# Wind as a climatic driver of biotic communities in the sub-Antarctic

By

**Mia Momberg**

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Supervisor: Prof. Peter C. le Roux

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## Declaration

I, Mia Momberg declare that the thesis, which I hereby submit for the degree Philosophiae Doctor (Plant Science) at the University of Pretoria, is my own work and has not previously been submitted by me for a degree at this or any other tertiary institution.

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**“The breath of life is in the sunlight and the hand of life is in the wind.”**

Kahlil Gibran

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## Abstract

The effects of temperature and precipitation, and the impacts of changes in these climatic conditions, on biological communities have been investigated extensively. The roles of other climatic factors are, however, comparatively poorly understood, despite potentially also strongly structuring community patterns. Wind, for example, is seldom considered when forecasting species responses to climate change, despite having direct physiological and mechanical impacts on plants, soil, and animals. It is, therefore, important to understand the magnitude of the potential impacts of changing wind conditions on biological communities. This has become increasingly relevant given that wind speeds have accelerated globally over the past decade, with the largest changes taking place in the Southern Ocean. Therefore, the aim of this thesis was to examine the role of wind in shaping biological systems in the sub-Antarctic, testing the influence of wind, across multiple spatial and organizational levels, on: 1) island-scale vegetation distribution, and the occurrence of vegetation types; 2) plant species richness, vegetation cover and composition at a community scale; 3) the fine-scale distribution and cover of individual vascular plant species; and 4) nest site selection by a surface-nesting seabird across an entire island.

At the broadest scale, across the whole of Marion Island, wind velocity was the second most important predictor (after elevation) driving the occurrence of vegetation types on the island, and the fourth most important predictor of total vegetation cover. Wind also affected a highly mobile species, the Wandering Albatross, at the island-scale. The nest-site selection of the world's largest pelagic bird was most strongly influenced by elevation, distance from the coast, terrain ruggedness and wind velocity. Nests had the highest probability of occurring in areas with intermediate wind velocities, which present favourable conditions for take-off and landing. Wind turbulence was, however, not important for either Wandering Albatross nest-site selection or vegetation patterns, emphasising the importance of considering wind velocity and wind exposure into future models.

At a finer spatial scale, using data from 1440 x 1 m$^2$ quadrats, wind stress significantly affected plant species richness, vegetation cover, and community composition, even after accounting for other ecophysiologically-important predictors. Species richness was highest under intermediate wind stress conditions, while the highest vegetation

cover occurred in plots that experienced the highest wind stress. The differences in community composition were driven by turnover due to species-specific responses to wind conditions. Wind stress had a significant effect on the occurrence of twelve out of sixteen species, and was a more important predictor than any temperature- or moisture-related variables for six of these species.

Wind conditions are, therefore, strongly related to multiple aspects of biological communities in this ecosystem that experiences chronic winds. Based on these findings, it is clear that wind has been overlooked as a climatic driver of ecological patterns, and that wind characteristics need to be incorporated into studies investigating the links between climate and biological communities, as well as explicitly included when forecasting the ecological impacts of climate change.

# Chapter 1:

# General introduction

Recent anthropogenic-driven climatic changes have altered ecosystems globally by impacting on the phenology, the occurrence, and the density of species (Walther et al., 2002; Parmesan and Yohe, 2003; Parmesan, 2006). These consequences of climate change are leading to species-level extinctions, shifts in community composition, and changes in ecosystem processes and functioning (Erasmus et al., 2002; Thomas et al., 2004; Worm et al., 2006). Climatic changes are predicted to accelerate and become more severe in coming years (IPCC, 2013), and, therefore, understanding the ways in which climate change will affect organisms, communities and ecosystems is important in order to conserve biodiversity and ecosystem services, both of which are crucial to human wellbeing (Pecl et al., 2017). Despite the fact that the majority of ecological research addressing climate change impacts has focussed on understanding the effects of changes in temperature and precipitation regimes, other climate characteristics may potentially also have large impacts on natural systems and human society (McInnes et al., 2011), and should, potentially, also be included when forecasting the future of biodiversity (e.g. Bellard et al., 2012).

Wind has been overlooked as an ecological driver for over six decades (Wilson, 1959). Extreme wind conditions have changed over the last 30-100 years, with, for example, an increase in the frequency and severity of hurricanes and tropical cyclones (Webster et al., 2005; Holland and Bruyère, 2014). The ecological impacts of these extreme wind events are relatively well understood (Laurance and Curran, 2008; Behie et al., 2014; Xuan and Chang, 2014). Furthermore, other wind conditions are already showing changes, with shifts in wind speed being documented over the past 30 years (Young et al., 2011; IPCC, 2013; Young and Ribal, 2019; Zeng et al., 2019). Additionally, shifts in wind direction and intensity have been observed at broad spatial scales, with, for example, the Southern Ocean westerlies having shifted northwards and increased in strength (Fyfe and Saenko, 2006). Over longer time periods, changes to westerly winds in the Southern Hemisphere have also been recorded, where westerly winds have strengthened and decreased coinciding with the Little Ice Age and early Holocene periods (Shulmeister et al., 2004). Northward and poleward shifts, in association with changes in strength, occurring in the southern westerly winds at different stages during the past glacial cycle also drove changes in precipitation across Patagonia (Moreno et al., 2012). While extreme wind events are constrained to specific time periods and occur only periodically, winds that occur daily or seasonally and are not linked to extreme phenomena like hurricanes, tornadoes or storms, are described here as “chronic” winds. Contrary to our understanding of extreme wind events, the influence that daily wind speed and direction, and changes to these wind characteristics, have on ecosystems and species is poorly understood (Møller, 2013; Sutherland et al., 2017).

Wind plays an important role in structuring natural systems at all scales, from determining the destination of a single grain of pollen, to determining the genetic composition of entire populations and affecting species’ geographical distributions (de Langre, 2008). Moreover, the impacts of wind can be seen across both the biotic and the abiotic components of ecosystems, from the geomorphology to the flora and fauna. Wind shapes landscapes through erosion, deflation and sediment deposition (Desonie, 2013), and alters soil properties through desiccation (Bertiller et al., 1996; Fitzgerald and Kirkpatrick, 2017) and the distribution of litter (influencing nutrient content and soil temperature; Fahnestock et al., 2000). Wind can also play a role in the redistribution of snow, and the depth and duration of this snow cover directly affects the extreme temperatures to which plants in these areas are exposed (Lord et al., 2018). Air flow can act as a mechanical stress and disturbance on plants, as well as affecting the thickness of plants’ boundary layer (Grace, 1977; Grime, 1979; Ennos, 1997; Gardiner et al., 2016). During windy conditions, plants may have a lower photosynthetic rate as a result of reducing stomatal conductance to combat water loss (Grace, 1977; de Langre, 2008), and a lower effective leaf area as leaves are curled or folded when fluttering in the wind (de Langre, 2008). Winds can also cause mechanical damage to plants by tearing leaves, breaking stems, and causing abrasion by wind-blown particles (de Langre, 2008; Gardiner et al., 2016). Additionally, wind may have indirect impacts on plant fitness by affecting the abundance and activity of pollinators, and by affecting dispersal of seeds and pollen (de Langre, 2008). Air movement affects plant growth, and, therefore, plants in windy conditions tend to be shorter in stature and more structurally robust (de Langre, 2008; Zhang et al., 2021), sometimes exhibiting pronounced asymmetry in growth and canopy structure (Smith, 1972; Fitzgerald and Kirkpatrick, 2017; Ramírez-Pinero et al., 2019). Despite our understanding of the physiological impacts of wind on plants, most of these studies were conducted on a narrow range of tree species (de Langre, 2008), limiting our understanding of wind on the majority of the world's plants. Plants may also make resource allocation trade-offs due to wind exposure, as a higher investment in structural compounds may, for example, come at the cost of carbon assimilation (Pammenter et al., 1986). Further, leaves with particular shapes and petiole characteristics may be beneficial in allowing leaves to survive high wind conditions (Vogel, 2009). Consequently, changes in wind conditions may have major implications for individual plant morphology and the overall vegetation structure in a community. In spite of the potential for wind to play a considerable role in structuring communities, we have a poor understanding of changing wind conditions as a component of global climate change.

The stresses and disturbances caused by wind are also ecologically relevant when scaling up from individual plants to the distribution of species and vegetation types. For example, wind-protected sites allow for tree establishment, which has a large impact on the position of the treeline (McIntire et al., 2016). Accordingly, the upslope expansion of species under climate changes could be influenced by changing wind conditions (Kullman and Loyer, 2005; Crabtree and Ellis, 2010; Holtmeier and Broll, 2010). The distribution of species at a fine scale may also be determined by wind, where, for example, mosses that are intolerant of wind are limited to protected microsites (Jia et al., 2012). The spread and distribution of invasive species may also be related to wind conditions, with *Agrostis stolonifera,* an alien grass species on Marion Island, being restricted to areas that do not frequently experience gale force winds since it has much less support tissue than indigenous congeneric species (Pammenter et al., 1986), and with functional traits of alien species on Kerguelen Island responding to wind (Saiz et al., 2021). Wind flow across a landscape can also drive the distribution of vegetation types and vegetation patterning. Due to wind-driven directionality in growth and mortality patterns, linear vegetation features (e.g. ribbon forests, forest hedges and parallel waves of plants) are limited to wind-swept landscapes (Burges, 1951; Holtmeier and Broll, 2010). Similarly, certain vegetation types are limited to areas that receive windblown salt-spray from the ocean, while this prevents other communities from establishing in these areas (Smith et al., 2001).

Wind conditions can also impact on the fitness and distribution of fauna, from influencing the dispersal of microscopic zooplankton (Gray and Arnott, 2011), to the choice of denning sites by Brown bears (DeGayner et al., 2005). Many flying bird species have also been shown to be affected by wind. Barn swallows, for example, have lower survival rates when wind speed increases (Møller, 2013). Windy conditions may also affect visual processing in birds, as seen through increased blinking in passerine birds under windier conditions (Yorzinski and Argubright, 2019). Some other aspects of avian life-history are, however, influenced more strongly by genetic triggers than by wind conditions, including, for example, the departure date of long-distance migratory birds (Schwemmer et al., 2021). The breeding success of some sub-Antarctic Albatrosses is positively related to seasonal windiness, which correlates with other pelagic variables that may influence foraging (Cooper and Lutjeharms, 1992). The largest challenge for ectotherms in tropical and desert areas is to avoid overheating, and finding areas with high wind speeds is one of the ways in which they increase heat loss (Kearney et al., 2009). At finer scales, impacts on invertebrate species have also been observed, with a higher abundance of microarthropods (the main herbivores on the sub-Antarctic islands) on the leeward side of cushion-forming plant species than on the windward side, as invertebrates are not resistant to the increased desiccation associated with greater wind exposure (Hugo et al., 2004).

### *Wind in the Southern Ocean*

When investigating the effects of wind on biota, the Southern Ocean is an excellent model system. Most of the wind-driven mixing in the world's ocean occurs in the Southern Ocean (Wunsch, 1998), and it has recently been shown that the Southern hemisphere westerly winds can shift abruptly (Buizert et al., 2018), making this region particularly vulnerable to climate-driven changes. Furthermore, winds in the Southern Ocean are almost uninterrupted by continental masses, in contrast to the Northern hemisphere, leading to stronger and more consistent bands of winds than in other regions. Therefore, the impacts of wind and changes in wind conditions may be pronounced in the sub-Antarctic (e.g. Young and Ribal, 2019; Zeng et al., 2019). A considerable amount of the global increase in ocean heat storage has occurred in the extratropical latitudes of the Southern hemisphere (Gao et al., 2018), with increases in westerly wind strengths also leading to changes in acidification (Xue et al., 2018). The interaction between wind and snow is less pronounced on these islands due to the fact that snow rarely persists for longer than a few days close to sea level. Further, the temperature buffering effect of snow is not as important as at equivalent latitudes in the Northern Hemisphere because of the hyper-oceanic climate. The moisture redistribution caused by the melting of snow is also not critical, because this is not a moisture-limited system. This allows to investigate the effects of wind while minimizing the impacts of snow.

Islands in the sub-Antarctic are experiencing exceptionally high rates of climatic change (Bergstrom and Chown, 1999; Pendlebury and Barnes-Keoghan, 2007; le Roux and McGeoch, 2008). Moreover, they are ideal “ecological laboratories” in which to study the effects of climate change since their isolation, low species richness and harsh climatic environments make them very sensitive to change (Smith, 2002) and they have experienced minimal other anthropogenic influences (Bergstrom and Chown, 1999). These islands are, additionally, of particular conservation importance as they are the only terrestrial habitats at these latitudes and provide nesting grounds for a large number of the world’s Procellariiform seabirds (Chown et al., 1998; Bergstrom and Chown, 1999), and areas where seals can haul out to rest, breed, and moult. Marion Island, in particular, has experienced pronounced climatic changes. A comparison of wind patterns between 1960 - 1980 and 1981 - 2000 revealed shifts in wind direction, a decrease in meridional wind speed and precipitation, and an increase in temperature extremes and sea surface temperature (Rouault et al., 2005).

**Figure 1** Wind on Marion Island creating waves on an inland lake.

The sub-Antarctic islands experience some of the world's highest mean wind speeds (Yuan, 2004) and their biotic and abiotic characteristics are highly influenced by wind (Löffler, 1984; French and Smith, 1985), although there are not many studies focusing on quantifying the effects of wind. The distribution of coarse and fine soil particles, for example, is influenced by the dominant wind direction (Hedding et al., 2015). The distribution of plants on these islands, as well as their productivity, and the outcome of plant-plant interactions have all been suggested to be linked to wind exposure, which affects salt-spray, and leads to more positive interactions (Smith, 1978; Bergstrom et al., 2002; le Roux and McGeoch, 2010). Cushion plants in sub-Antarctic environments show a clear response to wind, where plant death and erosion on the windward side of plants lead to crescent-shaped cushions (Fitzgerald and Kirkpatrick, 2017; Combrinck et al., 2020). Similarly, variability in mortality patterns in the cushion plant *Azorella selago*, a keystone species on these islands, were correlated with wind conditions (Le Roux et al., 2005). At fine scales, when examining individual *Azorella selago* cushion plants, there are clear differences between the windward and leeward sides of plants, with fewer frost cycles, higher snow accumulation, and more stable soil moisture (due to lower evapotranspiration) on the leeward sides (Haussmann et al., 2009). Graminoids in this region also respond to wind, where individuals were asymmetric in their basal shape or had their leaves or culms facing one direction (Fitzgerald and Kirkpatrick, 2017). These responses were contingent on topography and the direction not only of the most frequent strong winds, but also of the most damaging winds (Fitzgerald and Kirkpatrick, 2017). The fine-scale spatial genetic structure of *A. selago* across Marion Island was found to be highly variable, likely as a result of heterogenous wind directions and speeds across the island, which affect dispersal (Born et al., 2012). The fauna of the sub-Antarctic islands, from the activity and dispersal of invertebrates, to the behaviour, foraging and breeding success of the Wandering Albatross are also affected by wind patterns (Chown and Avenant, 1992; Greenslade et al., 1999; Weimerskirch et al., 2000; Chown et al., 2004; Weimerskirch et al., 2012).

## Thesis structure and objectives

The aim of this thesis is to examine the role of wind in shaping biological systems in the sub-Antarctic. To achieve this, my thesis consists of four research chapters, each with a distinct objective: To test for an influence of wind on:

1) island-scale vegetation limits, and the occurrence of vegetation types;

2) plant species richness, vegetation cover and composition at a community scale;

3) the fine-scale distribution and cover of individual vascular plant species; and

4) nest site selection by a surface-nesting seabird across an entire island.

Each research chapter was written as a stand-alone manuscript for submission to specific journals and, therefore, there is some repetition in the description of the study site and methods. In the final chapter of this thesis, I synthesize my findings from all of the preceding chapters.

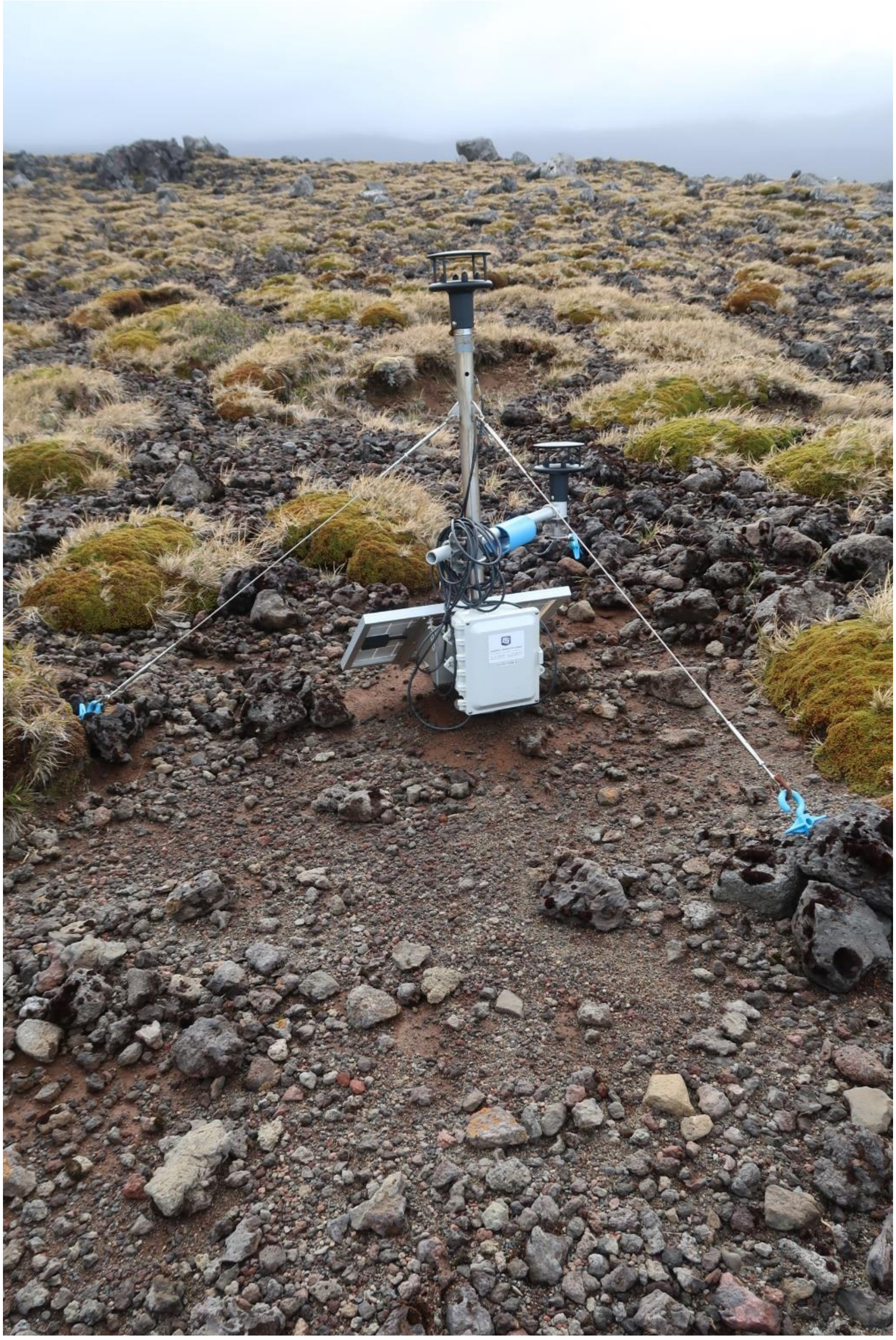

**Figure 2** A wind station installed in the wind-exposed fellfield vegetation type (dominated by *Azorella selago* and *Polypogon magellanicus*) on Marion Island.

This thesis sheds light on the role of wind in shaping biological systems in the sub-Antarctic, and provides an understanding of how wind drives vegetation and bird nesting patterns. By spanning different spatial and hierarchical scales, this study gives detailed insights into the effects of wind on different aspects of the biotic community. More broadly, this research will contribute to our understanding of how wind characteristics affect ecosystem structure, and highlights the paucity of studies considering a more complete set of potentially important climatic drivers.

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# Chapter 2:

# Wind shapes the island-scale distribution of vegetation

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**Authors' contributions:** MM, PCLR, DWH and KJC conceived the ideas and designed methodology; MM and PCLR analysed the data, with inputs from DWH; MM led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

## Abstract

Understanding relationships between climate and the distribution of vegetation are important in predicting patterns of vegetation occurrence under future climatic conditions. Temperature and precipitation have been studied extensively as climatic drivers of vegetation patterns, but to promote a more comprehensive understanding of these relationships, other components of climate must be considered. Little research has been conducted on how wind affects vegetation patterns, despite having clear physiological impacts on individual plants. Here, we investigate the relationship between wind velocity and wind turbulence and vegetation at a broad- (i.e. island-) scale on the chronically windy sub-Antarctic Marion Island. Total vegetation cover and the distribution of individual vegetation types were modelled, accounting for elevation, terrain ruggedness, curvature, geology, and potential solar radiation. Wind velocity was the fourth most important predictor in explaining vegetation cover (after elevation, solar radiation and terrain ruggedness), with lower vegetation cover in areas of higher wind velocity. After elevation, wind velocity was the most important predictor in explaining the occurrence of five out of the six vegetation types. Wind is, for example, critical in determining the distribution of salt-spray from the ocean, which shapes vegetation types. Therefore, wind may play an important role in the response of vegetation to future climatic change and, in particular, could explain differences in the distribution of vegetation types in topographically heterogenous environments that show pronounced variation in wind conditions.

## Introduction

Understanding the relationships between contemporary vegetation patterns and climate is crucial in predicting how vegetation will respond to future climate change. At broad spatial scales climate is the key driver of species distributions and, as a result, assemblages of species (McGill, 2010). For example, biomes and vegetation types are distributed chiefly along climatic gradients (Whittaker, 1975; Stephenson, 1990; Mucina, 2019). Traditionally, temperature and precipitation have been used to describe climate’s influence on vegetation cover and the occurrence of specific vegetation types (e.g. Whittaker, 1975; Liu et al., 2018). However, these parameters provide an incomplete description of climate when considered alone (Mather and

Yoshioka, 1968). Some other climatic drivers have not received much attention with regards to their effect on biotic communities, in particular relative humidity, solar radiation, and wind characteristics (Afuye et al., 2021).

Wind has seldom been considered as a climatic driver of vegetation patterns and the lack of studies has been noted, particularly in Arctic, sub-Antarctic and alpine areas, for over six decades (Wilson, 1959; Momberg et al., 2021a). Wind is directly linked to plant performance, affecting photosynthesis, evapotranspiration, physical damage to plants, soil available water, and soil temperature (Bertiller et al., 1996; Fahnestock et al., 2000; de Langre, 2008; Yang et al., 2014; Gardiner et al., 2016; Fitzgerald and Kirkpatrick, 2017). The redistribution of snow through wind changes patterns of plant exposure to extreme temperatures and frost damage (Lord et al., 2018). Since the performance of individual plants aggregate to determine the assemblages of species present in an area, it is reasonable to expect that individual plant- and population-level impacts of wind should scale up to impact the occurrence (and type of) vegetation in any given area. Indeed, in some systems there is evidence that wind may affect the distribution of vegetation, with, for example, the upper limit of the treeline in some boreal forests being constrained by wind (Kullman and Loyer, 2005; Holtmeier and Broll, 2010).

