have relatively low plant-plant interaction importance, compared to more temperate species-rich environments. Similarly, Lee et al. (2013) showed that species distribution models which are often criticised for neglecting biotic interactions (Kearney & Porter 2009), performed well in low-interaction environments such as the Antarctic, with only soil moisture as a predictor variable. While plant-plant interactions play a key role in regulating species composition with environmental change in many environments (Brooker 2006), these interactions are species-specific on MI and likely not as important as plant-plant interactions in species-rich environments. Indeed, facilitation in particular is known to be more prevalent in diverse, rather than species-poor vegetation (Schöb et al. 2018). Therefore, in low-interaction environments, either due to geographic isolation from source populations, such as islands (Ainsworth & Drake 2020), or strong environmental filtering due to harsh conditions, such as in the Antarctic (Lee et al. 2013), vegetation change should rather be viewed as an aggregation of individualistic responses to environmental conditions and biotic interactions.

In this study, my questioning the applicability of the Clementian view of vegetation patterns on MI led to the conclusion that species-level responses should be analysed to assess vegetation change, rather than community-level responses. An individualistic view of vegetation is commonly adopted, although not explicitly mentioned as such, for predictive ecologic research, particularly in forecasting future species distributions (Huntley et al. 1995; Franklin et al. 2013; Liautaud et al. 2019). Therefore, it was important to determine the conditions under which species respond individualistically or as an assemblage, as the choice of methodology is determined by how the vegetation is viewed. Future research should focus on identifying the environmental conditions under which continuous *vs.* discrete vegetation organisation exists along environmental gradients. Contrasting low- and high-interaction environments may shed light on the matter.

6.4. The utility of vegetation maps in low interaction environments

Since species respond individualistically to their environment in species-poor environments, where interaction importance is typically low, the utility of traditional categorical vegetation maps which use communities as the mapping unit, is questionable. Indeed, a robust community classification of the vegetation on MI could not be found (Chapter 2). As far as I am aware, the vegetation map of MI created in 2006 (Smith & Mucina 2006), has not been spatially utilised in research or management efforts, other than indicating previously identified units or for stratification of sampling sites (see example Treasure & Chown 2013 and van der Merwe et al. 2023). While traditional vegetation maps are inherently useful for vegetation monitoring and management over large scales and in diverse environments, in species-poor environments, maps with an assumed species composition may not be suitable, as communities are not easily differentiated. In other species-poor environments the utility of categorical classifications has also been questioned, with SDMs (Fitzgerald et al. 2022) or a combination of SDMs and other methods (Bricher et al. 2013) being suggested as more realistic alternatives. Instead of using discrete maps, mapping the probabilities of individual species occurrence will likely be a better alternative, since the probabilities of occurrence may change over time and space. Consequently, fuzzy mapping may be a useful alternative for future research, as it involves mapping probabilities of occurrence with gradual transitions in species composition as a floristic continuum (Feilhauer et al. 2021). On MI, conservation efforts will be more effective if species are targeted for monitoring and management rather than communities.

A significant portion of the vegetation might have been overlooked due to the taxonomic bias towards vascular plant species. Information on and the skills to identify bryophytes on MI is limited (Gremmen 1981). Since many more bryophyte species occur on MI (134 species) compared to vascular plant species (21 species), there is perhaps the potential for bryophyte species to expose the underlying patterns observed in the vegetation (Gremmen 1981).