Therefore, the aims of this study were to investigate the influence of wind velocity and wind turbulence (1) on the broad-scale spatial distribution of vegetation cover, and (2) on the distribution of vegetation communities, after accounting for the influence of elevation and other bio-physical variables.

## Methods

### *Study site*

This study was conducted on Marion Island (46°54’S, 37°43’E; 293 km$^2$), a remote sub-Antarctic island in the Southern Ocean (Rudolph et al., 2021), characterised by wet and windy weather on most days, with mild temperatures due to the strong oceanic influence (le Roux, 2008).

### *Data collection*

To model spatial variation in vegetation, satellite imagery from the Advanced Land Imager instrument on the Earth Observing One satellite platform, with 30 m resolution, was used to generate a Normalised Difference Vegetation Index (NDVI) and Soil Adjusted Vegetation Index (SAVI), using ArcGIS Pro. The 1 m resolution Digital Surface Model (DSM) for Marion Island (DRDLR, 2019) was resampled to 30 m to match the resolution of vegetation indices. The Terrain Ruggedness Index (TRI) and curvature were calculated at 30 m resolution using the resampled DSM. Geology was obtained from Rudolph et al. (2021). Wind speed and turbulence at 1 m above the ground (weighted by the frequency of 16 wind directions) were obtained from Goddard et al. (2022). Ten thousand random points were generated across the island (excluding lakes), with > 30 m between points. Slope and aspect were calculated from the DSM and used to calculate potential direct incident radiation (PDIR) (McCune and Keon, 2002; McCune, 2007). The NDVI, SAVI, TRI, curvature, elevation, wind turbulence, wind velocity, and geology type were extracted for all points.

To model vegetation types, the identity and cover of vascular plant species and bryophyte groups were recorded in 491 quadrats of 3 x 3 m in 24 altitudinal transects across Marion Island (see Figure A1 for the location of transects). These data were supplemented with 17 quadrats sampled from the high-altitude regions of the island. The data were used to classify each quadrat into one of seven vegetation types (as defined by Smith and Steenkamp, 2001). Due to low numbers of quadrats sampled in Biotic grassland (n=14) and Biotic herbfield (n=8), these two habitat types, were merged into one type (“Biotically influenced”), resulting in six vegetation types overall. For each quadrat, TRI, PDIR, curvature, elevation, wind turbulence, wind velocity, and geology type were extracted.

### *Statistical analysis*

None of the predictor variables were strongly correlated ($r < |0.4|$). Since elevation is the main driver of vegetation cover on Marion Island (Smith et al., 2001), a generalized additive model (GAM) with a Gaussian distribution, with only elevation as a predictor variable was created. The residuals from this model ("residual NDVI” and “residual SAVI”) were then analysed using a GAM with a Gaussian distribution to determine whether wind velocity, wind turbulence, geology, TRI, PDIR, and curvature can explain the remaining variation in NDVI and SAVI.

The occurrence of each of the six vegetation types was modelled using a GAM with a binomial distribution to determine the relationship between elevation, wind velocity, wind turbulence, geology, PDIR, and curvature and the distribution of each vegetation type. For each vegetation type, the quadrats classified as that type were used as presence points, and the remainder of the quadrats (i.e., those classified as other vegetation types) were used as absence points. Wind turbulence was log-transformed to reduce high leverage.

The variable importance for each predictor was calculated following (Niittynen and Luoto, 2018). All analyses were performed in R (R Core Team, 2021).

## Results

Elevation explained 52 % of the variation in NDVI. Five of the six predictor variables were significantly related to residual NDVI (turbulence did not have a significant effect). PDIR was the most important predictor in explaining the variation in the residuals, and had a positive effect, indicating higher NDVI than expected for a given elevation in areas of higher PDIR (Figure 1). The next most important variables were terrain ruggedness, wind velocity, and geology, with lower vegetation cover in areas with greater terrain ruggedness and higher wind velocities (Figure 1). Highest vegetation cover was found on black lava (i.e., rugged post-glacial lava flows from the Holocene; Rudolph et al., 2021), and lowest on recent lava flows (post-1980). The results for NDVI and SAVI were similar, and, therefore, results for SAVI are provided in the appendix.

The occurrence of all six vegetation types were significantly related to elevation (Table 2; Figure 2). The occurrence of five of the six vegetation types was additionally significantly affected by wind velocity, with only the coastal Biotically influenced vegetation not being constrained by wind speed. Wind turbulence, geology, PDIR and terrain ruggedness all had a significant impact on the occurrence of only one or two vegetation types.

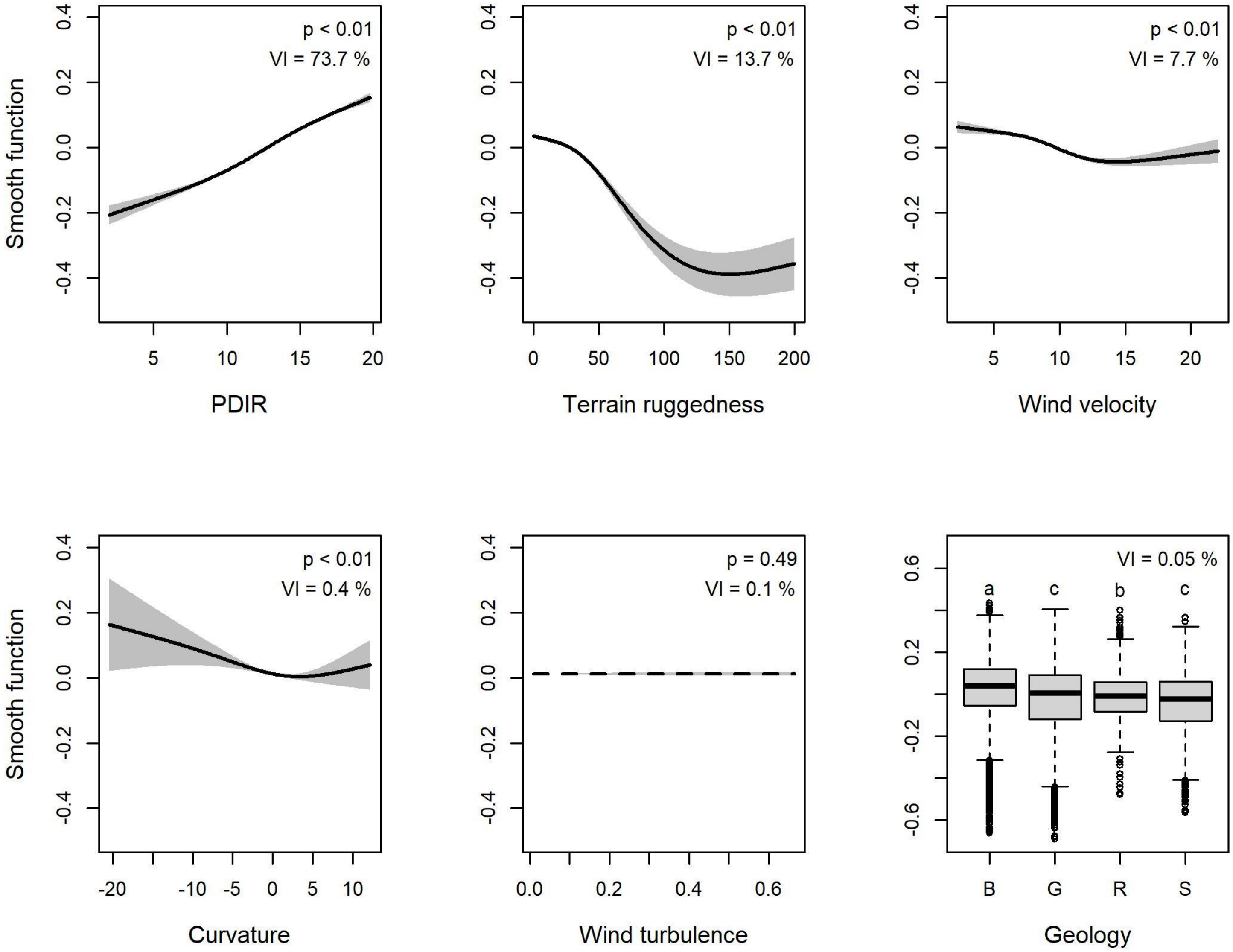

**Figure 1** Response curves for the six predictor variables explaining vegetation cover after accounting for elevation (i.e. residual NDVI, deviance explained = 27 %). PDIR = potential direct incident radiation. B=black lava (i.e. post-glacial lava flows), G=grey lava (i.e. pre-glacial flows), R=recent (i.e. post-1980 lava flows), S=scoria. Significance and variable importance values (VI) are indicated on each plot.

**Table 1** Variable importance (%) for each variable that was significantly related to each vegetation type's distribution. See Table A2 for full results. n = occurrences per vegetation type. TRI = terrain ruggedness index, PDIR = potential direct incident radiation.

| Vegetation type | n | Deviance explained (%) | Elevation | TRI | Curvature | Geology | PDIR | Wind velocity | Wind turbulence |
|---|---|---|---|---|---|---|---|---|---|
| Coastal salt-spray | 11 | 64.6 | 38 | | | | | 26 | 20 |
| Fellfield | 131 | 25.7 | 77 | 4 | | 6 | | 8 | |
| Fernbrake | 115 | 11.8 | 44 | | | 15 | 12 | 13 | |
| Biotically influenced | 22 | 32.9 | 35 | 23 | | | | | |
| Mire | 211 | 7.2 | 31 | | | | | 36 | |
| Polar desert | 18 | 47.7 | 47 | | | | | 23 | 28 |

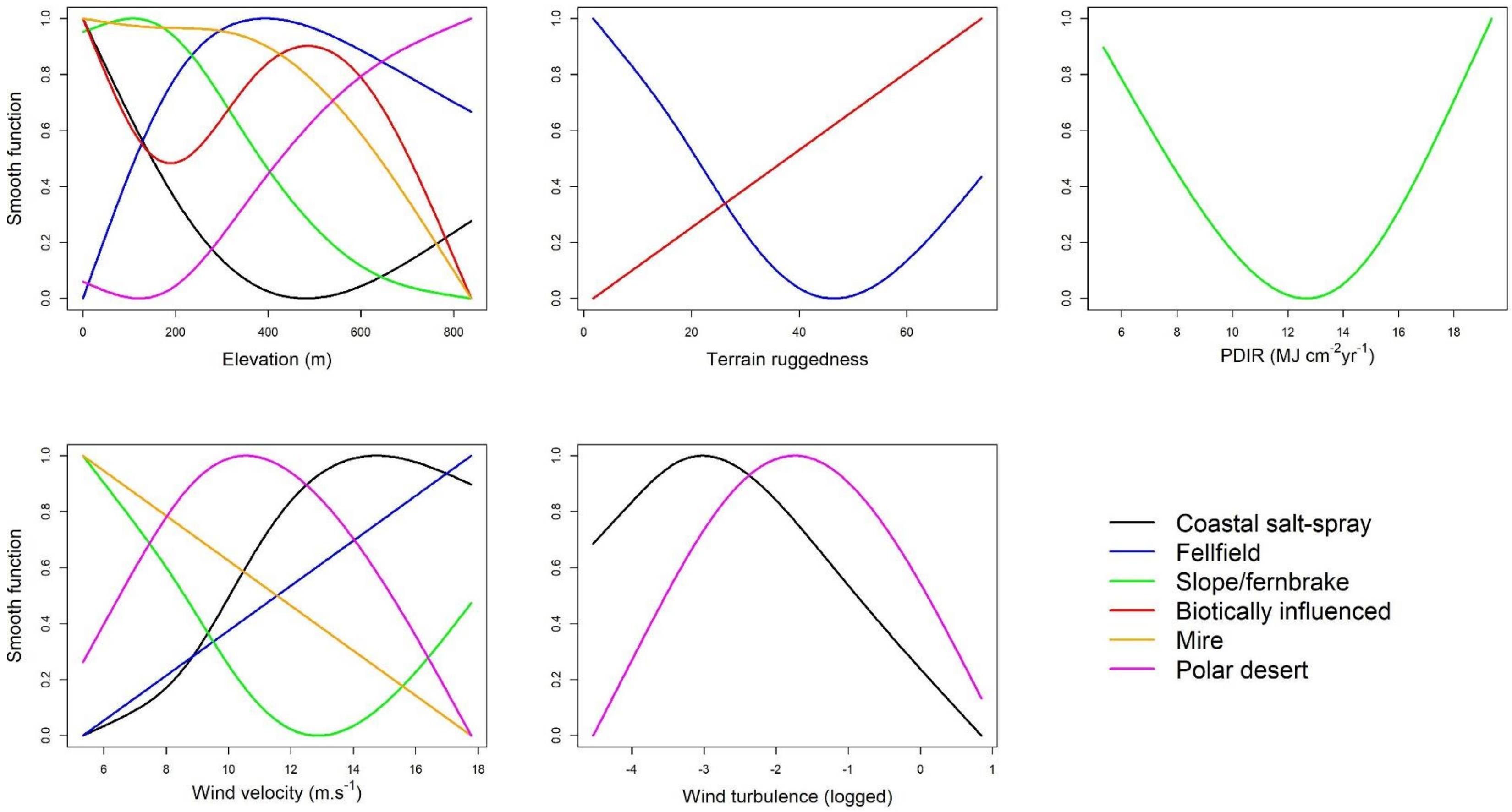

**Figure 2** Response curves of significant relationships for all six vegetation types for a) elevation, b) terrain ruggedness index, c) potential direct incident radiation, d) wind velocity, and e) wind turbulence (logged). Y-axis values of all curves were rescaled to allow for visualisation on the same panels. PDIR = potential direct incident radiation.

## Discussion

Wind velocity was significantly related to island-scale variation in vegetation cover and the distribution of the majority of vegetation types. For vegetation cover, wind velocity was the fourth most important predictor, while wind velocity was the second most important variable overall in determining the occurrence of all six vegetation types. Wind velocity determines the distribution of specific species, where under high wind velocities a lower density of plants occur, explaining the negative relationship between wind velocity and overall vegetation cover (Löffler, 1984; Momberg et al., 2021b). Under higher wind speeds coastal salt-spray and fellfield vegetation types had the highest probabilities of occurrence. Salt-spray communities are characterised by high soil salinity and are found further inland on the north and west coasts than on the east and south (Smith and Steenkamp, 2001) reflecting how the dominant (and strongest) westerly and north-westerly winds carry salt from the ocean further inland on these sides of Marion Island (le Roux, 2008; see also Whittle et al., 2019). Fellfield vegetation typically occurs on exposed ridges and plateaus (Smith and Steenkamp, 2001), where topography causes wind speeds to be higher than in adjacent lower-lying areas. In contrast, at lower wind speeds mire and fernbrake vegetation were more likely to occur. Mire habitats are typified by wet soils, and the desiccating effect of wind may limit these communities from establishing under high wind speeds (Bertiller et al., 1996). Fernbrake is most common in areas with low wind velocities, possibly due to ferns being very sensitive to drought stress, with only a small change in leaf water potential leading to permanent leaf death, instead of stomatal closure, as the drought response in some species (McAdam and Brodribb, 2013).

Elevation was most strongly related to vegetation cover at our site (in agreement with Huntley, 1971; Smith et al., 2001), possibly reflecting the strong correlation between elevation and temperature in this system (Leihy et al., 2018), with lower vegetation cover at cooler, higher elevations. Elevation was also the only predictor that contributed significantly to explaining the occurrence of all six vegetation types, in line with how these vegetation types have been previously described (Smith et al., 2001). Coastal salt-spray vegetation, for example, is limited to the lowest elevations along the coastline. The opposite pattern is seen for polar desert, which is the only vegetation type commonly present at elevations higher than 500 m (Smith and Steenkamp, 2001; Smith et al., 2001). This pattern is a global one, where the influence of salt-spray is strongly affected by the distance from the coast (Du and Hesp, 2020), and elevation is the greatest driver of the distribution of polar deserts (Lévesque, 1997).

Potential solar radiation played the largest role in determining vegetation cover, after accounting for elevation, and can be related to surface temperatures, evaporative demand, soil moisture, and light availability for photosynthesis (Ashcroft, 2006; Bennie et al., 2008). In the Maritime Antarctic, solar radiation also largely determines the distribution of vegetation, due to the greater solar radiation requirements of mosses than lichens (de Andrade et al., 2018). However, on Marion Island PDIR was only a significant predictor in the distribution of the Fernbrake vegetation type. This vegetation type is characteristic of slopes at low and mid altitudes (Smith and Steenkamp, 2001), and having peak occurrence at intermediate values of PDIR shows that this vegetation type has a higher probability of occurrence on east- and west-facing slopes. Even though solar radiation is related to the occurrence of some species, the cover of individual species is less affected by PDIR than their occurrence, and, therefore, the majority of vegetation types, which are defined by the cover attained by the species present, are not strongly affected (Momberg et al., 2021b).

Lower vegetation cover (than expected based on elevation) was found for areas with high terrain ruggedness. This likely reflects high rock cover in these areas, which limits vegetation growth. In particular, the probability of occurrence of the biotically-influenced vegetation type showed a strong positive relationship with terrain ruggedness. This vegetation type, which is strongly influenced by trampling and manuring by birds and seals, is mainly restricted to areas adjacent to coastal cliffs, which are particularly rugged features in this system. These results also show that the occurrence of fellfield tends to decrease as terrain ruggedness increases, which could be attributed to the fact that this vegetation type is typically constrained to exposed ridges and plateaus (Smith and Steenkamp, 2001) and may not establish on steep slopes.

Geology had an impact in determining overall vegetation cover whereby vegetation cover was highest on post-glacial lava flows (i.e. “black lava”), and lowest on recent (post-1980) lava flows, with pre-glacial “grey lava” and loose scoria supporting intermediate amounts of vegetation cover. This is likely because peat deposits (that support high vegetation cover) occur on these rugged black lava flows, while smooth pre-glacial flows do not allow for peat build-up (due to frequently having an approximately convex profile) and the recent lava flows have had inadequate time for sufficient substrate to form that would support higher vegetation cover. Indeed, many of the most recent lava flows are still largely devoid of vascular vegetation because ecological succession to support vascular plant cover on new lava flows takes centuries (Vilmundardóttir et al., 2018; see also Yeloff et al., 2007 for Marion Island).

Wind turbulence and landscape curvature had minimal impacts on both vegetation cover and the distribution of vegetation types. Wind turbulence was not related to variation in vegetation cover, but was negatively related to the occurrence of coastal salt-spray and polar desert. In areas of extreme turbulence, plants will likely experience more mechanical damage than when the wind flow is regular (e.g. Hamilton et al., 2020). Curvature has strong control over the flow of water and occurrence of erosion (and deposition). It is possible that curvature had a weak effect because this system is likely not limited by moisture, since it experiences rainfall on most days (le Roux, 2008), or sediment, since organic matter accumulates as peat in environments with high plant cover due to slow decomposition (Drewnik, 2006; Allison et al., 2010). However, in more arid environments, concave landforms typically have greater vegetation cover than flatter or convex surfaces (e.g. Yang et al., 2020), highlighting that this result may be contingent on resource availability.

In this study, wind velocity emerges as an important abiotic predictor of broad-scale spatial variation in vegetation patterns in a windy region. Therefore, including wind metrics into studies linking climate and biological patterns is paramount to develop a more comprehensive understanding of the relationships between wind conditions and vegetation distribution. Catastrophic wind disturbances, like hurricanes, can also reset succession, affecting the distribution of vegetation types and total vegetation cover in an area. The paucity of studies understanding the impacts of wind on vegetation at a broad spatial scale highlights the need to further investigate these relationships. Given the changes to wind patterns that have already taken place, and given that these changes are predicted to continue, understanding the relationships between wind and vegetation will provide more accurate estimates of vegetation characteristics in the future.

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## Appendix

**Table A1** The six vegetation types examined in this study, based on the classification of (Smith and Steenkamp, 2001). Species taxonomy following Chau et al. (2020).

| Vegetation type | Characteristic species | Key soil attributes |
|---|---|---|
| Coastal salt-spray | *Crassula moschata, Leptinella plumosa, Azorella selago* | High soil salinity |
| Fellfield | *Azorella selago* (with graminoids growing on the cushion plant), *Austroblechnum penna-marina* (low cover), bryophytes, lichens | High content of volcanic ash and weathered lava, high bulk density, dry |
| Fernbrake | *Austroblechnum penna-marina* (very high cover), *Acaena magellanica,* bryophytes | Deeper, well-drained soils, higher organic content and moisture than fellfield soils |
| Biotically influenced | *Poa cookii, Leptinella plumosa, Callitriche antarctica, Poa annua, Montia fontana, Austroblechnum penna-marina* | High organic content due to manuring |
| Mire | *Polypogon magellanicus, Juncus scheuchzerioides, Carex dikei*, bryophytes | High moisture content, low bulk density |
| Polar desert | *Azorella selago* (very low cover), bryophytes, lichens | No soils, bare rock or scoria covered in volcanic ash |

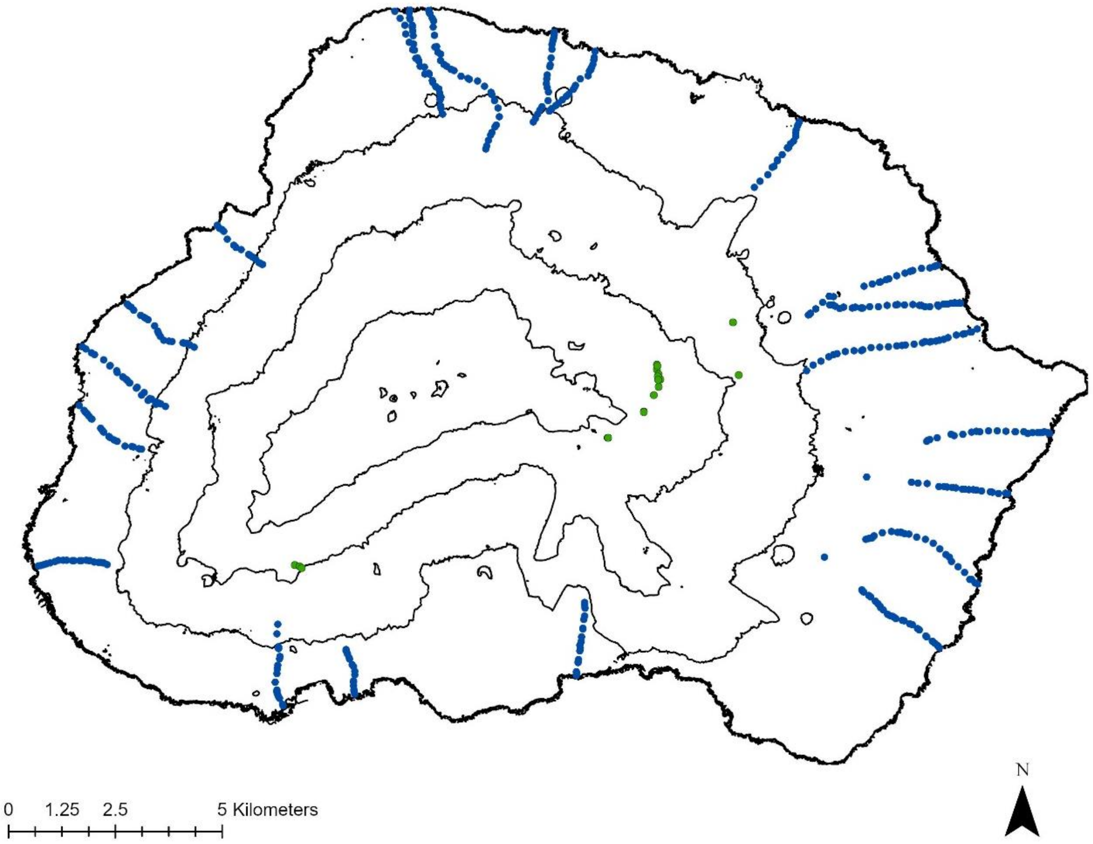

**Figure A1** Map of Marion Island indicating the sampled quadrats along transects in blue and additional high-altitude sampled quadrats in green. Contour lines are indicated at 300 m intervals.

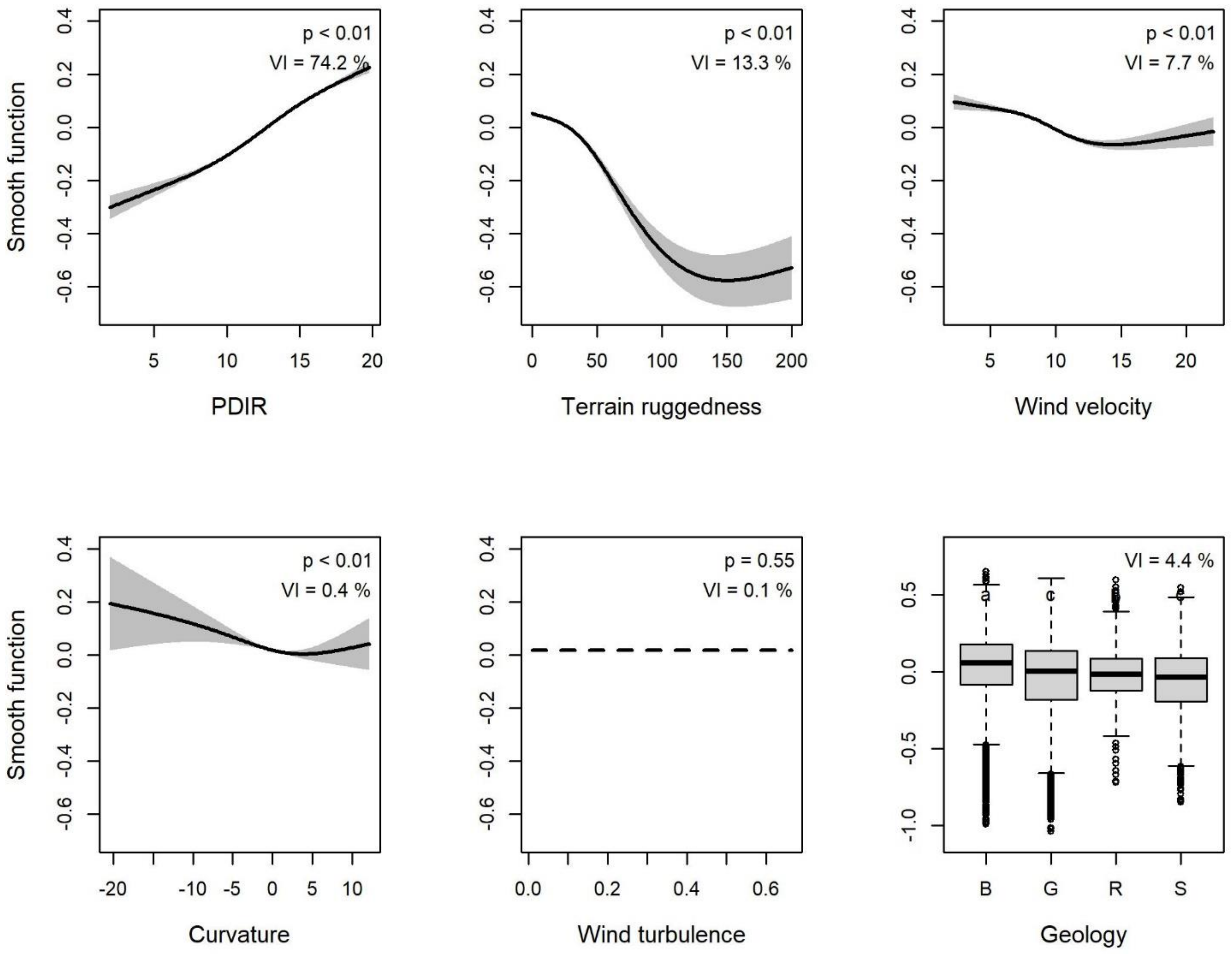

**Figure A2** Response curves from the Generalized Additive Model for the five predictor variables explaining vegetation cover after accounting for elevation (i.e. residual Soil Adjusted Vegetation Index, deviance explained = 27 %). Significant relationships are indicated with a solid line, while dashed lines represent non-significant relationships. PDIR = potential direct incident radiation. B=black lava (i.e. post-glacial lava flows), G=grey lava (i.e. pre-glacial flows), R=recent (i.e. post-1980 lava flows), S=scoria. Significance and percentage variable importance values (VI) are indicated on each plot.

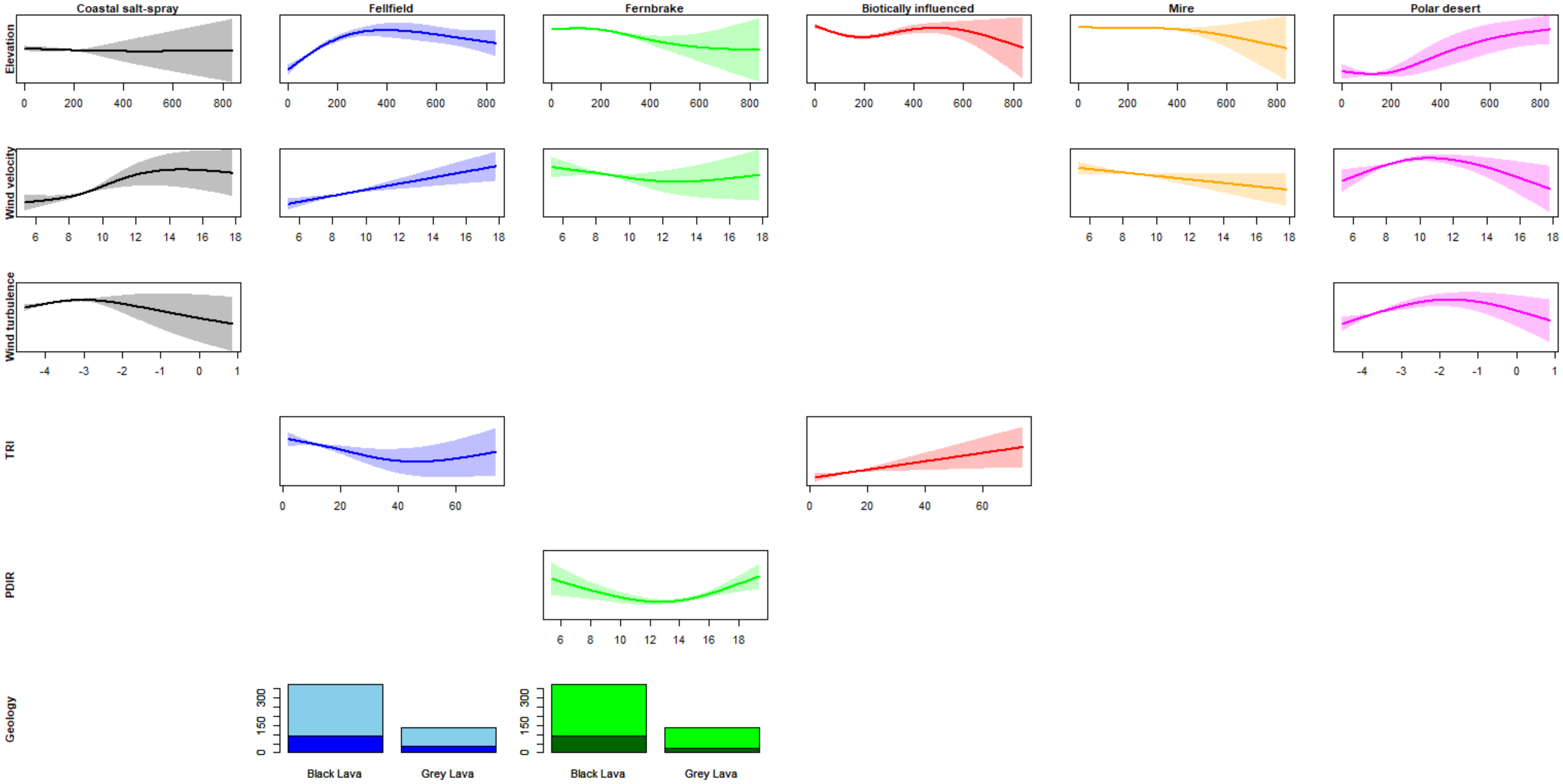

**Figure A3** Response curves and 95% confidence intervals for all significant relationships between vegetation type (columns) and the five continuous predictor variables (rows). Values on the x-axis represent the range for each predictor, while values on the y-axis represent the smooth function from the Generalized Additive Model. TRI = terrain ruggedness index; PDIR = potential direct incident radiation. Bar plots showing the presence of a vegetation type on black lava (B) and grey lava (G) in a darker shade and the absence of the vegetation type in a lighter shade. Fellfield: 25% occurrence on black lava, 27% occurrence on grey lava. Fernbrake: 25% occurrence on black lava, 17% occurrence on grey lava.

**Table A2** Variable importance values (%) for all predictor variables related to each vegetation type's distribution. n = number of quadrats in which the vegetation type occurred. TRI = terrain ruggedness index, PDIR = potential direct incident radiation.

| Vegetation type | n | Deviance explained (%) | Elevation | TRI | Curvature | Geology | PDIR | Wind velocity | Wind turbulence |
|---|---|---|---|---|---|---|---|---|---|
| Coastal salt-spray | 11 | 64.6 | 38 | 4 | 4 | 8 | 2 | 26 | 20 |
| Fellfield | 131 | 25.7 | 77 | 4 | 1 | 6 | 3 | 8 | 1 |
| Fernbrake | 115 | 11.8 | 44 | 7 | 6 | 15 | 12 | 13 | 2 |
| Biotically influenced | 22 | 32.9 | 35 | 23 | 2 | 1 | 9 | 19 | 12 |
| Mire | 211 | 7.2 | 31 | 13 | 5 | 2 | 3 | 36 | 11 |
| Polar desert | 18 | 47.7 | 47 | 0 | 1 | 1 | 0 | 23 | 28 |

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# Chapter 3:

# Exposing wind stress as a driver of fine-scale variation in plant communities

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**Authors' contributions:** PCLR, ML and MM conceived the ideas and designed methodology; MM, PCLR and DWH collected and processed the data; MM and PCLR analysed the data, with inputs from DWH and ML; MM led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

## Abstract

1. The effects of temperature and precipitation, and the impacts of changes in these climatic conditions, on plant communities have been investigated extensively. The roles of other climatic factors are, however, comparatively poorly understood, despite potentially also strongly structuring community patterns. Wind, for example, is seldom considered when forecasting species responses to climate change, despite having direct physiological and mechanical impacts on plants. It is, therefore, important to understand the magnitude of potential impacts of changing wind conditions on plant communities, particularly given that wind patterns are shifting globally.

2. Here, we examine the relationship between wind stress (i.e. a combination of wind exposure and wind speed) and species richness, vegetation cover and community composition using fine-scale, field-collected data from 1440 quadrats in a windy sub-Antarctic environment.

3. Wind stress was consistently a strong predictor of all three community characteristics, even after accounting for other potentially ecophysiologically important variables, including pH, potential direct incident solar radiation, winter and summer soil temperature, soil moisture, soil depth, and rock cover. Plant species richness peaked at intermediate wind stress, and vegetation cover was highest in plots with the greatest wind stress. Community composition was also related to wind stress, and, after the influence of soil moisture and pH, had a similar strength of effect as winter soil temperature.

4. Synthesis: Wind conditions are, therefore, clearly related to plant community characteristics in this ecosystem that experiences chronic winds. Based on these findings, wind conditions require greater attention when examining environment-community relationships, and changing wind patterns should be explicitly considered in climate change impact predictions.

## Introduction

Recent changes in climate have impacted all aspects of ecological communities, including species richness, total abundance, biomass, cover and species composition (e.g. Menéndez et al., 2006; Kardol et al., 2010; Liu et al., 2018). Given the implications of these community-level changes for conservation, ecosystem services and human health, predicting how further changes in climate will affect communities is a key challenge in ecology (Kolstad and Johansson, 2011; Pecl et al., 2017). While some trends, like species range shifts, have been observed fairly consistently (e.g. Morueta-Holme et al., 2015; Freeman et al., 2018), exceptions have also been noted (e.g. Lenoir et al., 2010; Zhang et al., 2019), suggesting that some key factors or processes still need to be accounted for. Indeed, many studies forecasting ecological responses to climate change consider only temperature and precipitation as climatic variables, and do not account for other components of climate. For example, the ten climatic variables most commonly used in plant species distribution modelling studies all just quantify aspects of temperature and precipitation (Gardner et al., 2019).

Other climatic factors may, however, also be influential in determining individual species distributions and, as a result, community characteristics (Barton, 2017; Cherry and Barton, 2017; Maclean, 2020). Therefore, to improve the quality of the predictions of the ecological impacts of climate change, it is important to consider a more comprehensive set of climatic variables that directly affect plant performance (Gardner et al., 2019). Indeed, other variables, such as snow cover duration and solar radiation, can have profound effects both on individual species and on communities (see Bennie et al., 2008; Austin and Van Niel, 2011; Niittynen and Luoto, 2018). For example, decreasing snow cover duration in the Arctic has a larger effect on species' probability of becoming locally extinct than rising temperatures alone (Niittynen et al., 2018). Thus, a more thorough understanding of the impacts of climatic factors, extending beyond conventional measures of temperature and precipitation, is required in order to more accurately predict how communities may be affected by changing climates (Mod et al., 2016).

Wind is a climatic variable that is currently underexplored as a driver of community patterns (see Table 1), despite representing an important stress and disturbance for many different taxa (Watanabe and Hasumi, 2005; Bintanja et al., 2014; Combes and Matano, 2018). It is relatively well understood how extreme winds (e.g. hurricanes and tornadoes) affect individuals, species, and communities (Mitchell, 2012; Møller, 2013; Behie et al., 2014; Xuan and Chang, 2014). However, these extreme conditions are limited in time and space (Nyberg et al., 2007; Lugo, 2008), and the impacts of chronic (i.e. continuous) wind conditions may be important but have received little focused attention. Exposure to wind has clear physiological impacts on plants, whereby, for example, plants typically close their stomata during windy conditions to reduce the rate of transpiration, consequently leading to lower rates of photosynthesis (Grace, 1977; de Langre, 2008). In addition, winds may desiccate the soil, creating a moisture stress for plants (Bertiller et al., 1996; Fitzgerald and Kirkpatrick, 2017), and redistribute litter which has an effect on soil temperature and nutrient content (Fahnestock et al., 2000). Wind may also have a range of mechanical impacts on plants, with, for example, strong winds potentially tearing leaves, causing abrasion and desiccation (Hadley and Smith, 1983; Hadley and Smith, 1986; de Langre, 2008; Gardiner et al., 2016), uprooting individuals (Yang et al., 2014), and causing flowers and fruits to be shed (e.g. Lahav and Zamet, 1999). As a result, lower wind speeds are typically associated with faster plant growth rates and higher productivity (e.g. Bang et al., 2010), although physiological responses to wind conditions may be species-specific (Onoda and Anten, 2011). Further, wind can shape the outcome of plant-plant interactions (severity-interaction-relationships; le Roux and McGeoch, 2010). Therefore, wind has the potential to directly affect vegetation patterns, from altering individual species' dominance (Okitsu and Ito, 1984) to impacting the distribution of different plant communities (Williams and Ashton, 1987; Lynch and Kirkpatrick, 1995; see Table 1 for an illustrative summary of what is currently known about the impacts of wind on vegetation). Consequently, differences in chronic wind conditions between sites and/or years has considerable potential to drive spatio-temporal variations in plant communities.

Wind stresses and disturbances may vary greatly over short distances (Katsaprakakis and Christakis, 2012; Chiras, 2017), and could therefore potentially contribute to fine-scale variation in ecological communities. For example, wind velocity can vary around individual plants (Combrinck et al., 2020) and models that do not account for fine-scale variation in wind patterns do not accurately predict seed dispersal (Lönnell et al., 2015). Variability in wind speed has also, for instance, been related to fine-scale differences in plant height, species richness, growth form diversity, and community type (Whitehead, 1954; Whitehead, 1959; Wilson, 1959). Nevertheless, wind is seldom considered as a driver of fine-scale variation in community patterns (see review by Gardner et al., 2019), and despite technological advances that have improved measurement and modelling of wind conditions, little work has recently examined the influence of wind on plant communities (although, see, e.g. Fitzgerald and Kirkpatrick, 2017; Sun et al., 2019; Sparacino et al., 2020; and Table 1). In addition, the reciprocal effect of vegetation on wind patterns, has also attracted limited attention (although see, e.g., Combrinck et al., 2020).

Based on our current understanding of the ecological impacts of wind, variation in prevailing wind conditions at fine spatial scales is likely to affect multiple measures of plant community structure. As wind exposure increases, vegetation cover generally declines due to wind pruning and slower growth rates (Bang et al., 2010; Gardiner et al., 2016), as evident, for example, on New Zealand’s off-shore islands (McGlone, 2002). Species richness may also decline in increasingly windy microclimates, especially in species-poor environments. However, in more species-rich communities, species may instead show a pattern of replacement along a wind stress gradient due to inter-specific differences in wind tolerance (i.e. more wind-tolerant species replace taller and/or more competitive species that are less tolerant of wind stress; e.g. Burke et al., 1989; Fernández-Palacios and Nicolás, 1995). Under such a scenario species richness would be predicted to remain relatively constant while species composition shifts in response to greater wind stress (i.e. a type of Gleasonian distribution; Gleason, 1939).

The paucity of studies investigating the effects of wind on vegetation was already noted six decades ago (Wilson, 1959; see also Whitehead, 1954; Whitehead, 1959), but this issue has yet to be explicitly and thoroughly addressed (see e.g. Sutherland et al., 2017). Furthermore, understanding how wind, and changes in wind patterns, affects biodiversity is increasingly relevant as, over the last decade, mean wind speeds have accelerated globally, with the largest changes happening in the Southern Ocean (Young and Ribal, 2019; Zeng et al., 2019), and current predictions suggesting that this trend will continue in the long-term (Jeong and Sushama, 2019; Zeng et al., 2019). Therefore, in this study, the impact of wind on fine-scale vegetation characteristics was assessed by examining the relationship between wind stress (i.e. a combination of wind exposure and wind speed) and 1) vascular plant species richness, 2) species cover, and 3) species composition in a wind exposed environment, after accounting for other potentially ecophysiologically important variables (Mod et al., 2016).

**Table 1** A summary of key papers highlighting the types of research questions that have been examined, and illustrating broadly the currently knowledge in this field.

| | **Study location** | **Ecosystem** | **Spatial scale** | **Result** | **Reference** |
|---|---|---|---|---|---|
| **Richness** | Mongolia, China | Semi-arid temperate steppe | 4 x 4 m plots | Wind erosion did not affect species richness, while dust deposition (due to wind erosion) reduced species richness. | Zheng et al. (2020) |
| **Vegetation cover** | Hill One, Southern range, Tasmania | Alpine | 1.5 x 1.0 m plots | Vegetation cover decreased over 11 years, mostly due to erosion, caused by an increase in wind speed. | Kirkpatrick et al. (2002) |
| | Sonoran Desert, Arizona, USA | Desert, desert remnants and urban sites | 20 individually potted plants at each site | Reduced wind speed increased cover of individuals in desert and desert remnants. In urban sites reduced wind speed had no effect on cover. | Bang et al. (2010) |
| | Mongolia, China | Semi-arid temperate steppe | 4 x 4 m plots | Wind erosion decreased total plant cover. Dust deposition by wind resulted in higher vegetation cover. | Zheng et al. (2020) |
| **Composition** | Swiss Alps | Alpine | 1 x 1 m plots | Wind speed was an important driver of species composition; $R^2 > 0.35$. | Vonlanthen et al. (2006a) |
| **Distribution of vegetation types** | North America, the Alps, European subarctic | Alpine | Review | Wind determines the treeline position in three different ecosystems and can override the role of heat deficiency. | Holtmeier and Broll (2010) |
| | Swedish Scandes | Alpine | 10 x 10 m plots | Wind determines the birch treeline and increasing wind circulation constrains upslope treeline expansion in response to warming temperatures. | Kullman and Loyer (2005) |
| | 5 mountain regions | Alpine | 50 $m^2$ plots | Wind exposure was the main determinant of the number of seedlings present at the treeline, with increased | McIntire et al. (2016) |

| | | | | | |
|---|---|---|---|---|---|
| | from 3 continents | | | wind exposure correlated with fewer tree seedlings. | |
| | Central Argentina | Forest patches | 396 individual saplings | Reduced wind speeds likely restrict the occurrence of forest to ravines. | Sparacino et al. (2020) |
| **Review** | Multiple locations | Boreal & temperate forest | | A review of the impact of disturbance agents on natural vegetation showed 146 studies of wind as a disturbance agent versus 677 for fire. More than 87% of these studies are from Europe or North America. There was no difference between the effects of wind, fire and bark beetles on biodiversity. | Thom and Seidl (2016) |

## Methods

### *Study site*

This study was conducted on the isolated sub-Antarctic Marion Island (46°54′ S, 37°45′ E). The sub-Antarctic provides an ideal study system to examine the ecological consequences of chronic winds as the region experiences consistently strong daily wind conditions (Pendlebury and Barnes-Keoghan, 2007; le Roux, 2008). Terrestrial habitats of Marion Island exhibit broad gradients of wind stress due to their complex topography, with sites ranging from sheltered to exposed often separated by only short distances. Marion Island lies approximately halfway between Africa and Antarctica, covers an area of 293 km2, and rises to 1240 m a.s.l. (Boelhouwers et al., 2008). The island is situated in the “roaring forties”, the region between 40 and 50°S, that experiences strong and relatively consistent westerly winds (Pendlebury and Barnes-Keoghan, 2007; le Roux, 2008) which can affect pedogenesis, vegetation growth, soil frost formation and aeolian transport of particles (Hedding et al., 2015). Gale force winds blow on >100 days per annum on Marion Island (with relatively consistent directionality; le Roux, 2008). The island has a hyper-oceanic climate (characterized by cool temperatures with little diurnal and seasonal variation) and high humidity, with near complete cloud cover and precipitation on most days (le Roux, 2008). Precipitation can occur in the form of rain, snow, hail, and mist, with rain being the dominant form of precipitation (le Roux, 2008). The mean daily maximum and minimum temperatures are 8.7 °C and 3.2 °C respectively, and the mean annual precipitation is c. 1800 mm (recorded at the island's meteorological station which is ~1 km away from the study site; average from 2008 - 2018).