6.5. Constraints to SDMs

The soil properties of MI were modelled and mapped to include in the environmental predictor set of plant SDMs (chapter 4), as many soil properties are an often-overlooked component of plant habitats, and thus rarely included in SDMs (Hageer et al. 2017; Roe et al. 2022). Including as many as possible "fixed" constraints to habitat suitability, such as topographic variables (Cramer et al. 2022), in SDMs will provide a more realistic representation of species habitat requirements, than only including “changing” variables such as temperature or rainfall (Austin & Van Niel 2011; Hageer et al. 2017). While soil properties are not “fixed”, soils may change much slower than climatic variables. Soil properties were retained in all SDMs, and soils were the most important predictor of five species, indicating the importance of their inclusion in modeling efforts. The distance to the coast and fauna is also associated with soil nutrients, since seals and seabirds are the main agents of nutrient-input to the island and mostly occur along the coast. Therefore, during the variable selection process, soil properties often explained more of the variance than did the distance to coast or to fauna (Chapter 4). If all constraints, or proxies thereof, to species distributions are not included in SDMs, misleading interpretations may arise. For instance, if soil nutrients were not included in the SDMs, the distribution of coprophilous species may not be correct, even though the models would inherently find the most important predictors in a predictor set, after which plausible alternative explanations for the distribution of coprophilous species may have been found. Hageer et al. (2017) has shown how opposing plausible explanations for species distributions can be made using different predictor sets in predicting the occurrence of the same species. Because soils are the growth medium for most plants, including soil properties in SDMs is thus fundamental in determining habitat suitability of plant species, and predicting realistic changes in habitat suitability.

A common challenge in using SDMs for future distribution, is that the future cannot be tested and thus remains uncertain (Wiens et al. 2009; Guillera-Arroita et al. 2015), even when all possible outcomes are considered. However, the vegetation of the past may be known and can be compared to the present, and thus a retrodicted trend can be validated. There was some general agreement between the changes observed in the repeat photography analysis (Chapter 3) and those predicted to have occurred by the SDMs (Chapter 5). For instance, the range expansion of generalist species predicted in the SDMs was verified by the increase in cover of generalists observed in the repeat photography. This was particularly evident in the range expansion of *A. penna-marina* and *P. magellanicus*. However, there were also insightful differences between the two approaches that provided a more realistic view of the often-overestimated changes predicted by SDMs (Austin & Van Niel 2011; Guillera-Arroita et al. 2015). In particular, *C. dikei* was predicted to have expanded its range by the SDMs, but the repeat photography did not validate this prediction because there was a decrease in cover of mire graminoids. This is likely because the impact of mice predation and the drying of the island were not included in the SDMs. Therefore, using repeat photography as a test for model predictions can deepen the understanding of past vegetation change at a site (Hoffman et al. 2019) and provide a more accurate prediction of the future. A key constraint in this study is that only two time points were compared. While comparing the vegetation at two time points may give insights into broader changes that may have occurred at a site, increasing the number of time points to understand the trajectories of change may help to disentangle the more nuanced underlying processes of vegetation change.

Studying vegetation change in remote regions presents unique challenges primarily due to the paucity of data availability. Data collection and monitoring efforts are expensive and logistically challenging. This is because the sub-Antarctic islands have limited human presence, are far removed from continental lands and the rugged terrain on MI causes physical constraints to data collection. Consequently, the limited long-term and high resolution data poses constraints to our understanding of vegetation dynamics. While data availability is increasing substantially for distant and inaccessible regions due to remote sensing advances (Xie et al. 2008), some climate aspects, and thus aspects of habitat suitability to plant species, were not available to include in the SDMs. Firstly, rainfall data is still unavailable for MI, other than the single point records at the meteorological station. Since rainfall has decreased significantly on MI (Chapter 3), excluding rainfall in SDMs may disregard a significant component of potential impacts of climate change. Secondly, the resolution of the temperature data (1 km) may also not capture the fine-scale habitat requirements of plant species to environmental gradients on MI and may play a crucial role in influencing the accuracy of the model outcomes. Consequently, sub-Antarctic research faces the intricate challenge of making inferences from limited datasets with innovative approaches, such as spatial modelling techniques (Chapter 4; Leihy et al. 2018; Goddard et al. 2022). Addressing the data paucity challenge is necessary to fully understand the underlying vegetation dynamics of the unique ecosystems in the sub-Antarctic.