### *Data collection*

Data were collected from early 2016 to early 2017 on the eastern side of Marion Island, with sampling focused in a topographically-, geologically- and biotically-heterogenous area (comprising a smooth pre-glacial lava flow north of the Van den Boogaard river and a rugged post-glacial lava flow south of the river; Fig. 1). A survey approach was used that has previously been applied in other high-altitude and high-latitude systems (e.g. le Roux et al., 2013b; Kemppinen et al., 2019; Niittynen et al., 2020a), where vegetation composition and abiotic conditions are measured across steep environmental gradients within a single landscape unit (avoiding differences in macroclimate and regional species pools). Nine grids of 8 x 20 m were sampled, each comprising 160 contiguous quadrats of 1 m2 (resulting in 1440 quadrats sampled in total; Figure 1, Table 2). These grids encompassed fellfield, mire vegetation, and fern-dominated slopes, and contained 18 vascular plant species. Grids were located to sample the full range of conditions within the site, covering the range of vegetation types, vegetation cover and topography present. The distance between grids was 70 - 915 m, with the grids covering an altitudinal range of c. 40 to 100 m a.s.l. Individual grids, in turn, were orientated to encompass as much local environmental variability as possible.

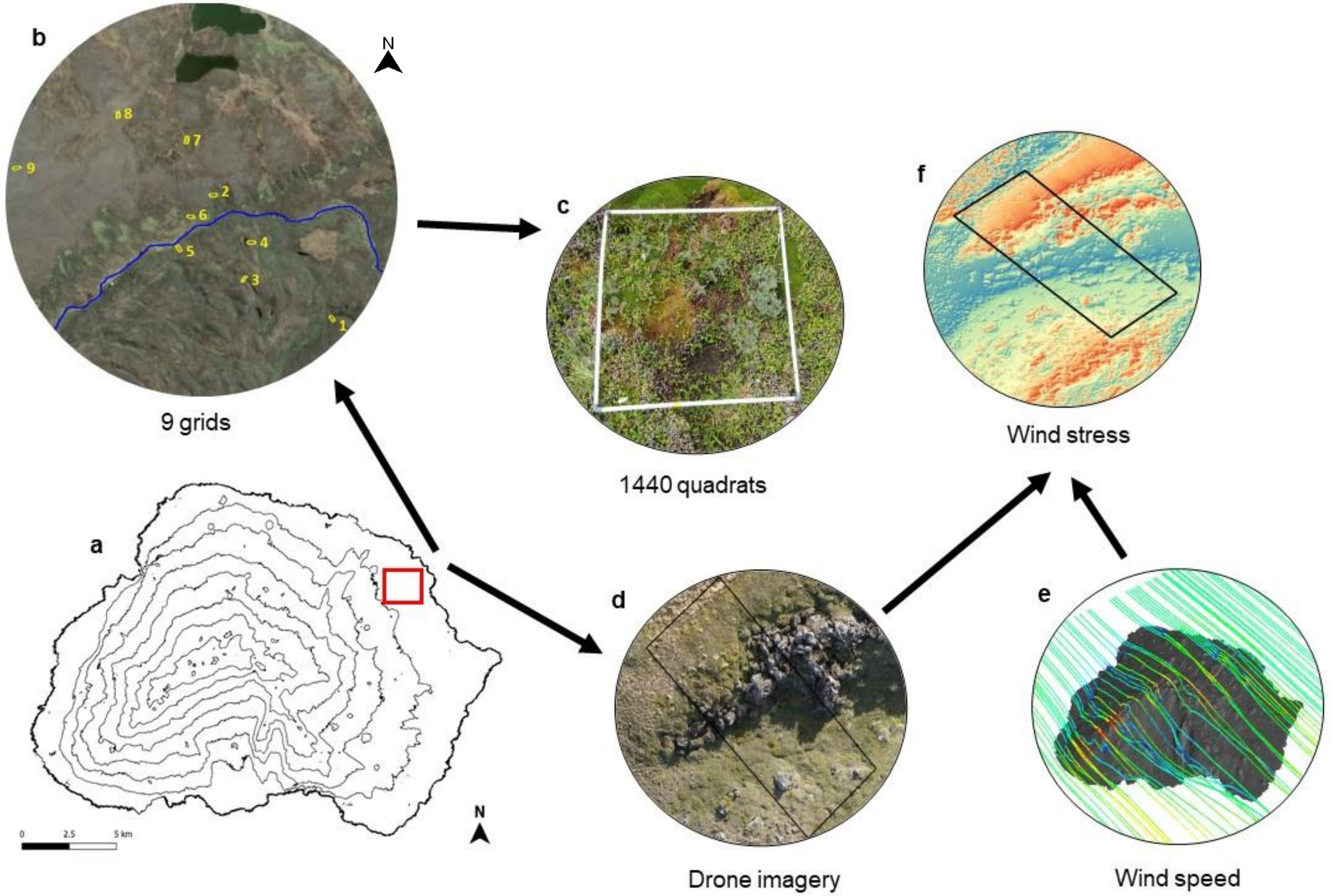

**Figure 1** Study site location on Marion Island and study design. a: Marion Island, with contour intervals of 150 m and study location indicated by the red block; b: the location of all 9 study grids (each 8 x 20 m; the distance from grid 1 to grid 9 is ~900 m; Google Earth imagery), with the Van den Boogaard river indicated in blue; c: biotic and abiotic data were sampled from 160 quadrats within each grid, resulting in a total of 1440 quadrats (each 1 x 1 m in size; indicated here with the white frame); d: drone imagery was obtained for each grid, from which a digital surface model was created and used to calculate the wind exposure of each quadrat; e: wind speed for each grid was obtained from a computational fluid dynamics model of island-scale wind speed; f: wind exposure (calculated from drone imagery products) and wind speed were combined to create a wind stress metric for each quadrat.

Within each of the 1 m2 quadrats several abiotic and biotic variables were measured. The cover and identity of all vascular plant species in each quadrat were recorded and then used to determine the species richness and composition for each quadrat. Percentage plant cover, rock cover (i.e. the cover of rocks or boulders large enough to inhibit plant growth) and bare soil cover were visually estimated. Soil depth was measured using a thin metal rod (diameter of 8 mm) at three points randomly located in each quadrat, and an average soil depth then calculated for the quadrat (where soil depth exceeded 60 cm, a value of 70 cm was assigned). The slope and aspect of each quadrat were recorded and these values were then used to calculate potential annual direct incident radiation (PDIR; McCune and Keon, 2002; McCune, 2007). Soil samples were taken from 16 - 32 quadrats per grid and used to determine soil pH in the laboratory using the CaCl2 method (Hendershot et al., 2008). Soil pH was then interpolated to the unsampled quadrats using bilinear interpolation (Bovik, 2009).

Instantaneous soil temperature and soil moisture measurements were taken in each quadrat in June, July and October 2016 and January and April 2017. These readings were only taken on days when there had been at least 24 hours since the last rainfall event. Volumetric soil moisture content was measured using a handheld time-domain soil moisture meter (using 7.5 cm probes; FieldScout TDR 300; Spectrum Technologies), and soil temperature was measured using a corkscrew thermometer (EXTECH Instruments, TM40) at a depth of 5 cm. To test whether the order in which measurements were taken had an effect on soil moisture or temperature readings (i.e. testing for an effect of time of the day), the grid which was measured first was revisited at the end of the measurement period and partly remeasured (20 quadrats). The average difference in instantaneous soil moisture readings between the initial and final measurements in resampled quadrats was 0.8%, and, therefore, the raw data for soil moisture readings were used in analyses. Soil temperature, however, showed a significant difference (t-test: $p<0.001$) between the temperature measured at the start of the measurement time period versus the end of the measurement period for the quadrats which were remeasured. Therefore, to account for the effect of the measurement time on soil temperature, readings were corrected using a linear adjustment. This correction was based on soil temperature data logged in 3 – 9 cells per grid using temperature loggers (Thermochron iButton DS1921G; Maxim

Integrated), with data from the specific day on which instantaneous measurements were made being used (following le Roux et al., 2013a).

Soil temperatures in the winter months were positively correlated (June and July), while there was minimal correlation between winter and summer temperatures (Figure A1). Therefore, one measurement of summer soil temperature (January; mid-summer) and one measurement of winter soil temperature (June; mid-winter) were used in all subsequent analyses. Soil moisture was significantly positively correlated across all months (Figure A2), and, therefore, moisture data from only one month (October) were included in further analyses.

Wind speed and direction were measured at 17 locations across Marion Island using two sonic anemometers (Gill Windsonic: Gill Instruments, UK), mounted at 0.5 m and 1 m above ground at each of the locations. The anemometers measured wind speed and direction in the horizontal plane (two-dimensional) at a 0.01 m.s-1 resolution, with measurement accuracy of 2% (at 12 m.s-1). Wind speed and direction were sampled at 0.5 Hz, with mean direction and speed logged every 10 minutes using a CR300 datalogger (Campbell Scientific, USA). Both the anemometers and the logger were powered using a 12 V DC battery continuously charged using a 25 W solar panel. Wind direction data for the study site showed one clear and dominant wind direction, and, therefore, only the dominant wind direction was extracted from the wind station located closest to the study site (< 700 m from the furthest grid) over a 12-month period (April 2018 - March 2019). Wind at the study site predominantly comes from a north-westerly direction (68 % of readings were from 260-330° from N), with the strongest wind speeds being even more limited to the north-westerly sector (88 % of all wind speeds greater than 11 m.s-1 were recorded between 260-330°; Figure 1; in agreement with long-term data from the island's weather station; le Roux, 2008).

Photographic images of each grid were taken using an unmanned aerial vehicle (UAV; DJI Phantom 4 Pro fitted with a 20-megapixel camera) at a ground sample distance of 0.7 cm during April 2019. The aerial images from the UAV were processed in Agisoft Photoscan using the principle of structure-from-motion to produce a point dense cloud which in turn was used to generate a Digital Surface Model (DSM) at 2 cm resolution, which captures the elevation of the surface. From the DSM's, a within-grid wind exposure metric was calculated for each 1 m2 quadrat using the Wind Effect module in SAGA-GIS (Conrad et al., 2015), specifying the wind direction as North-West (with the majority of the wind coming from 292 - 338°; based on the data from the wind station at the site). The minimum, maximum, and mean of the wind effect values were extracted for each quadrat. Wind effect is a dimensionless index, where values below 1 indicate areas that are sheltered from wind and values above 1 indicate areas that are exposed to wind in terms of the specified wind direction (Böhner and Antonić, 2009). To account for differences in coarser-scale wind stress between grids (since some grids were more wind-exposed than others; Fig. 1), the mean simulated wind speed for each grid was extracted from a computational fluid dynamics (CFD) model of Marion Island (maximum 50 m resolution) using ANSYS Fluent 2019R3 (Ansys, USA). The CFD model uses a full-scale digital elevation model of Marion Island (DRDLR, 2019) and simulates air flow over the topology by iteratively solving a set of partial differential equations (the Reynolds-Averaged Navier Stokes Equations; see Versteeg and Malalasekera, 2007 for a detailed consideration of CFD; and Cindori et al., 2018 for a recent implementation). A westerly wind was assumed as the free-stream condition with a reference speed of 5 m.s-1 at 1.5 m above ground, based on measured data from the wind stations. The model includes considerations for the atmospheric boundary layer and the effect of the Coriolis force (Breedt et al., 2018). This estimate of grid-level wind speed was multiplied by quadrat-level wind index indices (for minimum, maximum, mean, and range wind stress) to estimate wind stress values that are comparable across and within grids (i.e. accounting for grids differing considerably in landscape-level wind stress). The wind stress metric provides relative values, enabling comparisons between sites within this particular study system, where higher values indicate higher wind stress. Here wind stress represents the combined influence of wind exposure to the dominant wind direction and the simulated mean wind speed at each grid when the wind is blowing from the dominant wind direction. These values, therefore, provide an estimate of the mean physical and mechanical strain that plants experience (i.e. representing chronic wind stress). The resulting wind stress metrics were highly correlated (r > |0.8|; Figure A3), and, therefore, only maximum wind stress was used in subsequent analyses.

### *Statistical analyses*

None of the predictor variables in the final dataset were strongly or significantly correlated with each other (r < |0.8| and Variance Inflation Factor < 3.1; Figure A4).

The relationship between species richness (and cover) and predictor variables was analysed using three different statistical methods to reduce uncertainties due to modelling approach: generalized linear models (GLZ; Müller, 2012), generalized additive models (GAM; Wood and Augustin, 2002), and generalized boosted regression models (GBM; Friedman et al., 2000; Friedman, 2001). These three methods were chosen due to their differing flexibility and complexity. All of the statistical methods were run assuming a Poisson (for species richness) or quasibinomial (for vegetation cover; which was significantly over-dispersed) distribution.

For all three statistical methods, a first model was run with PDIR, soil depth, rock cover, winter temperature, summer temperature, moisture, and pH as predictor variables (hereafter referred to as the “simple model”). A second model was then run with all of the above variables, as well as the maximum wind stress (hereafter referred to as the “full model”). The GLZs included quadratic terms for all predictor variables to allow for non-linear relationships. For GAMs, the initial degree of smoothness for each predictor was set to four. The tree complexity was set to 6 for GBMs and the tree threshold to 1000. To determine whether the addition of wind stress improved the performance of the models, each pair of simple and full models from GAMs and GLZs were compared using a likelihood ratio test (for species richness) and an F-test (for vegetation cover). Similar model comparisons are not possible for GBMs, but response curves and variable importance could be compared between GBMs and the other two methods. Variable importance for GAMs and GLZs was calculated by comparing the Pearson correlation between predictions made on the original data and predictions made on the data where the predictor variable of interest has been randomly shuffled (following Niittynen and Luoto, 2018). The calculations of variable importance were calculated 10 times and the mean importance value reported.

**Table 2** Vegetation and abiotic characteristics of each grid. Soil temperatures for summer (measured in January) and winter (measured in June) are reported. Minimum and maximum temperatures reflect the extreme values in in grid, while the mean temperature was calculated across all 160 quadrats within each grid. See Fig. 1 for the location of the sampling grids. VWC: volumetric water content.

| **Grid** | **Vascular plant cover (mean; %)** | **Total vascular plant richness** | **Summer temperature (°C)** | | | **Winter temperature (°C)** | | | **Soil moisture range (% VWC)** | **Wind stress** | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | **Minimum** | **Mean** | **Maximum** | **Minimum** | **Mean** | **Maximum** | | **Mean maximum** | **Absolute maximum** |
| 1 | 72 | 9 | 2.92 | 6.28 | 8.12 | 1.62 | 4.02 | 5.92 | 76.2 | 5.50 | 6.06 |
| 2 | 65 | 15 | 2.91 | 6.35 | 7.71 | 2.66 | 4.70 | 6.46 | 41.2 | 6.52 | 7.02 |
| 3 | 65 | 12 | 5.56 | 7.70 | 12.86 | 2.61 | 4.83 | 6.21 | 69.2 | 7.62 | 8.22 |
| 4 | 55 | 12 | 2.72 | 5.77 | 11.22 | 2.19 | 4.10 | 5.49 | 68.6 | 8.22 | 8.53 |
| 5 | 48 | 10 | 4.42 | 5.50 | 6.62 | 3.58 | 5.34 | 6.28 | 48.7 | 6.22 | 6.46 |
| 6 | 67 | 9 | 4.24 | 6.12 | 10.54 | 2.48 | 4.81 | 6.48 | 38.7 | 6.10 | 6.60 |
| 7 | 64 | 9 | 4.60 | 6.66 | 8.10 | 4.13 | 5.73 | 7.63 | 48.1 | 6.18 | 6.46 |
| 8 | 25 | 11 | 3.83 | 5.02 | 6.33 | 0.00 | 1.06 | 2.45 | 27.6 | 7.18 | 7.64 |
| 9 | 19 | 10 | 4.72 | 5.97 | 7.22 | 0.36 | 1.70 | 3.26 | 53.4 | 7.48 | 7.60 |

Species composition was modelled using non-metric multidimensional scaling (nMDS) and permutational multivariate analysis of variance (PERMANOVA) based on species occurrence. Two dimensions, 200 random starts and the standard transformation (Wisconsin double standardization) were used in nMDS analyses. Nestedness analyses were also conducted on the species composition data to determine whether species were nested along the wind stress gradient (Ulrich, 2009). The species-site matrix was first ordered by maximum wind stress, and the nestedness metric based on Overlap and Decreasing Fill (NODF) was calculated. NODF is less prone to type I statistical errors and is insensitive to matrix size and shape, and, therefore, provides a more conservative approach than other nestedness metrics (Almeida-Neto et al., 2008). Finally, the nestedness analysis was complemented by calculating the overall beta diversity between quadrats using the Sørensen dissimilarity index, with the contribution of species turnover (measured as Simpson dissimilarity) and nestedness (measured as the nestedness-resultant fraction of the Sørensen dissimilarity index) being partitioned to explain the observed differences in community composition (Baselga and Orme, 2012).

All analyses were run in R statistical software, version 3.5.0 (R Core Team, 2018), using additional functions from the vegan (Oksanen et al., 2018), mgcv (Wood, 2006), spind (Carl et al., 2018), and betapart (Baselga et al., 2018) libraries.

## Results

Wind stress ranged from 4.5 to 8.5, with grid one experiencing the overall lowest wind stress, and grid four the highest wind stress (Figure 2). Species richness varied between zero and eight species per 1 m² quadrat, and between 9 and 15 species per grid (Figure 3), while vascular plant cover varied between a minimum of zero and a maximum of 100 % (Figure A5).

The full model, including wind stress, performed significantly better than the simple model for species richness in the GAM, and marginally significantly so in the GLZ. For vegetation cover the full model performed significantly better in both statistical approaches (GLZ and GAM; likelihood ratio test and F-test, $p < 0.05$; Table A1). The full model for species richness improved the deviance explained by 0.8 % for the GLZ and by 3.5 % for the GAM relative to the simple models that did not include a measure of wind stress. For vegetation cover, the full model improved the deviance explained by 1.4 % for the GLZ and by 1.4 % for the GAM (Table A1).

Both GLZ and GAM models for species richness contained maximum wind stress within the top five predictor variables (i.e. on the basis of variable importance; Table 3; wind stress was the second most important predictor in the GBM model, Table A2). Response curves from the GAM model for species richness showed that species richness has a complex relationship with maximum wind stress, with the highest species richness observed at intermediate maximum wind stress (Figure 4, with raw data shown in Figure A6; similar response curves were observed from the GLZ model, Fig. A8; and for the GBM model, Fig. A10). The addition of wind stress to the model changed the shape of the response curve between species richness and PDIR (from negative to nearly horizontal), winter soil temperature (the slope of the positive response becomes less steep), and summer soil temperature (remains hump-shaped, but high temperatures result in a smaller drop in species richness). Species richness also showed non-linear relationships with both rock cover and pH (which were also consistently in the top five predictors), where species richness peaked at c. 60% rock cover and 4.6 pH (Figure 4).

Vegetation cover was significantly predicted by maximum wind stress, and wind stress was the second most important predictor when modelling vegetation cover for both the GLZ and the GAM (Table 3; and third most important in the GBM model, Table A2). The response curves for vegetation cover showed that maximum wind stress had a valley-shaped relationship with vegetation cover (Figure 5 and Figure A7; see Fig. A9 and A11 for GLZ and GBM response curves which showed similar patterns). Rock cover had a strong negative relationship with vegetation cover, and was the most important predictor in both statistical approaches (Table 3).

**Table 3** Model fit and variable importance for all variables when predicting spatial variation in species richness and vegetation cover in the full model. The five most important predictors for each approach are highlighted in bold and significant predictors are indicated with an asterisk. GAM = generalized additive model; GLZ = generalized linear model. See Table A2 for results from the generalized boosted regression models.

| | **Richness** | | **Cover** | |
|---|---|---|---|---|
| | **GAM** | **GLZ** | **GAM** | **GLZ** |
| Deviance explained (%) | 24.9 | 19.5 | 67.7 | 66.9 |
| | Relative importance (%) | | | |
| Rock cover | **16.7*** | **12.6*** | **94.15*** | **94.63*** |
| Wind stress: maximum | **33.8*** | **6.0** | **3.00*** | **2.88*** |
| Soil pH | **19.4*** | **16.0*** | 0.04 | 0.06 |
| Soil depth | **12.2*** | **13.8** | 0.17 | 0.21 |
| Temperature: summer | 1.5 | 1.7 | **0.90*** | 0.12 |
| Temperature: winter | **13.8*** | **44.5*** | 0.49 | **0.64** |
| PDIR | 0.0 | 1.3 | **0.70*** | **0.52*** |
| Soil moisture | 2.6 | 4.0 | **0.65*** | **0.94*** |

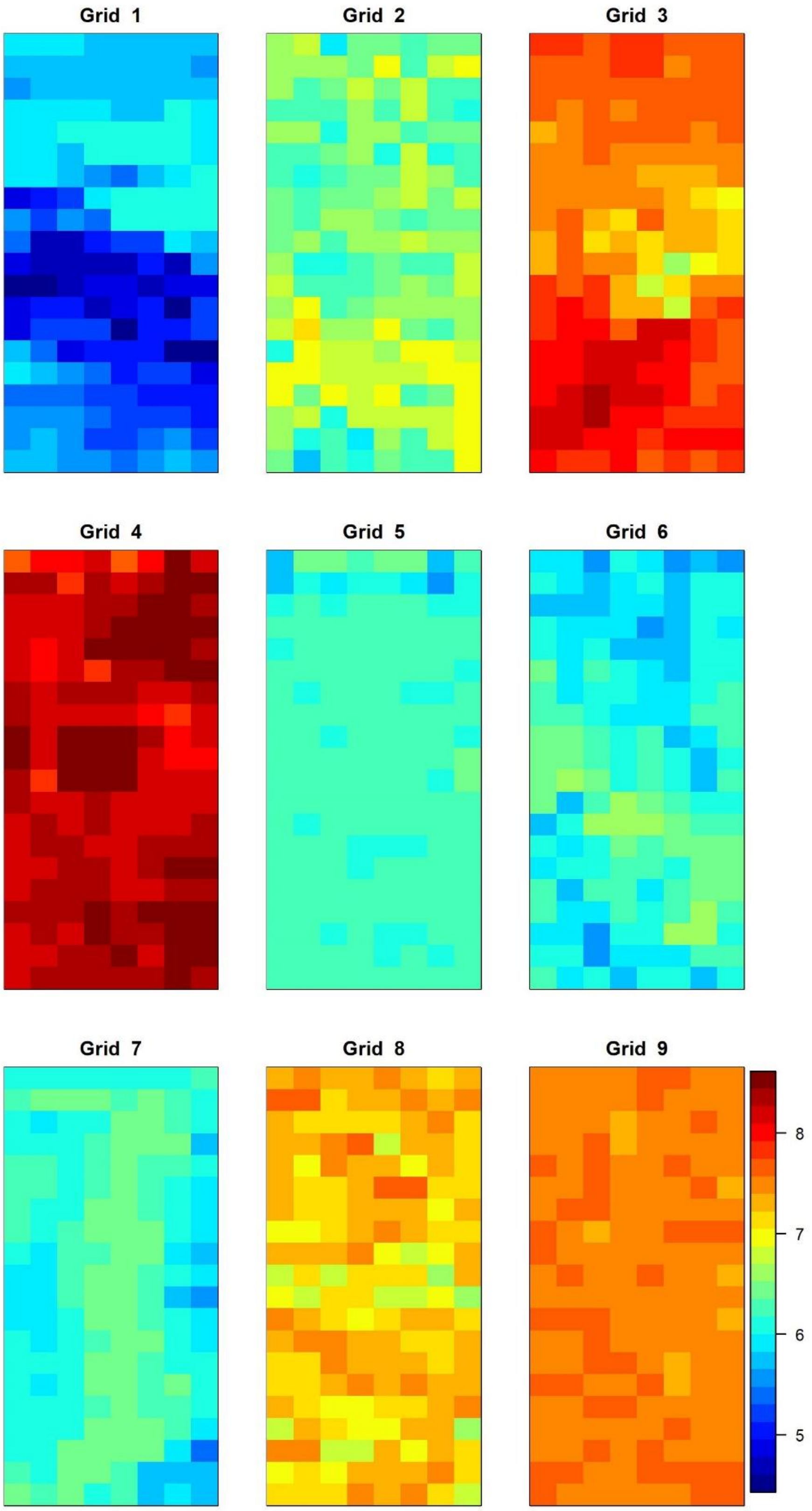

**Figure 2** Variation in maximum wind stress in all nine study grids (see Fig. 1 for location of the grids) indicated for each 1 $m^2$ quadrat. Cooler colours indicate low wind stress and warmer colours indicate higher wind stress.

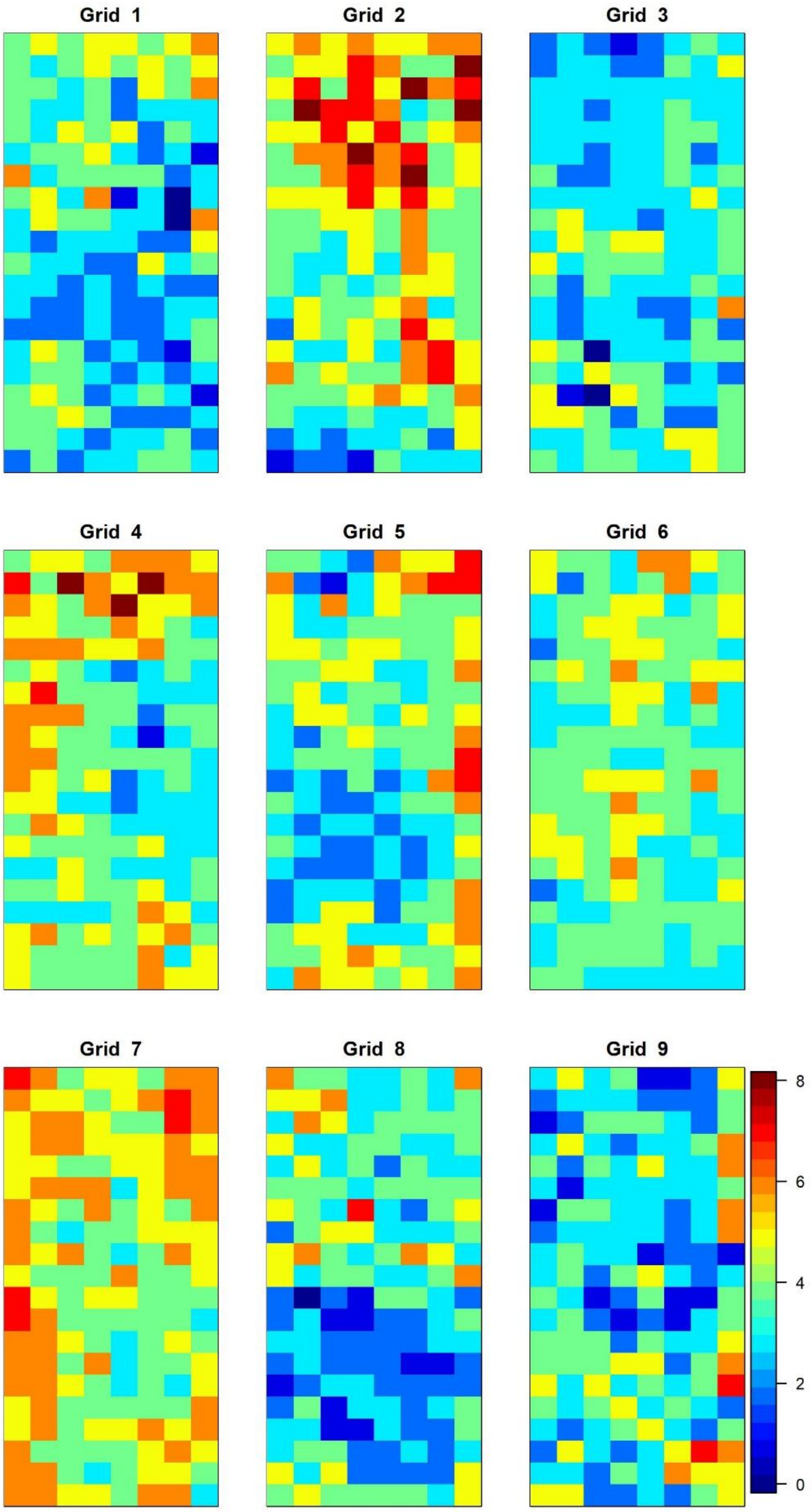

**Figure 3** Species richness across all nine study grids (see Fig. 1 for location of the grids), with vascular plant species richness indicated for each 1 $m^2$ quadrat. Cooler colours indicate low species richness and warmer colours indicate higher richness.

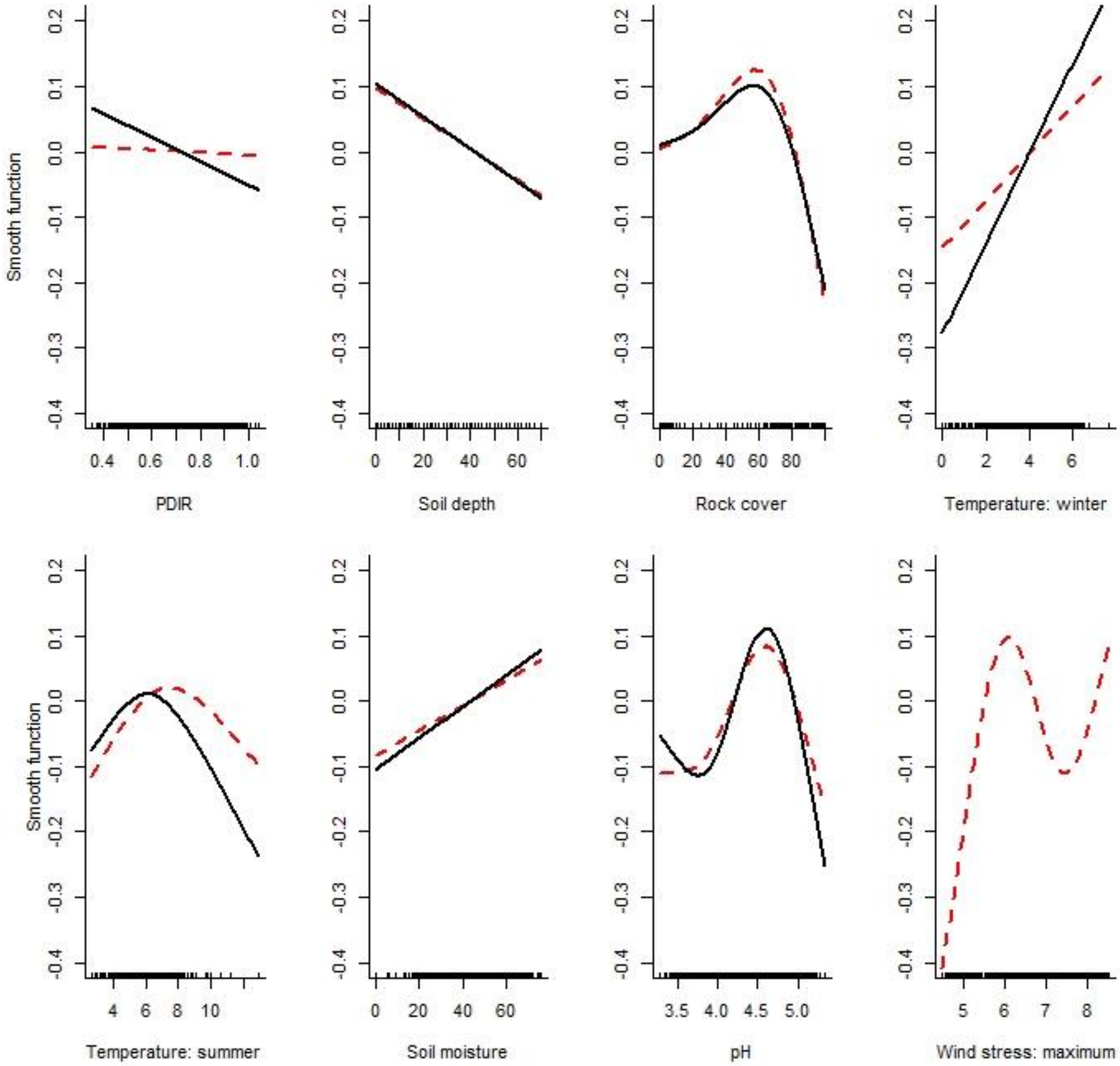

**Figure 4** Individual predictor variables' response curves for species richness in GAM models. Tick marks on the x-axis indicate observed values. Solid black lines represent the response curves from the simple model (excluding wind stress predictor variables), while dashed red lines represent the response curves from the full model.

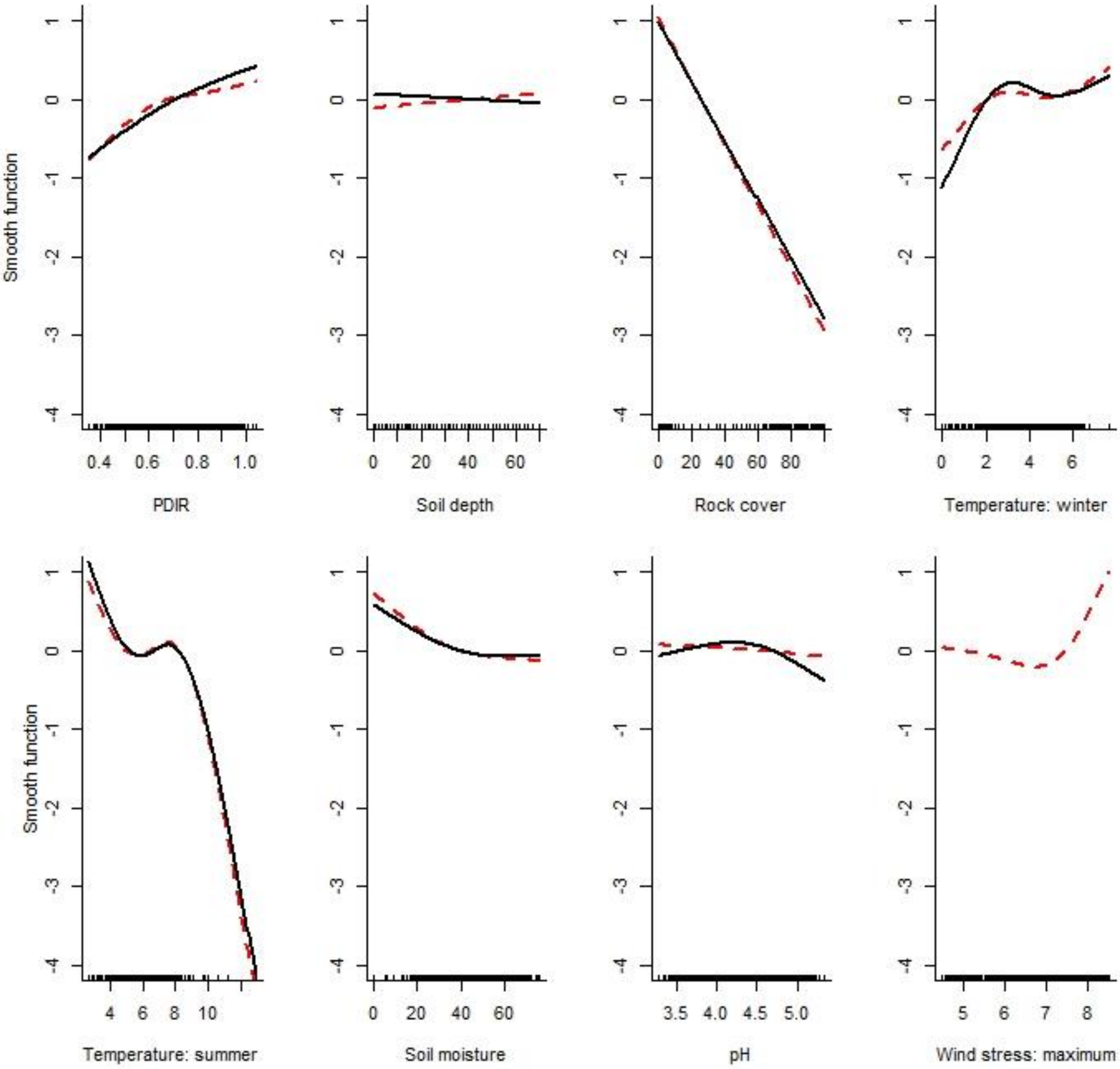

**Figure 5** Individual predictor variables' response curves for vegetation cover in GAM models. Tick marks on the x-axis indicate observed values. Solid black lines represent the response curves in the simple model (excluding wind stress predictor variables), while dashed red lines represent the response curves in the full model.

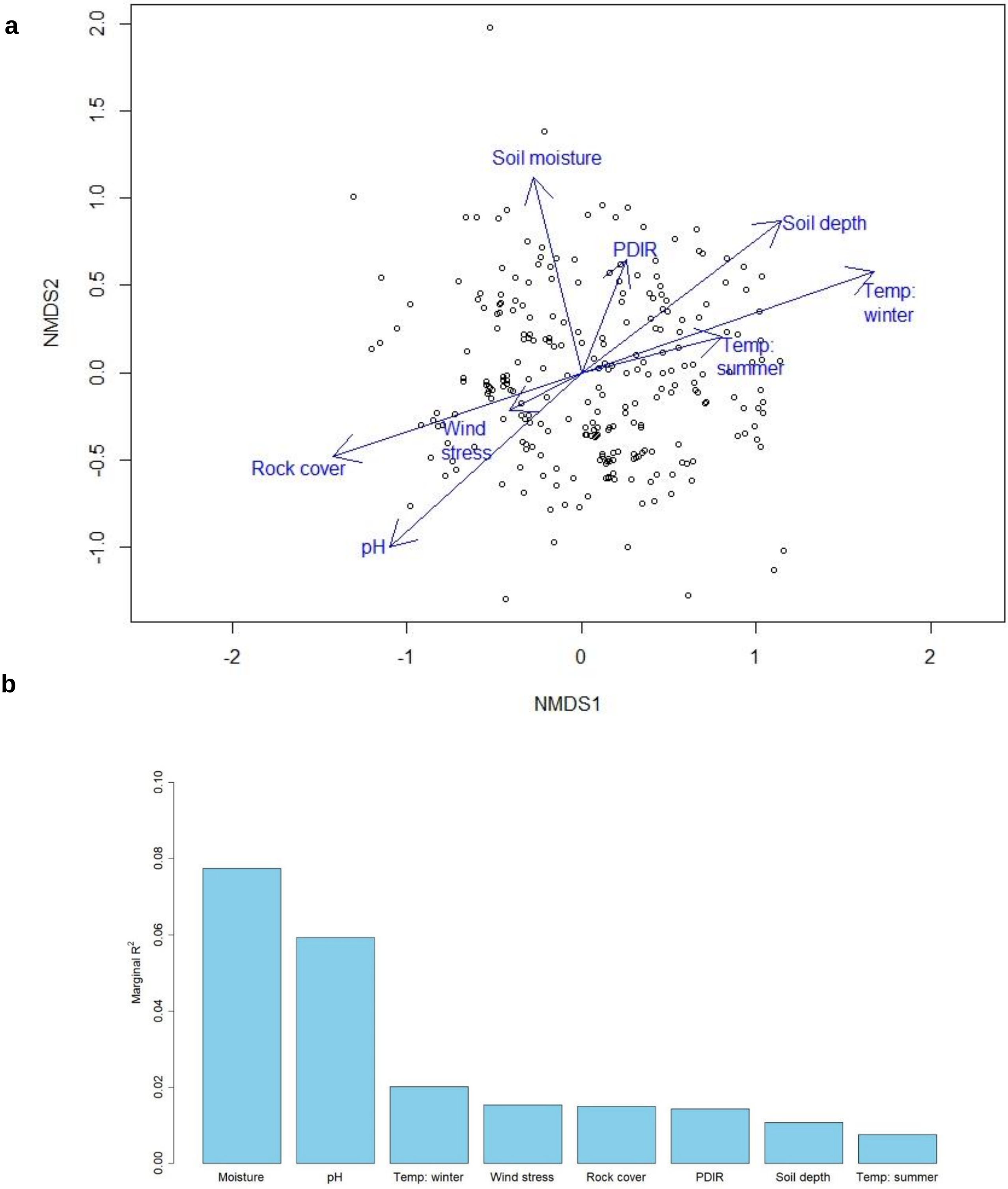

**Figure 6** a) Non-metric multidimensional scaling (nMDS) ordination plot showing variables impact on species composition (Stress = 0.18), symbols indicate sampled quadrats; b) Variable importance, as assessed by marginal $R^2$ values, from the PERMANOVA. Temp = soil temperature.

All eight of the predictor variables in the full model contributed significantly to explaining variation in species composition, and together explained 33.9 % of the variation (the simple model explained 32.4 %). Wind stress was the fourth most important predictor in explaining species composition, after soil moisture, pH, and winter soil temperature. Species composition was weakly nested by wind stress, with NODF = 31.0, whereas NODF = 57.9 when the species matrix is arranged to maximize nestedness. This result was mirrored by the partitioning of beta diversity into species turnover and nestedness, where an overall Sørensen dissimilarity index value of 0.996 (indicating high dissimilarity in the species composition between quadrats) was predominantly driven by species turnover (0.994), with nestedness having a much smaller effect (0.003).

## Discussion

Wind stress was consistently prominent in explaining fine-scale spatial variation in species richness, vegetation cover, and species composition, as evidenced both by models including wind stress performing better than models without wind stress and by wind stress repeatedly having among the highest relative importance values. These results agree with findings across broader scales, where, for example, wind protection is important in determining the distribution of high-altitude forests and tree sapling growth (Sparacino et al., 2020), and wind patterns improved the accuracy of future temperature forecasts and resulting predictions of climate refugia (Ashcroft et al., 2009).

Both species richness and species cover were significantly related to wind stress. Species richness responded non-linearly to wind stress, with the highest species richness at intermediate maximum wind stress. This suggests that in ecosystems with high wind stress, such as sub-Antarctic islands, areas that do not have sheltered microsites have a constrained species richness, and that the largest number of species co-occur where the maximum stress conditions in an area are neither entirely sheltered nor exposed. Vegetation cover follows the same trend as species richness, where maximum wind stress is one of the key predictors. Wind stress and vegetation cover have a non-linear relationship (i.e. both low and high maximum wind stress values are correlated with higher vegetation cover), but the highest vegetation cover is found in microsites with the highest maximum wind stress. It is possible that in this system where bryophytes can be co-dominant (e.g. in both the wettest habitats; Smith and Steenkamp, 2001; Smith et al., 2001), that at high wind speeds evapotranspiration causes too great a moisture stress for bryophytes (which are poikilohydric and are highly dependent on external water availability; Vitt et al., 2014), allowing vascular plants to achieve greater cover.

Species composition was also significantly related to wind stress, and differed strongly between quadrats, driven chiefly by species replacement. The low nestedness exhibited by vascular plant species along the wind stress gradient, which matches the observation that species richness did not decline uniformly with increasing wind stress, suggests that species may be replacing each other as wind conditions become progressively more stressful. For example, on Marion Island, the alien grass *Agrostis stolonifera*, is limited to sites which are sheltered due to its lack of supportive tissue, while the indigenous congeneric *A. magellanica* grows in more wind exposed locations (Pammenter et al., 1986). Further, presumably due to the wind-sheltered nature of streambanks, *Agrostis stolonifera* disproportionately invades these communities, but is absent from windier habitats (Gremmen et al., 1998). Irrespective of the mechanism driving the influence of wind on community composition, these results agree with previous studies in other temperature-limited systems that have also identified wind (acting, e.g., via erosion) as a driver of variation in species composition (Vonlanthen et al., 2006a; le Roux and Luoto, 2014). Therefore, in terms of species richness, cover and composition, wind is an important driver of plant community structure at fine-scales in an environment that is exposed to chronic winds.