6.6. Recommendations to environmental managers

The research conducted here, provided compelling data for evidence-based conservation decision-making in the sub-Antarctic. Species-level monitoring of the impacts of climate change and invasive species on the native and non-native flora is recommended. Since species on MI mostly respond individualistically, and only a few vascular plant species occur on MI, it is possible to monitor the vegetation at the species-level. In terms of climate change, *A. penna-marina* can be used as an indicator species. Since this fern is sensitive to temperature change and can only grow in soils that are not waterlogged (Huntley 1971), it is a good indicator of temperature and precipitation trends (see Chapter 3). For example, the increase of *A. penna-marina* in mires may indicate the drying of the island and its predicted range expansion across the island may also indicate warmer temperatures (Chapters 3 & 5). Pteridophytes have also been suggested to be good indicator species of climate change, since their distribution is independent of biotic vectors and changes in cover or abundance are likely a response to climate (Abotsi et al. 2020).

While the impacts of climate change are not straightforward to control, invasive species may be more effectively managed. Options for their control of the three most widely spread invasive plant species, *Poa annua, Sagina procumbens* and *A. stolonifera* to avoid negative impacts, such as displacement of native plant species, should be seriously considered. *P. annua* only occurs where there is biotic disturbance and nutrient-input by seals and seabirds, thus its distribution is localised to areas with faunal influence. *A. stolonifera* was more widespread in the past, but has been successfully controlled at some sites. However, *S. procumbens* has spread across the island, and is not restricted to the coast as most other alien plant species. I therefore suggest that *S. procumbens* be eradicated, because it can fill the niche space of native species, and likely outcompete natives.

This research also provides further support for the eradication of the house mouse from MI, although plans for this eradication by 2024 are already underway. This is a key opportunity to monitor and study the recovery of the vegetation, especially *C. dikei, A. selago* and *A. magellanica,* after the eradication of an invasive rodent. Establishing monitoring sites along environmental gradients before the start of the eradication programme, is crucial. Lessons learnt from Macquarie Island on the eradication of non-native vertebrates have provided insights into the indirect impacts of their sudden removal from an island (Bergstrom et al. 2009). Non-native rabbits had a devastating impact on the vegetation after removal of predation pressure by the key invasive predator, cats, once they were eradicated in 2000 to conserve seabird (Bergstrom et al. 2009). Similarly, the mouse eradication will likely affect non-native species as much as native species, and thus an interesting research and monitoring opportunity is presented to assess the impacts of invasive vertebrate removal on non-native plant and invertebrate species. Mice are both the key predator for invertebrates and some seabird species, such as albatross, and the only mammalian herbivore on MI. Therefore, the indirect trophic cascade effects of their eradication will likely be severe. Marion Island is one of few cases in the world where the vegetation may recover and adapt relatively naturally to climate change, if released from invasive species pressure. Therefore, it is important to focus on non-native species responses to the eradication, as once mice are removed, rapid changes may be expected in the vegetation, especially if invertebrate abundance increases suddenly as a result. I recommend that during the risk assessment of the eradication management plan, substantial focus should be placed on the indirect effects of the removal of mice on vegetation and not only on seabirds.

References

Abotsi, K.E., Bose, R., Adjossou, K., Deblauwe, V., Rouhan, G., Segla, K.N., Atsri, K.H., & Kokou, K. 2020. Ecological drivers of pteridophyte diversity and distribution in Togo (West Africa). *Ecological Indicators* 108: 105741.

Ainsworth, A., & Drake, D.R. 2020. Classifying Hawaiian plant species along a habitat generalist-specialist continuum: Implications for species conservation under climate change. *PLOS ONE* 15: e0228573.

Angel, A., Wanless, R.M., & Cooper, J. 2009. Review of impacts of the introduced house mouse on islands in the Southern Ocean: are mice equivalent to rats? *Biological Invasions* 11: 1743–1754.