The other abiotic variables that were strongly related to vascular plant richness, cover and composition exhibited patterns consistent with other studies conducted at high altitude and/or latitude sites. For example, pH was a consistently strongly correlated with species richness, in agreement with findings from other temperature-limited systems (e.g. Vonlanthen et al., 2006b; Filibeck et al., 2019). Soil moisture played the largest role in driving community composition, and this variable has been highlighted as a key driver of species composition in other low-energy systems (le Roux et al., 2013a). Indeed, wind and soil moisture may potentially have an interactive relationship, with strong winds desiccating upper soil layers (Bertiller et al., 1996). Because wind stress was related to plant community properties even after accounting for these other abiotic variables, these results clearly highlight the importance of wind in driving variation in floral communities.

### Wind as a globally underexplored environmental driver

While wind may be important in high latitude and high altitude regions (e.g. Whitehead, 1954; Wilson, 1959 and this study), and experiments have shown it to have widespread effects on plant growth in other regions too (Wilson, 1959), it is still partly unclear if the patterns observed here can be generalized to other systems. At a minimum, it is likely that wind will be important in (1) areas with strong winds (chronic and/or extreme winds) as it is a mechanical stress, (2) areas with fine and loose material available for aeolian transport (e.g. due to erosion, deposition and wind scouring in dune environments; Nylén et al., 2015; Nylén and Luoto, 2015), (3) dry areas where wind enhances evaporation and the potential for plants to experience greater moisture stress (Zhang et al., 2007), (4) areas with thin soils which are more susceptible to desiccation (Bertiller et al., 1996), and (5) Arctic and alpine areas where it affects snow drift (Sturm et al., 2001; Dadic et al., 2010). The redistribution of snow by wind, leading to differences in the depth and duration of seasonal snow cover has large impacts on alpine plant communities, since species are protected from temperature extremes and frost when covered by snow (Lord et al., 2018). Wind may also have an indirect effect by interacting with other climatic factors (see e.g. Kullman and Loyer, 2005; Ashcroft et al., 2009). As a result, the large recent changes in global wind patterns may have direct consequences for species distributions and interactions between species (Young et al., 2011; Young and Ribal, 2019), as well as indirect impacts (e.g. by affecting seed dispersal; Kling and Ackerly, 2020).

Predictions of the ecological impacts of changing wind conditions may be complicated by species- and site-specific responses. For example, wind may differentially impact on groups of species within communities. Since understory species are less exposed, for example in forest communities, it is expected that canopy species will show the greatest responses to changes in wind (as observed for changes in temperature; Mau et al., 2018). Further, species growing on ridge crests or slopes will likely be more affected than those growing in protected valleys, since changes to wind speed and/or direction in wind exposed locations will be less buffered by other vegetation or topographic features. An added challenge in making predictions on the impacts of changing wind conditions is that altered wind patterns may contribute to the development of “novel climates”, representing climatic conditions not currently present elsewhere (sensu Williams and Jackson, 2007; Dahinden et al., 2017). Plants and animals may lack adaptations to changes in wind conditions; similar to some species’ inability to adapt fast enough to recent changes in temperature and precipitation (e.g. Parmesan and Hanley, 2015; Gómez-Ruiz and Lacher Jr, 2019; Radchuk et al., 2019). Shelter from wind could also be a facilitative mechanism in extreme environments, where cushion plants, for example, may ameliorate conditions for benefactor species (Schöb et al., 2014). Although wind shelter does not appear to benefit the dominant grass species on Marion Island (van der Merwe et al., 2020), other species growing on the periphery of the cushion plants here may receive more shelter from wind. Therefore, the impacts of changes in wind patterns on plant communities will likely be dependent on interactions with microclimatic and/or topographic conditions, and will vary between habitat types and species groups.

To further understand the ecological impact of wind, future studies should investigate not only community-level metrics (e.g. as in this study), but also the responses of the individual species that comprise the community. Species may, for example, respond to wind stress through trading-off resources between different processes or traits, as seen in response to changes in other climatic factors (Gandin et al., 2011; Liu et al., 2013). Indeed, recent evidence has shown that, for example, some plant species respond to higher wind speeds by increasing their foliar silicon content (which may provide protection against mechanical stress; Song et al., 2020). Functional traits have been used to examine how species react to changes in other environmental variables (e.g. Bjorkman et al., 2018; Niittynen et al., 2020b; Thomas et al., 2020), and traits related to resource allocation (e.g. specific leaf area) and leaf toughness (e.g. leaf dry matter content and tensile strength) may provide useful metrics for quantifying functional variation within species in response to spatio-temporal variation in wind patterns.

Here we show that spatial variation in wind stress has a defining impact on vegetation communities in an ecosystem that experiences chronic winds. Therefore, temporal variation in wind patterns, which are currently shifting due to global climate change (Young et al., 2011; Young and Ribal, 2019; Zeng et al., 2019), may also likely affect plant community characteristics through time, in the same way that wind currently affects their spatial patterning. The growing availability of wind data at a coarse spatial scale needs to be (1) examined in the context of landscape-level biological patterns (i.e. related to topography), and (2) refined to also describe variation in wind characteristics at the scales affecting individual plants and local communities (Maclean, 2020). Wind has been an understudied climatic driver of biotic communities for more than 60 years (Wilson, 1959), and, especially in light of the global challenge of climate change, it is now time to advance our understanding of where, and to what extent, wind acts as a driver of vegetation patterns at multiple spatial scales.

## References

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# Appendix

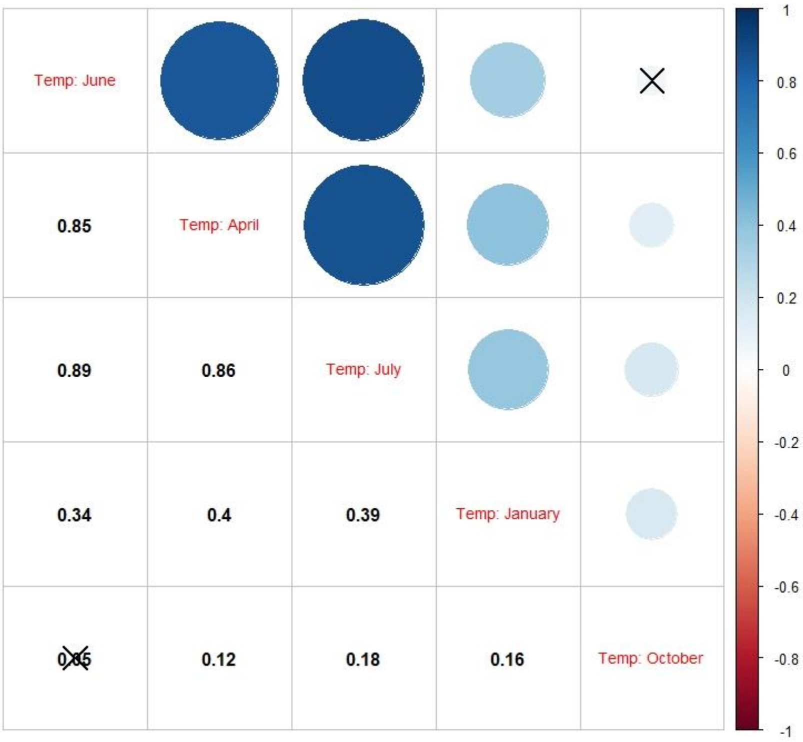

**Figure A1** Pairwise Pearson correlation coefficients between soil temperature variables. “X” indicates non-significant correlations.

**Figure A2** Pairwise Pearson correlation coefficients between soil moisture variables. “X” indicates non-significant correlations.

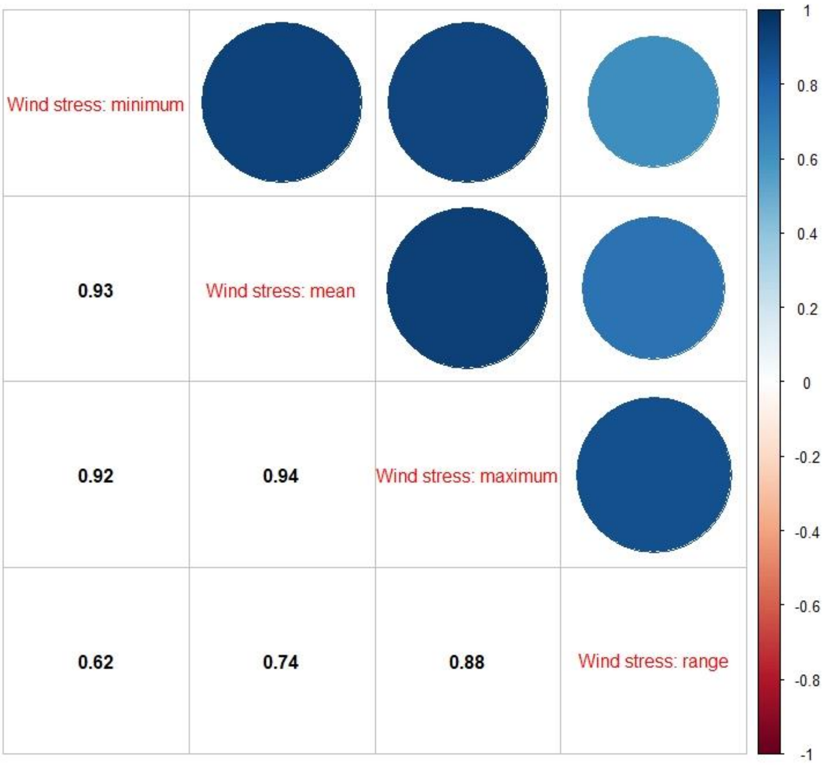

**Figure A3** Pairwise Pearson correlation coefficients between wind stress variables. “X” indicates non-significant correlations.

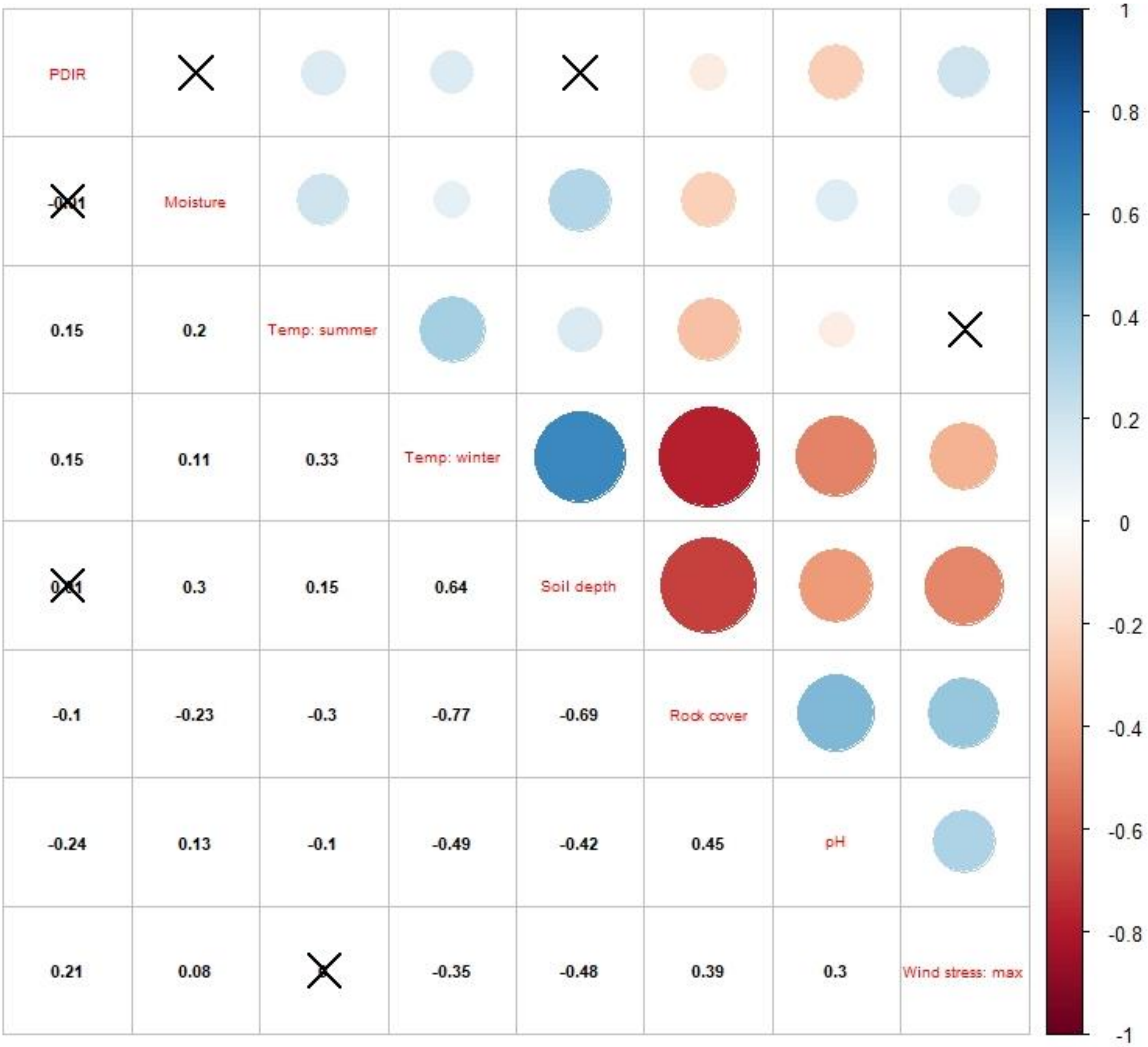

**Figure A4** Pairwise Pearson correlation coefficients between all of the predictors included in the final full models. “X” indicates non-significant correlations.

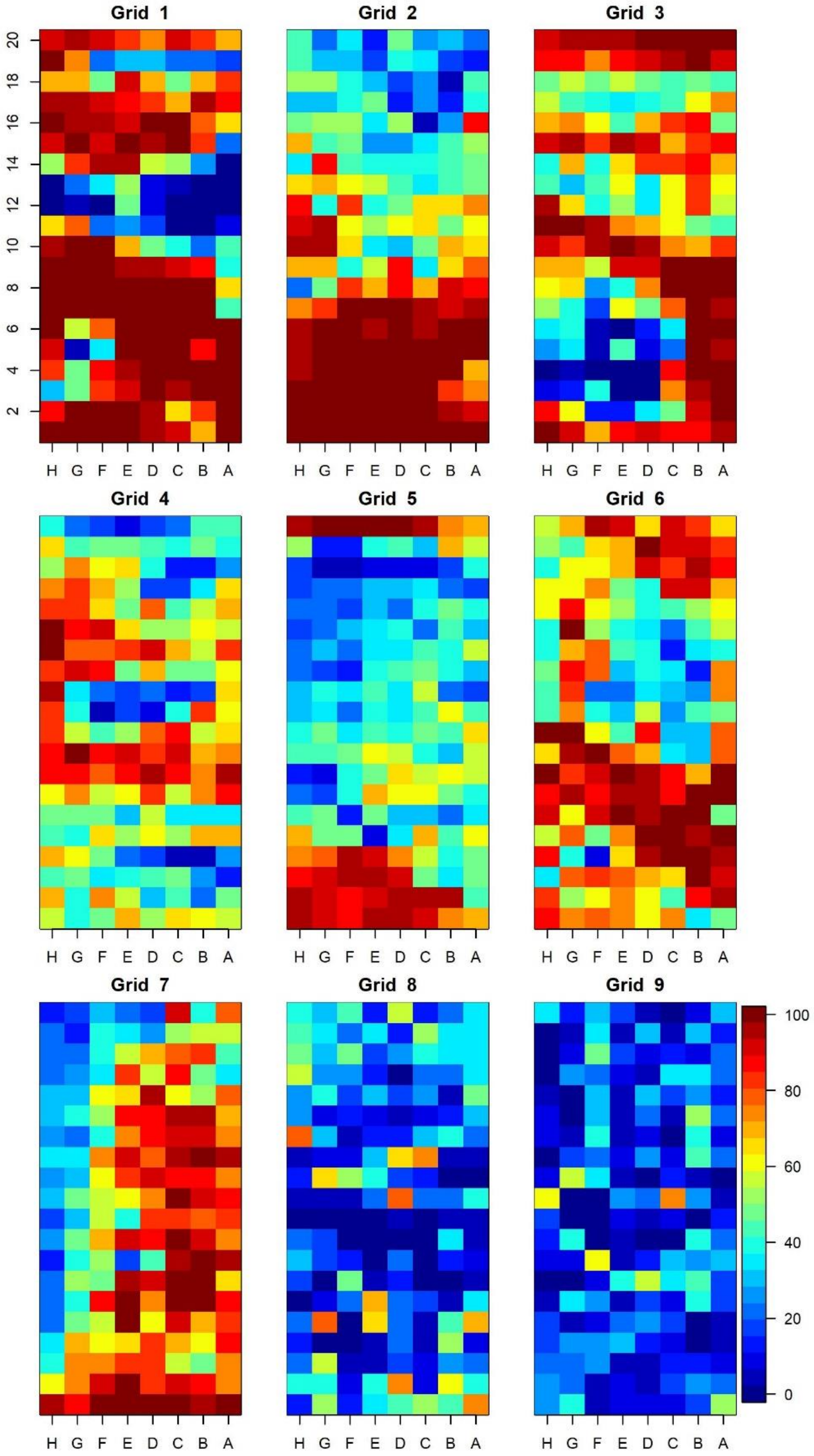

**Figure A5** Vascular plant cover (%) across all nine study grids (see Fig. 1 for location of the grids). Cooler colours indicate low plant cover and warmer colours indicate higher vegetation cover. Each cell represents a 1 x 1 m quadrat, with all 180 quadrats per grid being contiguous.

**Table A1** Performance of the simple versus full models for species richness and vegetation cover across the two statistical methods. GAM = generalized additive model; GLZ = generalized linear model.

| | **Richness** | **Cover** |
|---|---|---|
| **GAM** | | |
| Deviance explained (%): simple model | 21.4 | 66.3 |
| Deviance explained (%): full model | 24.9 | 67.7 |
| p-value | < 0.001 | < 0.001 |
| **GLZ** | | |
| Deviance explained (%): simple model | 18.7 | 65.5 |
| Deviance explained (%): full model | 19.5 | 66.9 |
| p-value | 0.06 | < 0.001 |

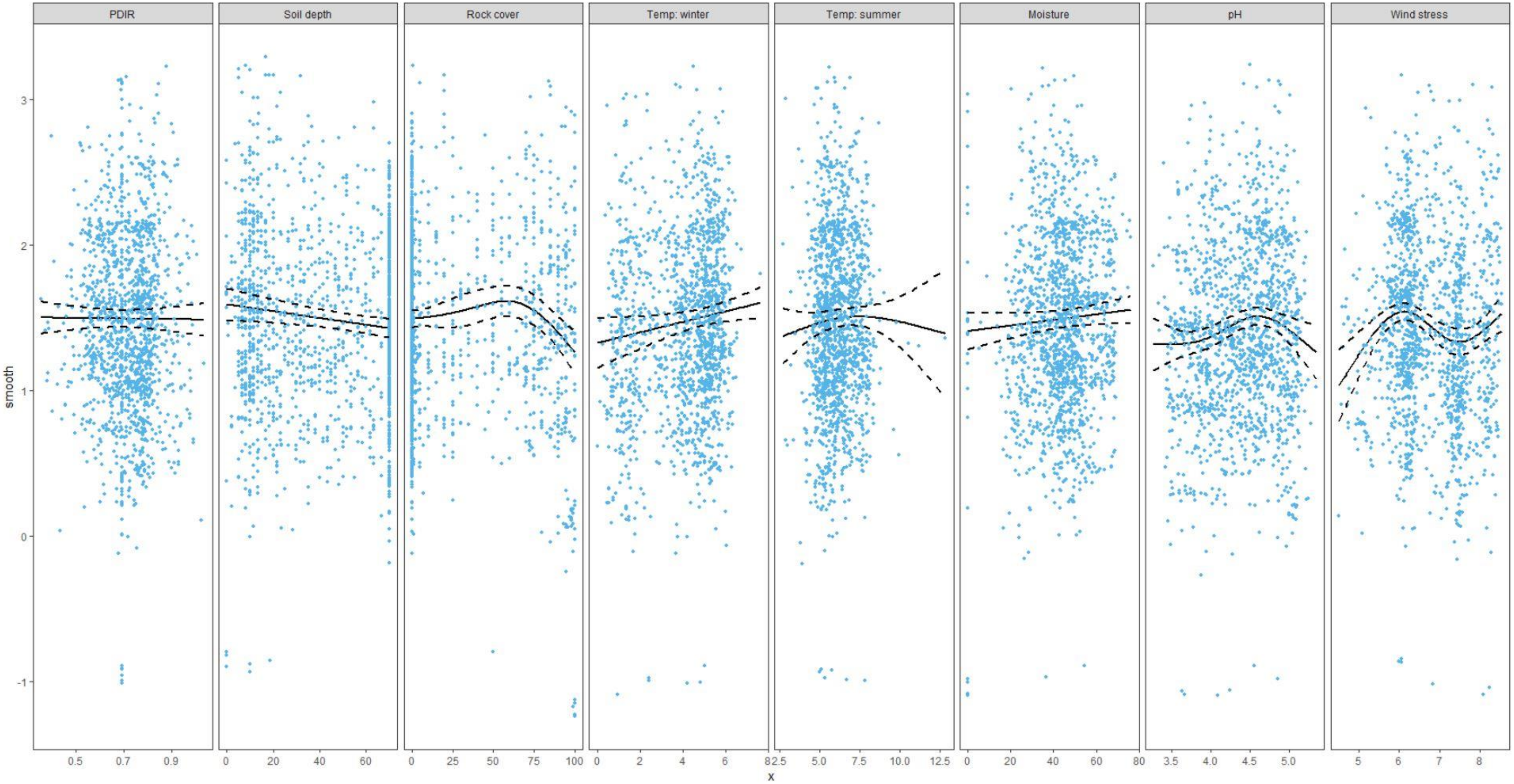

**Figure A6** Individual predictor variables' response curves for species richness in the full GAM model, with raw data indicated by blue symbols. Black solid lines represent the response curves while black dashed lines represent 95 % confidence intervals.

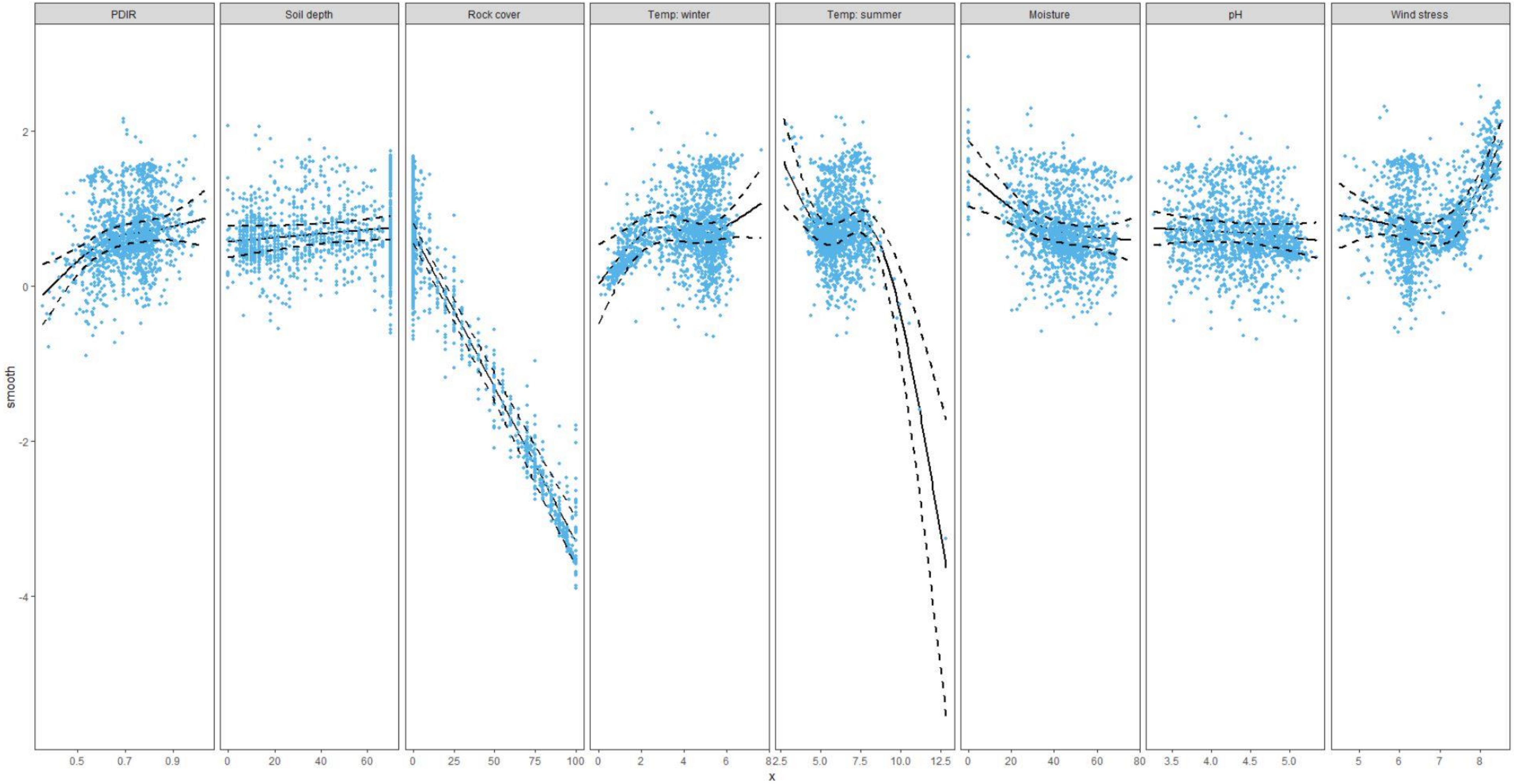

**Figure A7** Individual predictor variables' response curves for vegetation cover in the full GAM model, with raw data indicated by blue symbols. Black solid lines represent the response curves while black dashed lines represent 95 % confidence intervals.

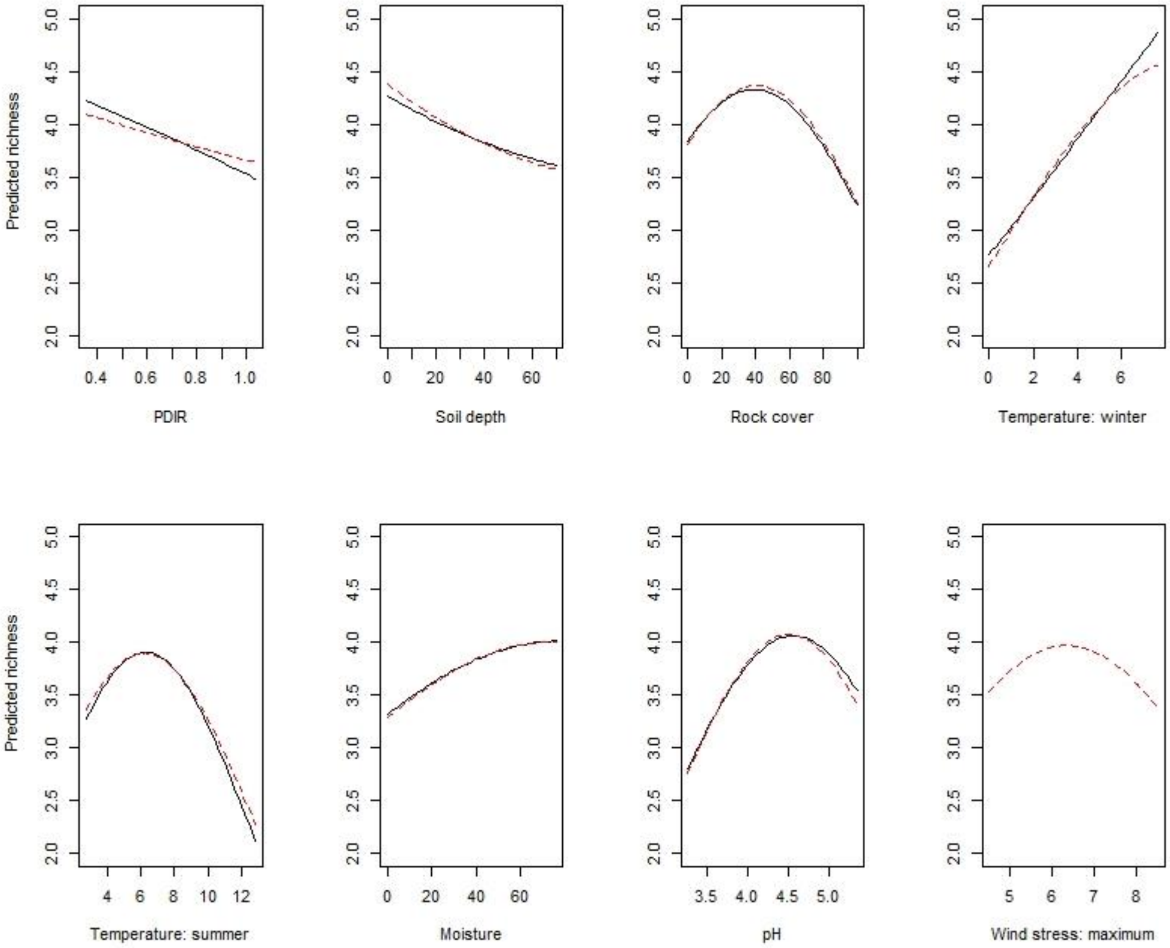

**Figure A8** Individual predictor variables' response curves for species richness in GLZ models. Black solid lines represent the response curves in the simple model (excluding wind index predictor variables), while red dashed lines represent the response curves in the full model.

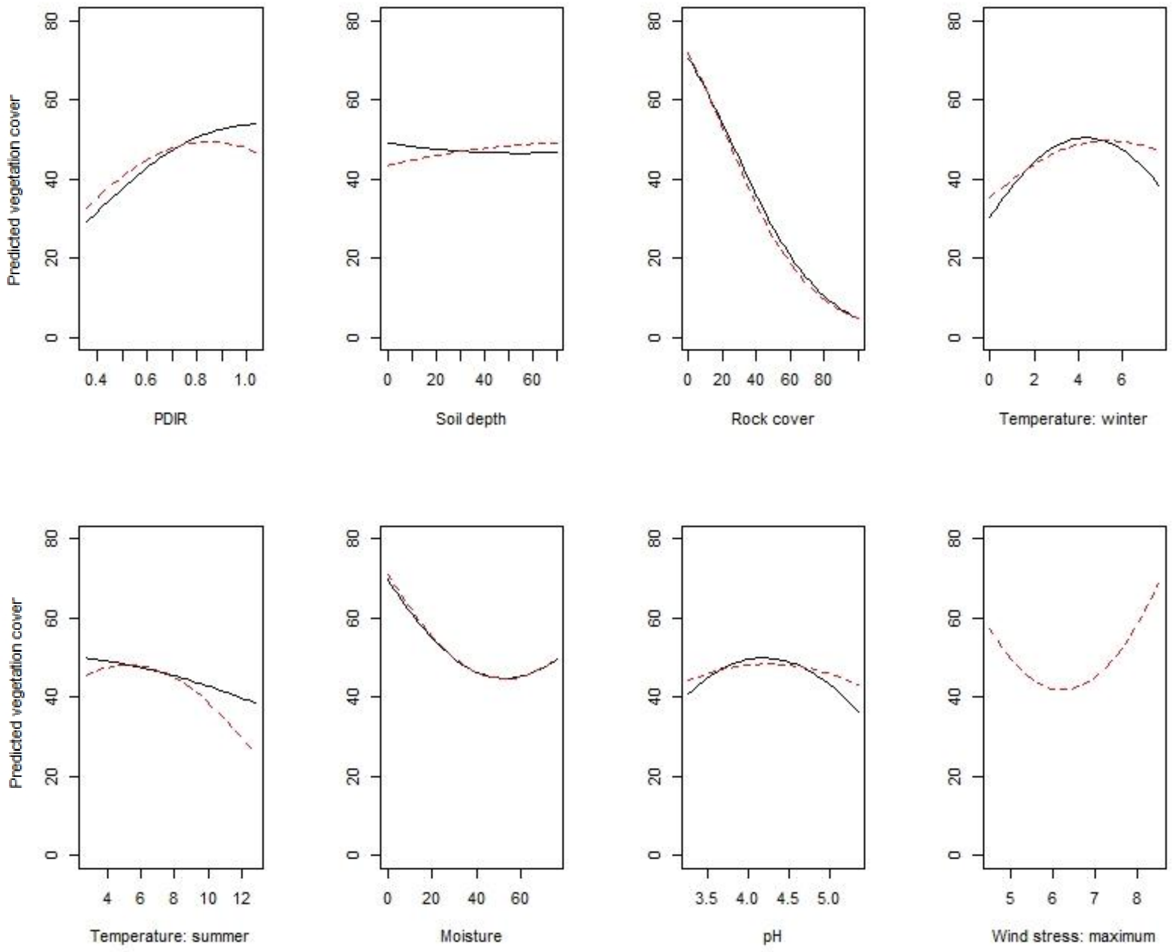

**Figure A9** Individual predictor variables' response curves for vegetation cover in GLZ models. Black solid lines represent the response curves in the simple model (excluding wind index predictor variables), while red dashed lines represent the response curves in the full model.

**Table A2** Variable importance for all variables when predicting spatial variation in species richness and vegetation cover in the full generalized boosted regression model (GBM). The five most important predictors for each response variable are highlighted in bold.

| | **Richness** | **Cover** |
|---|---|---|
| | **Relative importance (%)** | |
| Rock cover | **15.47** | **52.96** |
| Wind stress: maximum | **18.77** | **3.59** |
| Soil pH | **20.91** | **26.75** |
| Soil depth | 7.24 | **3.04** |
| Temperature: summer | **10.78** | 2.59 |
| Temperature: winter | 7.66 | **8.44** |
| PDIR | **10.61** | 0.69 |
| Soil moisture | 8.59 | 1.93 |

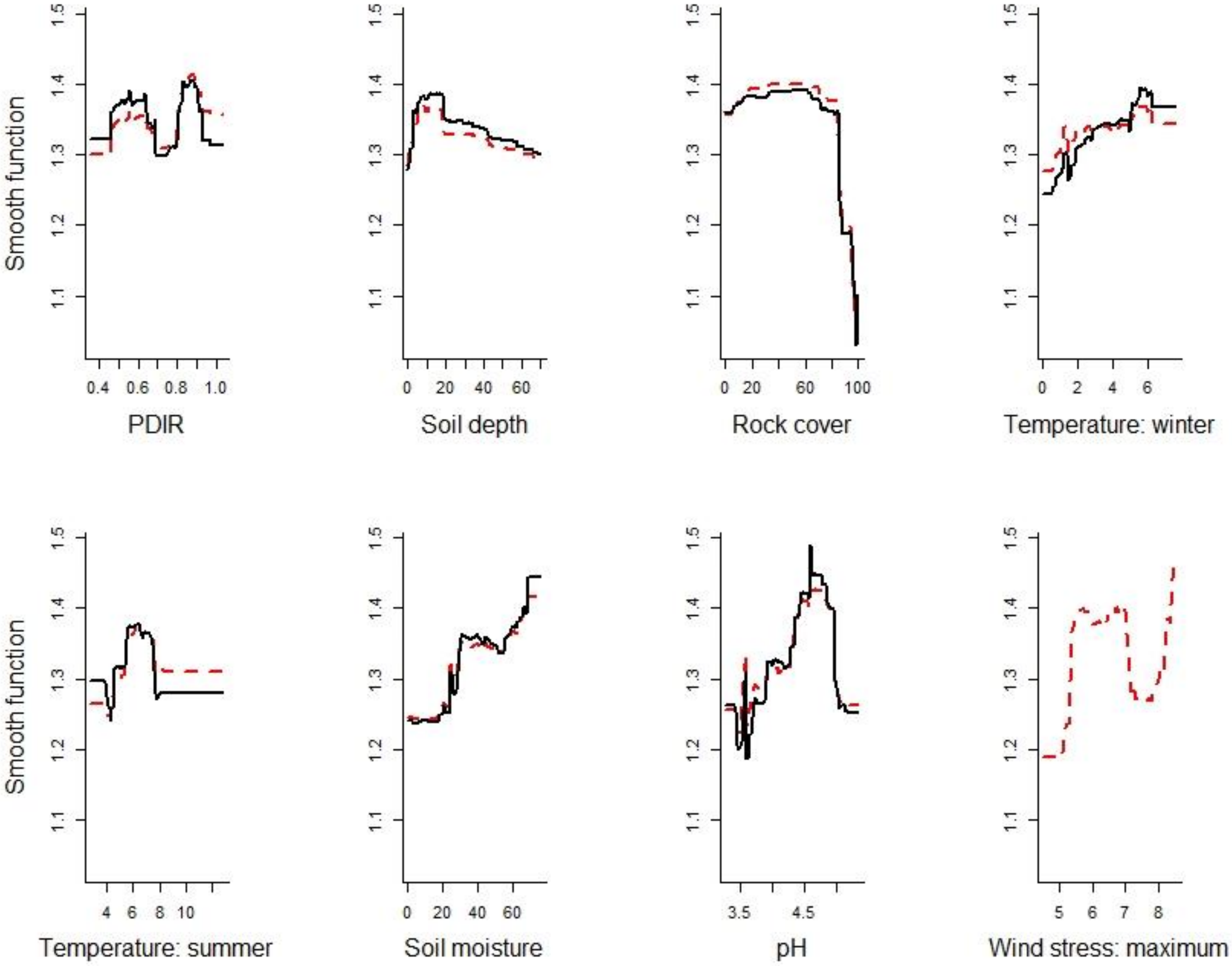

**Figure A10** Individual predictor variables' response curves for species richness in GBM models. Black solid lines represent the response curves in the simple model (excluding wind index predictor variables), while red dashed lines represent the response curves in the full model.

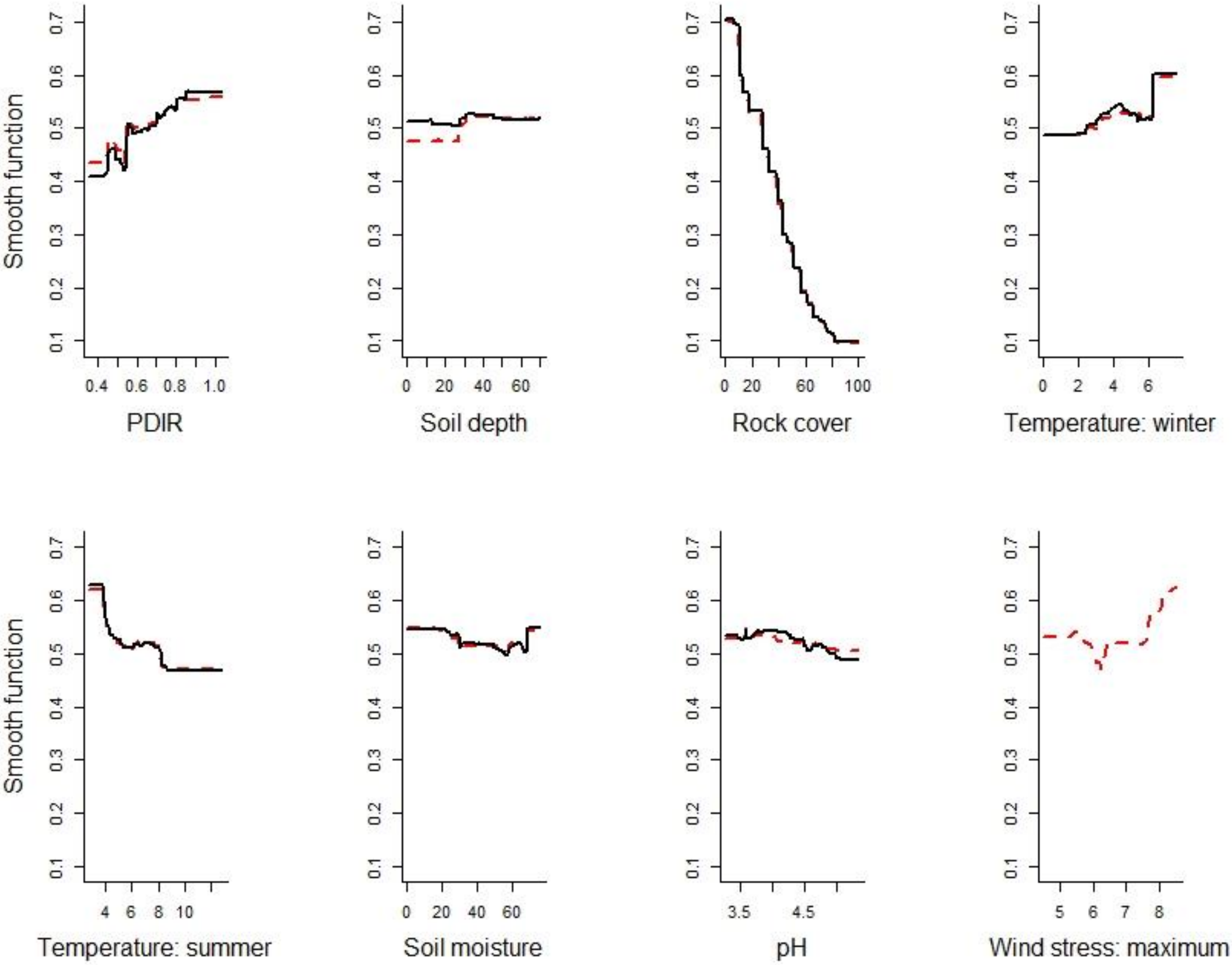

**Figure A11** Individual predictor variables' response curves for vegetation cover in GBM models. Black solid lines represent the response curves in the simple model (excluding wind index predictor variables), while red dashed lines represent the response curves in the full model.

# Chapter 4:

# Species differ in their responses to wind: The underexplored link between species fine-scale occurrences and variation in wind stress

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**Authors' contributions:** PClR, ML and MM conceived the ideas and designed the methodology; MM, PClR and DWH collected and processed the data; MM and PClR analysed the data, with inputs from DWH and ML; MM led the writing of the manuscript. All the authors contributed critically to the drafts and gave final approval for publication.

## Abstract

*Questions*

Species distribution models have traditionally relied heavily on temperature and precipitation, often ignoring other potentially important variables. However, recent advances have shown other climatic variables, including snow cover and solar radiation, may strongly improve predictions of species occurrence. Wind has long been known to have mechanical and physiological impacts on plants, but has not yet received adequate attention as a driver of species distributions.

*Location*

Marion Island, sub-Antarctic.

*Methods*

Using data from 1440 plots in a chronically windy system, we test if wind stress (a combination of wind exposure and wind speed) improves species distribution models of vascular plant species, examining predictions for both species occurrence and cover.

*Results*

Wind stress was a significant predictor of the occurrence of twelve out of the sixteen species, even after accounting for seven other ecophysiologically-important abiotic variables. Species showed differential responses to wind, but wind stress was among the four most important drivers for the majority of species when modelling occurrence patterns (10 out of 16) and variation in cover (12 out of 16). Further, wind stress was more important than all temperature and precipitation variables in predicting the occurrence of six species (and three species' cover).

*Conclusions*

Wind conditions were most influential for species which are characteristic of open, wet environments and for pteridophyte species, likely due to high wind speeds and exposure increasing the potential for moisture loss. This research highlights the value of incorporating wind metrics into species distribution models, particularly under changing wind patterns.

## Introduction

The distributions of many species are shifting in response to global environmental change (Pecl et al., 2017). Traditionally, temperature and precipitation have most often been examined as drivers of species ranges (Austin and Van Niel, 2010). However, for the most accurate predictions of where species occur, currently and under future climate scenarios, all biologically-meaningful environmental variables need to be included in these biogeographical models (Mod et al., 2016). By considering more ecophysiologically-relevant predictors, the predictions of plant species distributions can be improved (e.g. Qiu et al., 2021). For example, when considering soil moisture, instead of traditional precipitation data (which may be weakly correlated with plant-available moisture), plant species distribution models perform better (Kemppinen et al., 2019; Buri et al., 2020). In addition, snow conditions have an important role in driving taxonomic and functional diversity in ecosystems with seasonal snow cover, (Niittynen and Luoto, 2018; Niittynen et al., 2020a; Niittynen et al., 2020b).

Wind is an environmental variable that potentially has profound impacts on plant growth and species' distributions (Whitehead, 1959; Wilson, 1959). For example, investigation of six wind-dispersed alien plant species reflects that wind has an effect on species' habitat distributions in all biomes, but that the nature of this effect varied (Wan et al., 2017). Wind can be expected to affect species distributions as it has direct physiological impacts on plants, through affecting rates of transpiration and photosynthesis (Grace, 1977; de Langre, 2008). Additionally, stronger winds lead to faster soil desiccation which, as a result, can affect plant moisture uptake (Bertiller et al., 1996; Fitzgerald and Kirkpatrick, 2017). Recent work has shown that decreases in wind have contributed to delayed autumn foliar senescence dates in the high latitudes of the northern hemisphere (Wu et al., 2021). Wind conditions also affect surface litter distribution which, in turn, influences soil nutrient content and temperature (Fahnestock et al., 2000). In addition to these physiological impacts, wind affects plants as a consequence of its' mechanical impacts, including abrasion and desiccation (Hadley and Smith, 1983; Gardiner et al., 2016), uprooting (Yang et al., 2014), and premature shedding of leaves or flowers (Lahav and Zamet, 1999). Tree failure in both boreal forests and urban spaces has also been linked to wind events, with certain tree characteristics increasing their susceptibility to succumbing (Jahani, 2019; Jahani and Saffariha, 2021). Wind has, however, not yet been investigated in the context of species distribution modelling (SDM) at a fine scale, to test whether, in a single system, wind conditions affect where species occur.