Austin, M.P. 1985. Continuum concept, ordination methods, and niche theory. *Annual Review of Ecology and Systematics* 16: 39–61.

Austin, M.P. 2005. Vegetation and environment: discontinuities and continuities. In van der Maarel, E. (Ed.), *Vegetation Ecology*, Blackwell Publishing, Oxford, UK.

Austin, M.P., & Van Niel, K.P. 2011. Improving species distribution models for climate change studies: variable selection and scale. *Journal of Biogeography* 38: 1–8.

Austin, M., & Smith, T. 1989. A new model for the continuum concept. *Vegetatio* 83: 35–47.

Bazzichetto, M., Massol, F., Carboni, M., Lenoir, J., Lembrechts, J.J., Joly, R., Renault, D. 2021. Once upon a time in the far south: Influence of local drivers and functional traits on plant invasion in the harsh sub-Antarctic islands. *Journal of Vegetation Science* 32, e13057.

Bergstrom, D.M., Bricher, P.K., Raymond, B., Terauds, A., Doley, D., McGeoch, M.A., Whinam, J., Glen, M., Yuan, Z., Kiefer, K., Shaw, J.D., Bramely-Alves, J., Rudman, T., Mohammed, C., Lucieer, A., Visoiu, M., van Vuuren, B.J., & Ball, M.C. 2015. Rapid collapse of a sub-Antarctic alpine ecosystem: the role of climate and pathogens. *Journal of Applied Ecology* 52: 774–783.

Bergstrom, D.M., Lucieer, A., Kiefer, K., Wasley, J., Belbin, L., Pedersen, T.K., & Chown, S.L. 2009. Indirect effects of invasive species removal devastate World Heritage Island. *Journal of Applied Ecology* 46: 73-81.

Bester, M.N., Bloomer, J.P., Van Aarde, R.J., Erasmus, B.H., Van Rensburg, P.J.J., Skinner, J.D., Howell, P.G., & Naude, T.W. 2002. A review of the successful eradication of feral cats from sub-Antarctic Marion Island, Southern Indian Ocean. *South African Journal of Wildlife Research* 32: 65-73.

Bricher, P.K., Lucieer, A., Shaw, J., Terauds, A., & Bergstrom, D.M. 2013. Mapping sub-Antarctic cushion plants using random forests to combine very high resolution satellite imagery and terrain modelling. *PLOS ONE* 8: e72093.

Brooker, R.W. 2006. Plant-plant interactions and environmental change. *New Phytologist* 171: 271–284.

Brouat, C., Chevallier, H., Meusnier, S., Noblecourt, T., & Rasplus, J.Y. 2004. Specialization and habitat: spatial and environmental effects on abundance and genetic diversity of forest generalist and specialist Carabus species. *Molecular Ecology* 13: 1815–1826.

Brown, L.R., & Bredenkamp, G.J. 2018. An overview of the vegetation classification approach in South Africa. *Phytocoenologia* 48: 163–170.

Chown, S.L., Lee, J.E., & Shaw, J.D. 2008. Conservation of Southern Ocean Islands: Invertebrates as exemplars. *Journal of Insect Conservation* 12: 277–291.

Chown, S.L., le Roux, P.C., Ramaswiela, T., Kalwij, J.M., Shaw, J.D., & McGeoch, M.A. 2013. Climate change and elevational diversity capacity: do weedy species take up the slack? *Biology Letters* 9: 0120806.

Chown, S.L., & Smith, V.R. 1993. Climate change and the short-term impact of feral house mice at the sub-Antarctic Prince Edward Islands. *Oecologia* 96: 508-516.

Cooper, J. 2008. Human history. In Chown, S. & Froneman, P. (Eds.), *The Prince Edward Islands: land-sea interactions in a changing ecosystem*, pp. 331–350. Sun Press, Stellenbosch, South Africa.

Cramer, M.D., Hedding, D., Greve, M., Midgley, G.F., & Ripley, B.S. 2022. Plant specialisation may limit climate-induced vegetation change to within topographic and edaphic niches on a sub-Antarctic island. *Functional Ecology* 36: 2636–2648.

Cushman, S., Evans, J., McGarigal, K., & Kiesecker, J. 2010. *Toward Gleasonian landscape ecology: From communities to species*. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, USA.

Feilhauer, H., Zlinszky, A., Kania, A., Foody, G.M., Doktor, D., Lausch, A., & Schmidtlein, S. 2021. Let your maps be fuzzy!-Class probabilities and floristic gradients as alternatives to crisp mapping for remote sensing of vegetation. *Remote Sensing in Ecology and Conservation* 7: 292–305.

Fitzgerald, N.B., Kirkpatrick, J.B., Dickson, C.R., Williams, L.K., Fergus, A.J., & Whinam, J. 2022. Determining the distributions of plant communities in subantarctic vegetation using species distribution models. *Australian Journal of Botany* 70: 311–322.

Franklin, J., Davis, F.W., Ikegami, M., Syphard, A.D., Flint, L.E., Flint, A.L., & Hannah, L. 2013. Modeling plant species distributions under future climates: how fine scale do climate projections need to be? *Global Change Biology* 19: 473–483.

Frenot, Y., Chown, S.L., Whinam, J., Selkirk, P.M., Convey, P., Skotnicki, M., & Bergstrom, D.M. 2005. Biological invasions in the Antarctic: extent, impacts and implications. *Biological Reviews* 80: 45–72.

Gellie, N.J.H., Hunter, J.T., Benson, J.S., Kirkpatrick, J.B., Cheal, D.C., McCreery, K., & Brocklehurst, P. 2018. Overview of plot-based vegetation classification approaches within Australia. *Phytocoenologia* 48: 251–272.

Gleason, H.A. 1927. The individualistic concept of the plant association. *Bulletin of the Torrey Botanical Club* 53: 7–26.

Goddard, K.A., Craig, K.J., Schoombie, J., & le Roux, P.C. 2022. Investigation of ecologically relevant wind patterns on Marion Island using Computational Fluid Dynamics and measured data. *Ecological Modelling* 464: 109827.

Gonzalez-Orenga, S., Boscaiu, M., Verdeguer, M., Sanchez-Moreiras, A.M., Gonzalez, L., & Vicente, O. 2022. Adaptability of invasive plants to climate change. *Agrolife Scientific Journal* 11: 58–65.

Gremmen, N.J.M. 1981. The vegetation of the Subantarctic islands Marion and Prince Edward. Dr W. Junk Publishers, The Hague, Netherlands.

Gremmen, N.J.M., Chown, S.L., & Marshall, D.J. 1998. Impact of the introduced grass *Agrostis stolonifera* on vegetation and soil fauna communities at Marion Island, sub-Antarctic. *Biological Conservation* 85: 223-231.

Greve, M., Mathakutha, R., Steyn, C., & Chown, S.L. 2017. Terrestrial invasions on sub-Antarctic Marion and Prince Edward Islands. *Bothalia* 47: a2143.

Guillera-Arroita, G., Lahoz-Monfort, J.J., Elith, J., Gordon, A., Kujala, H., Lentini, P.E., McCarthy, M.A., Tingley, R., & Wintle, B.A. 2015. Is my species distribution model fit for purpose? Matching data and models to applications. *Global Ecology and Biogeography* 24: 276–292.

Hageer, Y., Esperon-Rodriguez, M., Baumgartner, J.B., & Beaumont, L.J. 2017. Climate, soil or both? Which variables are better predictors of the distributions of Australian shrub species? *Peerj* 5: e3446.

Haussmann, N.S., Rudolph, E.M., Kalwij, J.M., & McIntyre, T. 2013. Fur seal populations facilitate establishment of exotic vascular plants. *Biological Conservation* 162: 33–40.

Hoffman, M.T., Rohde, R.F., & Gillson, L. 2019. Rethinking catastrophe? Historical trajectories and modelled future vegetation change in southern Africa. *Anthropocene* 25: 100189.

Hoffmann, A.A., Rymer, P.D., Byrne, M., Ruthrof, K.X., Whinam, J., McGeoch, M., Bergstrom, D.M., Guerin, G.R., Sparrow, B., Joseph, L., Hill, S.J., Andrew, N.R., Camac, J., Bell, N., Riegler, M., Gardner, J.L., & Williams, S.E. 2019. Impacts of recent climate change on terrestrial flora and fauna: Some emerging Australian examples. *Austral Ecology* 44: 3–27.

Huntley, B. 1971. Vegetation. In E. M. Van Zinderen Bakker (Ed.), *Marion and Prince Edward Islands,* pp. 98-160, A.A. Balkema, Cape Town, South Africa.

Huntley, B., Berry, P.M., Cramer, W., & McDonald, A.P. 1995. Modelling present and potential future ranges of some European higher plants using climate response surfaces. *Journal of Biogeography* 22: 967–1001.

Kappes, P.J., Benkwitt, C.E., Spatz, D.R., Wolf, C.A., Will, D.J., & Holmes, N.D. 2021. Do invasive mammal eradications from islands support climate change adaptation and mitigation? *Climate* 9: 172.

Kearney, M., & Porter, W. 2009. Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. *Ecology Letters* 12: 334–350.

Lee, J.E., Le Roux, P.C., Meiklejohn, K.I., & Chown, S.L. 2013. Species distribution modelling in low-interaction environments: Insights from a terrestrial Antarctic system. *Austral Ecology* 38: 279–288.

Leihy, R.I., Duffy, G.A., Nortje, E., & Chown, S.L. 2018. High resolution temperature data for ecological research and management on the Southern Ocean Islands. *Scientific Data* 5: 180177.

Liautaud, K., van Nes, E.H., Barbier, M., Scheffer, M., & Loreau, M. 2019. Superorganisms or loose collections of species? A unifying theory of community patterns along environmental gradients. *Ecology Letters* 22: 1243–1252.

McClelland, G.T.W., Altwegg, R., Van Aarde, R.J., Ferreira, S., Burger, A.E., & Chown, S.L. 2018. Climate change leads to increasing population density and impacts of a key island invader. *Ecological Applications* 28: 212–224.

van der Merwe, S., Greve, M., Olivier, B., & le Roux, P.C. 2021. Testing the role of functional trait expression in plant-plant facilitation. *Functional Ecology* 35: 255–265.

van der Merwe, S., Greve, M., Skowno, A.L., Hoffman, M.T., & Cramer, M.D. 2023. Can vegetation be discretely classified in species-poor environments? Testing plant community concepts for vegetation monitoring on sub-Antarctic Marion Island. *Ecology And Evolution* 13: e9681.

Mod, H.K., Heikkinen, R.K., le Roux, P.C., Wisz, M.S., & Luoto, M. 2016. Impact of biotic interactions on biodiversity varies across a landscape. *Journal Of Biogeography* 43: 2412–2423.

Moncrieff, G.R., Bond, W.J., & Higgins, S.I. 2016. Revising the biome concept for understanding and predicting global change impacts. *Journal Of Biogeography* 43: 863–873.

Mucina, L. 1997. Classification of vegetation: Past, present and future. *Journal of Vegetation Science* 8: 751–760.

Mucina, L., Bueltmann, H., Dierssen, K., Theurillat, J.-P., Raus, T., Čarni, A., Šumberová, K., Willner, W., Dengler, J., Garcia, R.G., Chytrý, M., Hajek, M., Di Pietro, R., Iakushenko, D., Pallas, J., Daniels, F.J.A., Bergmeier, E., Santos Guerra, A., Ermakov, N., Valachovic, M., Schaminee, J.H.J., Lysenko, T., Didukh, Y.P., Pignatti, S., Rodwell, J.S., Capelo, J., Weber, H.E., Solomeshch, A., Dimopoulos, P., Aguiar, C., Hennekens, S.M., & Tichy, L. 2016. Vegetation of Europe: hierarchical floristic classification system of vascular plant, bryophyte, lichen, and algal communities. *Applied Vegetation Science* 19: 3–264.

Oepik, M., de Bello, F., Price, J.N., & Fraser, L.H. 2014. New insights into vegetation patterns and processes. *New Phytologist* 201: 383–387.

Øvstedal, D.O., & Gremmen, N.J.M. 2001. The lichens of Marion and Prince Edward Islands. *South African Journal of Botany* 67: 552–572.

Pandit, S.N., Kolasa, J., & Cottenie, K. 2009. Contrasts between habitat generalists and specialists: an empirical extension to the basic metacommunity framework. *Ecology* 90: 2253–2262.

Penuelas, J., Prieto, P., Beier, C., Cesaraccio, C., de Angelis, P., de Dato, G., Emmett, B.A., Estiarte, M., Garadnai, J., Gorissen, A., Lang, E.K., Kroeel-Dulay, G., Llorens, L., Pellizzaro, G., Riis-Nielsen, T., Schmidt, I.K., Sirca, C., Sowerby, A., Spano, D., & Tietema, A. 2007. Response of plant species richness and primary productivity in shrublands along a north-south gradient in Europe to seven years of experimental warming and drought: reductions in primary productivity in the heat and drought year of 2003. *Global Change Biology* 13: 2563–2581.

Phiri, E.E., Mcgeoch, M.A., & Chown, S.L. 2009. Spatial variation in structural damage to a keystone plant species in the sub-Antarctic: interactions between *Azorella selago* and invasive house mice. *Antarctic Science* 21: 189–196.

Preston, G.R., Dilley, B.J., Cooper, J., Beaumont, J., Chauke, L.F., Chown, S.L., Devanunthan, N., Dopolo, M., Fikizolo, L., Heine, J., Henderson, S., Jacobs, C.A., Johnson, F., Kelly, J., Makhado, A.B., Marais, C., Maroga, J., Mayekiso, M., McClelland, G., Mphepya, J., Muir, D., Ngcaba, N., Ngcobo, N., Parkes, J.P., Paulsen, F., Schoombie, S., Springer, K., Stringer, C., Valentine, H., Wanless, R.M., & Ryan, P.G. 2019. South Africa works towards eradicating introduced house mice from sub-Antarctic Marion Island: the largest island yet attempted for mice. In Veitch, C.R., Clout, M.N., Martin, A.R., Russell, J.C., West, C. (Eds.), *Island invasives: scaling up to meet the challenge,* pp. 40–46. IUCN, Gland, Switzerland.

Raath-Krüger, M.J., McGeoch, M.A., Schöb, C., Greve, M., & le Roux, P.C. 2019. Positive plant-plant interactions expand the upper distributional limits of some vascular plant species. *Ecosphere* 10: e02820.

Ricciardi, A., Iacarella, J.C., Aldridge, D.C., Blackburn, T.M., Carlton, J.T., Catford, J.A., Dick, J.T.A., Hulme, P.E., Jeschke, J.M., Liebhold, A.M., Lockwood, J.L., MacIsaac, H.J., Meyerson, L.A., Pysek, P., Richardson, D.M., Ruiz, G.M., Simberloff, D., Vila, M., & Wardle, D.A. 2021. Four priority areas to advance invasion science in the face of rapid environmental change. *Environmental Reviews* 29: 119–141.

Ripley, B.S., Edwardes, A., Rossouw, M.W., Smith, V.R., & Midgley, G.F. 2020. Invasive grasses of sub-Antarctic Marion Island respond to increasing temperatures at the expense of chilling tolerance. *Annals of Botany* 125: 765–773.

Roe, N.A., Ducey, M.J., Lee, T.D., Fraser, O.L., Colter, R.A., & Hallett, R.A. 2022. Soil chemical variables improve models of understorey plant species distributions. *Journal of Biogeography* 49: 753–766.

le Roux, P.C., & McGeoch, M.A. 2010. Interaction intensity and importance along two stress gradients: adding shape to the stress-gradient hypothesis. *Oecologia* 162: 733–745.

le Roux, P.C., & McGeoch, M.A. 2008. Rapid range expansion and community reorganization in response to warming. *Global Change Biology* 14: 2950-2962.

le Roux, P.C., Ramaswiela, T., Kalwij, J.M., Shaw, J.D., Ryan, P.G., Treasure, A.M., McClelland, G.T.W., McGeoch, M.A., & Chown, S.L. 2013. Human activities, propagule pressure and alien plants in the sub-Antarctic: Tests of generalities and evidence in support of management. *Biological Conservation* 161: 18–27.

Ryan, P.G., Smith, V.R., & Gremmen, N.J.M. 2003. The distribution and spread of alien vascular plants on Prince Edward Island. *African Journal of Marine Science* 25: 555–562.

Schöb , C., Brooker, R.W., & Zuppinger-Dingley, D. 2018. Evolution of facilitation requires diverse communities. *Nature Ecology & Evolution* 2: 1381–1385.

Scott, D. 1995. Vegetation - A mosaic of discrete communities, or a continuum. *New Zealand Journal of Ecology* 19: 47–52.

Shaw, J.D. 2013. Southern Ocean Islands Invaded: Conserving Biodiversity in the World's Last Wilderness. In Foxcroft, L., Pyšek, P., Richardson, D., & Genovesi, P. (Eds.), *Plant Invasions in Protected Areas. Invading Nature - Springer Series in Invasion Ecology, vol 7*, Springer, Dordrecht.

Smith, V.R., Avenant, N., & Chown, S.L. 2002. The diet and impact of house mice on a sub-Antarctic island. *Polar Biology* 25: 703–715.

Smith, V.R., & Mucina, L. 2006. Vegetation of sub-Antarctic Marion and Prince Edward Islands. In Mucina, L., Rutherford, M.C., & Powrie, L.W. (Eds.), *Vegetation of South Africa, Lesotho and Swaziland*, pp. 699–723. South African National Biodiversity Institute, Pretoria, South Africa.

Treasure, A.M., & Chown, S.L. 2014. Antagonistic effects of biological invasion and temperature change on body size of island ectotherms. *Diversity and Distributions* 20: 202–213.

Treasure, A.M., & Chown, S.L. 2013. Contingent absences account for range limits but not the local abundance structure of an invasive springtail. *Ecography* 36: 146–156.

Weaver, J., & Clements, F. 1929. *Plant Ecology*. McGraw-Hill Book Company, New York.

Wiens, J.A., Stralberg, D., Jongsomjit, D., Howell, C.A., & Snyder, M.A. 2009. Niches, models, and climate change: Assessing the assumptions and uncertainties. *Proceedings of the National Academy of Sciences of The United States of America* 106: 19729–19736.

Wiser, S.K., & De Cáceres, M. 2018. New Zealand's plot-based classification of vegetation. *Phytocoenologia* 48: 153–161.

Xie, Y., Sha, Z., & Yu, M. 2008. Remote sensing imagery in vegetation mapping: a review. *Journal of Plant Ecology* 1: 9–23.

Yang, B., Cui, M., Du, Y., Ren, G., Li, J., Wang, C., Li, G., Dai, Z., Rutherford, S., Wan, J.S.H., & Du, D. 2022. Influence of multiple global change drivers on plant invasion: Additive effects are uncommon. *Frontiers in Plant Science* 13: 1020621.