In order to understand what impacts changes in wind conditions will have on species into the future, it is of value to examine wind as a driver of contemporary patterns in species distributions. Indeed, deeper insight into the role of wind conditions in driving variation in species distributions is particularly relevant, given that global wind patterns are currently shifting (due to broader changes in climate; Young et al., 2011; Young and Ribal, 2019), and that these changes are predicted to continue (Jeong and Sushama, 2019; Zeng et al., 2019). Wind has previously indirectly been considered in species future distributions by including dispersal into SDMs, where species' dispersal syndromes affect maximum dispersal distance (Di Musciano et al., 2020; see also Monsimet et al., 2020 as a study which incorporates ballooning into distribution models for fishing spiders). Therefore, understanding the direct effects of wind on species occurrence and cover remains an important unanswered question.

Therefore, the aim of this study was to determine whether wind acts as a biogeographical driver by investigating its effect on the occurrence and cover of individual plant species. The sub-Antarctic region experiences some of the strongest and most consistent winds globally (Pendlebury and Barnes-Keoghan, 2007), and recent research has shown that spatial variation in wind conditions on Marion Island is significantly related to species richness, vegetation cover and community composition (Momberg et al., 2021). Therefore, in this study, the effect of wind on the distribution of the vascular plant species of Marion Island was investigated, using fine-scale vegetation and abiotic data from 1440 quadrats.

## Methods

### *Study site*

The sub-Antarctic, defined as the region between 45° and 60° S, is an ideal region in which to focus on the impacts of wind since the islands here experience strong and constant winds (Pendlebury and Barnes-Keoghan, 2007). Data was collected in the north-eastern region of sub-Antarctic Marion Island (46°54′ S, 37°45′ E; 293 km$^2$). Marion Island is located in the southern Indian Ocean, approximately halfway between the southern tip of Africa and the Antarctic continent. The island is volcanic in origin, and is comprised of smoothed pre-glacial and rugged post-glacial lava flows (Rudolph et al., 2020). Marion Island experiences strong and consistent westerly winds on most days of the year (Pendlebury and Barnes-Keoghan, 2007; le Roux, 2008), with a mean annual wind speed of approximately 8 m/s (le Roux and McGeoch, 2008). Weather records from the meteorological station (approximately 1 km from the study site) indicate mean daily minimum and maximum temperatures of 3.2 and 8.7 °C, respectively, and a mean annual precipitation of approximately 1800 mm (2008 – 2018; South African Weather Service). The island has a hyper-oceanic climate, resulting in narrow daily and seasonal temperature ranges (le Roux, 2008). Marion Island supports 23 indigenous vascular plant species (Gremmen and Smith, 2008) and currently hosts 16 alien vascular plant species, of which 6 are considered to be invasive (Greve et al., 2017). The island is dominated by low-growing species and there are no trees occurring on the island, despite the intentional introduction of *Salix* and *Pinus* species in 1950, of which none survived (La Grange, 1954; Gremmen, 1975).

### *Data collection*

Nine study grids (8 x 20 m each), located on the north-eastern side of Marion Island, individually comprising 160 contiguous 1 $m^2$ quadrats (following le Roux et al., 2013), were sampled between April 2016 and May 2017, resulting in data from a total of 1440 quadrats (see Appendix S1). Grids were located at least 70 m apart, with a maximum distance of 915 m between the farthest two grids. The grids were positioned to sample as much environmental variability as possible within the local environment and covered a heterogenous area in terms of topography, geology and biology (see Momberg et al., 2021 for detailed design). Previous work has illustrated that fine-scale differences in species richness, vegetation cover, and species composition may be related to wind stress at this site (Momberg et al., 2021), but the influence of wind stress on the occurrence and cover of individual species has not yet been examined. All pteridophytes and angiosperms were identified (taxonomy following Chau et al., 2020), their occurrence recorded, and their canopy cover visually estimated across all 1440 quadrats. In total, 18 species were found within the nine study grids (see Appendix S2 for photographs of selected species). Only species with at least 14 occurrence records (i.e. present in >1 % of the quadrats), and which were present in at least two of the nine grids (to allow for cross-validation), were used in further analyses. Two species, *Montia fontana* and *Poa pratensis*, did not meet these requirements, resulting in a total of 16 species used in the analyses (Table 1). Four of these species are invasive (Greve et al., 2017), while the remaining 12 are indigenous to Marion Island. Therefore, 52 % of the indigenous vascular flora for Marion Island are included in these analyses. Of the most widespread indigenous plants, only *Leptinella plumosa* and *Crassula moschata* were not recorded in the sampling grids (because these species are limited to coastal areas; Smith and Steenkamp, 2001).

In addition to species occurrence and cover data, several abiotic variables were characterised within each 1 $m^2$ quadrat. Soil depth, soil temperature, soil moisture, and rock cover (as a percentage of each quadrat) were measured in the field. Soil temperature and soil moisture were measured on five occasions throughout the sampling year. One measure of winter (June) and summer (January) soil temperatures were used in analyses as these were not significantly correlated (all summer temperature readings were correlated with each other, and all winter temperature readings were correlated with each other), while for soil moisture only one set of readings were used since soil moisture readings were significantly correlated across all five sampling occasions (see Momberg et al., 2021). Soil samples from a subset of quadrats in each grid (16 to 32 samples per grid) were analysed to determine soil pH (using the $CaCl_2$ method; Hendershot et al., 2008). These data were then interpolated to other quadrats in each sampling grid using a bilinear interpolation (Bovik, 2009). Potential direct incident radiation (PDIR) was calculated for each quadrat using field-collected slope and aspect values (McCune and Keon, 2002; McCune, 2007). A wind stress metric was calculated based on dominant wind direction, wind speed and exposure (see Momberg et al., 2021). First, wind exposure was calculated in SAGA GIS (Conrad et al., 2015) using a digital surface model created from 2 cm resolution drone imagery and specifying the dominant wind direction at the site based on data collected at the site between April 2018 and March 2019 at a height of 1 m above the ground surface (maximum wind speed recorded at the site = 22.39 m/s, mean ± SD wind speed = 6.87 ± 3.42 m/s). Then, the wind speed for each grid was extracted from a computational fluid dynamics model of windflow across Marion Island (for details see Momberg et al., 2021). Finally, the wind exposure for each quadrat was multiplied by the grid-level wind speed to obtain a wind stress value for each quadrat.

Trait data were obtained for all of the sampled species for five plant functional traits: plant height, leaf area, specific leaf area, leaf nitrogen content and leaf phosphorous content (Rossouw, 2014; Louw, 2016; Bjorkman et al., 2018). Trait measurements are described in detail in the publications from which they were obtained. Wind stress was hypothesized to have stronger effects on taller- than short statured vegetation (Saiz et al., 2021). Leaf traits were expected to show a correlation with wind stress due to the mechanical damage and desiccating effect that wind could have on leaves (see e.g. Russell and Grace, 1978), with windier conditions expected to favour smaller leaves (as observed by Niklas, 1996) and leaves with greater structural investment and, therefore, lower specific leaf area, lower leaf nitrogen content and lower phosphorous content (Pérez-Harguindeguy et al., 2013).

### *Statistical analyses*

None of the measured variables were highly collinear ($r<|0.8|$; Momberg et al., 2021) and, therefore, all were used in analyses (see Appendix S3 for correlation values between all predictors). To minimise uncertainty due to modelling approach, three different statistical techniques were used. Generalised linear models (GLM), generalised additive models (GAM), and boosted regression trees (GBM) were used to model the occurrence and cover of all species. For both species occurrence and cover, a binomial distribution was used for GAM and GLM models, while GBM models were run with Bernoulli distribution for occurrence and a Gaussian distribution for cover.

The influence of wind on the vascular plants at the study site was first examined using a univariate model, testing the relationship between wind stress and the occurrence and cover of all species. A second model was then run, including all eight predictor variables to determine the significance of predictors and the deviance explained by these models.

To assess the transferability of the relationships (i.e. as a measure of model accuracy), a nine-fold cross-validation approach with non-random assignment was used to validate multivariate models. In this approach, each grid was left out once in training and used for validation (i.e. eight grids were used for training and one for validation, with this repeated once for each of the nine grids, resulting in nine folds). This method provides a strong test of the transferability of the model (Wenger and

Olden, 2012). This resulted in two models per statistical approach, a model excluding wind stress (“simple model” hereafter) and a model including wind stress (“full models”), both of which were calibrated on eight grids, and then used to predict species occurrence and cover for the excluded ninth grid. Predictions for species occurrences under the simple and full validation models were then compared to the observed data using the true skill statistic (TSS; Allouche et al., 2006), and the area under the receiver operating characteristic curve (AUC; Çoban et al., 2020). The accuracy of predictions for species cover were assessed by determining the Spearman correlation between predicted and observed cover values.

Variable importance was calculated for the full calibration model based on the entire dataset for each predictor by comparing the Pearson correlation between predictions made on the original dataset and predictions made on a version of dataset where the predictor variable of interest had been randomly ordered, with this procedure being repeated ten times (Niittynen and Luoto, 2018). The mean of the ten resulting correlation values was used as the variable importance score, with the scores from all eight predictors scaled to percentage values (Niittynen and Luoto, 2018). Response curves were produced for each species, showing the relationship between species occurrence or cover and each of the eight predictor variables, while accounting for all of the other predictors in the full model based on the entire dataset.

A Pearson correlation test was used to determine whether there were significant correlations between the variable importance for wind stress and plant functional traits (plant height, specific leaf area, leaf area, leaf nitrogen content, and leaf phosphorous content). Leaf nitrogen and leaf phosphorous content were significantly positively correlated ($r=0.89$, $p<0.05$), while other traits were not strongly correlated ($r<|0.65|$). Since the traits were investigated against the variable relative importance of wind stress independently, collinearity was not a reason for excluding any traits. All statistical analyses were conducted in R statistical software, version 3.5.0 (R Core Team, 2021), using additional functions from the vegan (Oksanen et al., 2018), mgcv (Wood, 2006), and Hmisc (Harell, 2018) libraries.

## Results

Results from all three statistical approaches were similar, and, therefore, only results from the GAM models are reported here (see the supplementary material for results from the GLM and BRT models). Wind stress alone explained between 0.08 and 25.4 % of the deviance observed in the occurrence and cover of each species ($p < 0.05$ in 14 of 16 univariate models; Table 2). Models containing all eight predictors improved the proportion of deviance explained by 0.15 - 65.79 % (resulting in full models with % deviance explained ranging from 0.23 to 72.00 %). Wind stress was a significant predictor in the multivariate models of species occurrence for 12 of the 16 species (Table 2; comparison between univariate and multivariate models from the GLM for species occurrence and for GAM and GLM for species cover in Appendix S12 - S14).

The inclusion of wind stress into models already comprising the seven other environmental variables did not, however, strongly improve AUC and TSS across all species. The mean change in model performance across all the species showed no significant improvement in model performance when wind stress was added as a predictor (mean AUC improvement = 0.005; mean TSS improvement = -0.017; $p > 0.05$).

*Juncus scheuchzerioides* and *Ranunculus biternatus* occurrence and cover were better predicted when including wind stress (i.e. had higher AUC and TSS values for the full models than for the simple models; see Appendix S20 for values and for results from GLM and GBM). In addition, one species' occurrence had higher AUC, but not TSS (*Agrostis stolonifera*), while four species showed higher TSS values, but not AUC, when including wind (*Cerastium fontanum, Lycopodium magellanicum, Poa annua, Poa cookii*). For models of species cover, a further three species had higher AUC values in the model accounting for wind (*Agrostis stolonifera, Lycopodium magellanicum, Sagina procumbens*), and two species had higher TSS values (*Poa annua, Poa cookii*; see Appendix S20 for values and for results from GLM and GBM).

**Table 2** Names and details of species used in analyses. Alien species are preceded by *. Plant functional trait values from Bjorkman et al. (2018), Rossouw (2014), and Louw (2016). Plant height values for the three species indicated with ▲ are based on personal observations.

| **Species** | **Clade** | **Family** | **Plant height (m)** | **Specific leaf area ($mm^2/mg$)** | **Leaf area ($mm^2$)** | **Leaf nitrogen content (g/g)** | **Leaf phosphorous content (g/g)** | **Percentage of quadrats present** | **Mean cover across all quadrats (%)** |
|---|---|---|---|---|---|---|---|---|---|
| *Acaena magellanica* (Lam.) Vahl | Angiosperm | Rosaceae | 0.09 | 11.97 | 3619.63 | 2.47 | 0.22 | 37.8 | 3.20 |
| **Agrostis stolonifera* L. | Angiosperm | Poaceae | 0.17 | 47.31 | 272.19 | 2.83 | 0.35 | 1.0 | 0.31 |
| *Austroblechnum penna-marina* (Poir.) Gasper & V.A.O.Dittrich | Pteridophyte | Blechnaceae | 0.18 | 13.08 | 1535.93 | 1.53 | 0.19 | 89.9 | 27.52 |
| *Azorella selago* Hook.f. | Angiosperm | Apiaceae | 0.14 | 8.71 | 63.75 | 1.67 | 0.18 | 65.8 | 7.19 |
| *Carex dikei* (Nelmes) K.L.Wilson | Angiosperm | Cyperaceae | 0.08 | 9.94 | 793.72 | 1.62 | 0.16 | 30.3 | 5.17 |
| **Cerastium fontanum* Baumg. | Angiosperm | Caryophyllaceae | 0.20 | 20.07 | 133.33 | 4.37 | 0.68 | 2.0 | 0.01 |
| *Hymenophyllum peltatum* (Poir.) Desv. | Pteridophyte | Hymenophyllaceae | 0.01▲ | NA | NA | NA | NA | 8.5 | 0.35 |
| *Juncus scheuchzerioides* Gaudich. | Angiosperm | Juncaceae | 0.03 | 14.48 | 62.17 | 1.95 | 0.17 | 12.9 | 1.07 |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| *Lycopodium magellanicum* (P.Beauv.) Sw. | Pteridophyte | Lycopodiaceae | 0.01$^{\blacktriangle}$ | NA | NA | 1.51 | 0.14 | 1.4 | 0.01 |
| *Notogrammitis crassior* (Kirk) Parris | Pteridophyte | Polypodiaceae | 0.03 | 14.6 | 109.86 | 1.31 | 0.09 | 2.8 | 0.16 |
| *Phlegmariurus saururus* (Lam.) B.Øllg. | Pteridophyte | Lycopodiaceae | 0.10$^{\blacktriangle}$ | NA | NA | 1.03 | 0.11 | 3.4 | 0.02 |
| **Poa annua* L. | Angiosperm | Poaceae | 0.15 | 42.01 | 304.55 | 5.23 | 0.46 | 5.1 | 0.11 |
| *Poa cookii* Hook.f. | Angiosperm | Poaceae | 0.32 | 10.49 | 5335.06 | 2.06 | 0.21 | 16.0 | 1.09 |
| *Polypogon magellanicus* (Lam.) Finot | Angiosperm | Poaceae | 0.18 | 18.12 | 2102.62 | 1.99 | 0.19 | 81.2 | 6.90 |
| *Ranunculus biternatus* Sm. | Angiosperm | Ranunculaceae | 0.02 | 15.02 | 104.96 | 2.68 | 0.29 | 20.9 | 0.24 |
| **Sagina procumbens* L. | Angiosperm | Caryophyllaceae | 0.12 | 43.85 | 4.87 | NA | NA | 8.1 | 0.18 |

Variable importance for wind stress varied between wind being the most important predictor and the second least important predictor. However, ten out of the sixteen species included wind stress as one of the top four predictor variables in determining the species' distribution (i.e. occurrence) based on variable importance (Table 3; values ranging between 12.99 % and 42.60 % for those ten species; importance for GLM and GBM in Appendix S15 and S16). When considering species cover, ten of the sixteen species had wind stress among the first four most important variables (Appendix S17; values ranging between 7.92 % and 30.41 % for those ten species, with GLM and GBM results in Appendix S18 and S19).

Response curves showed similar patterns within some species groups, while there were no consistent patterns across groups (Figure 1, see also Appendix S4 - S11 for response curves for all predictor variables). Pteridophytes generally had a lower probability of occurrence at higher wind stress, with the magnitude of this response varying between species (Figure 1a). Most of the grass species, showed higher probability of occurrence under high wind stress, with the exception of *Poa annua* that showed a hump-shaped relationship with wind stress (Figure 1b). Mire species (i.e. species characteristic of the wettest terrestrial habitats) showed more complex response curve shapes, with *Juncus scheuchzerioides* having higher chances of occurrence at both intermediate and high wind stress, *Ranunculus biternatus* having the highest probability of occurrence at intermediate wind stress, and *Carex dikei* showing an increasing chance of being present with higher wind stress (Figure 1c). For the remaining species, the two indigenous species (*Azorella selago* and *Acaena magellanica*) were more likely to occur in sites with higher wind stress (with *Azorella selago* also having a higher probability of occurrence at low wind stress), while the probability of occurrence of the two invasive species (*Sagina procumbens* and *Cerastium fontanum*) decreased under higher wind stress conditions (Figure 1d).

There were no significant correlations between the importance of wind stress in explaining species occurrence or cover and any of the traits (with one exception), irrespective of the modelling approach. The only exception was the significant relationship between leaf nitrogen and the importance of wind stress in the GLM model for species occurrence (r=0.55, p=0.04).

## Discussion

The majority of the species in this chronically windy sub-Antarctic environment were limited in their occurrence and cover, to some degree, by wind. For example, wind stress was a significant predictor for the occurrence of twelve of the sixteen species, even after accounting for multiple other variables known to strongly affect plant species performance and distribution. Notably, wind stress was a more important predictor than either soil temperature or soil moisture for six species' occurrence and five species' cover. This highlights that, despite temperature and precipitation receiving the majority of attention as drivers of plant species distribution models to date (Gardner et al., 2019), other environmentally meaningful predictors also need to be accounted for to improve predictions of species current and future distributions (Mod et al., 2016). While data are lacking for some biologically important environmental variables (e.g. soil pH; Mod et al., 2016), global estimates of wind speed (up to a spatial resolution of 30 second; equivalent to c. 1 km at the equator) are available (through WorldClim; Fick and Hijmans, 2017). However, these data are not as commonly considered in models, probably, at least in part, due to a lack of future wind scenarios.

Both invasive and native species' fine-scale biogeography were affected by wind stress. The invasive species distributions, with the exception of *Agrostis stolonifera*, were all strongly (i.e. significantly and with high variable importance) related to wind stress. *Poa annua*, *Cerastium fontanum,* and *Sagina procumbens* all had high variable importance scores for wind stress, and were all absent from sites with high wind stress. *Agrostis stolonifera* was more tolerant of higher wind stress than the other three invasive species, but was still less likely to occur in very windy microsites compared to the two indigenous grasses, in agreement with the species being limited to less windy sites than *Polypogon magellanicus* due to its lower investment in support tissue (Pammenter et al., 1986). Wind is considered in terms of dispersal when examining alien species distributions (Egawa, 2017; Wan et al., 2017), but clearly also needs to be considered in terms of habitat suitability as well.

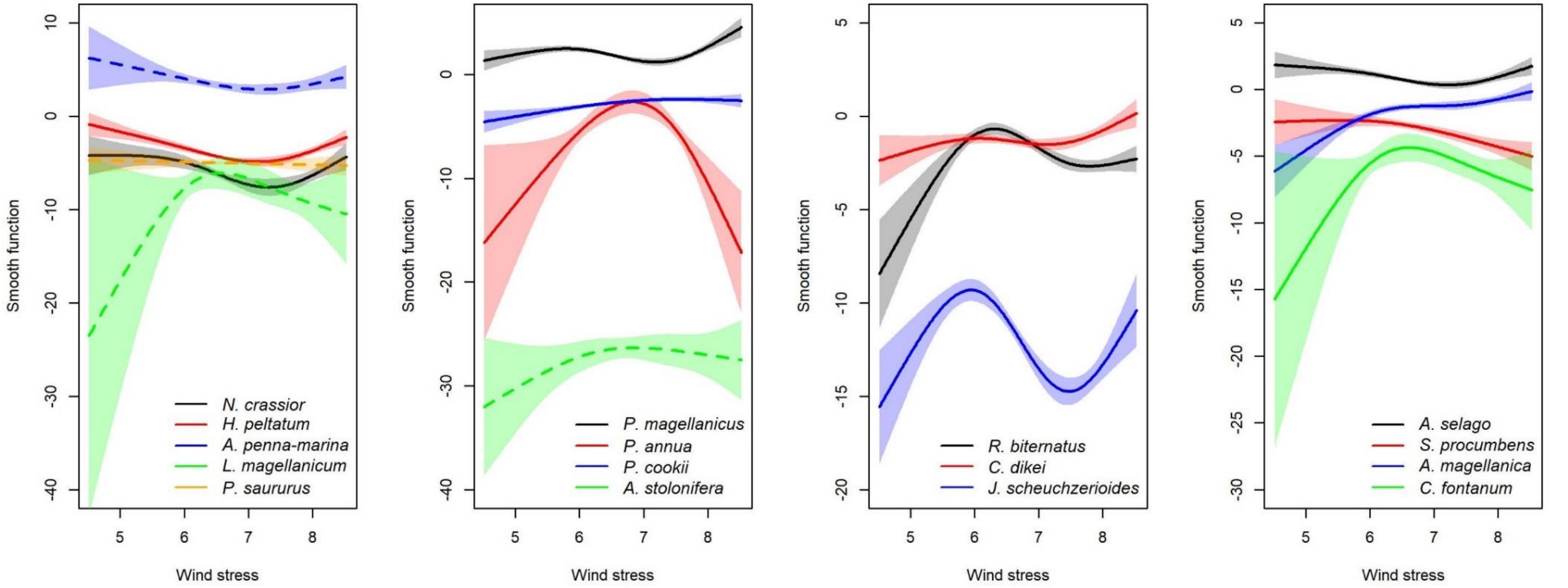

**Figure 3** Response curves from the full GAM of the occurrence of all species in response to wind stress. Dashed lines represent models where wind stress was not a significant predictor of species occurrence in the multivariate models. a) Pteridophytes; *N. crassior* = *Notogrammitis crassior*, *H. peltatum* = *Hymenophyllum peltatum*, *A. penna-marina* = *Austroblechnum penna-marina*, *L. magellanicum* = *Lycopodium magellanicum*, *P. saururus* = *Phlegmariurus saururus*. b) Poaceae; *P. magellanicus* = *Polypogon magellanicus*, *P. annua* = *Poa annua*, *P. cookii* = *Poa cookii*, *A. stolonifera* = *Agrostis stolonifera*. c) Mire species; *R. biternatus* = *Ranunculus biternatus*, *C. dikei* = *Carex dikei*, *J. scheuchzerioides* = *Juncus scheuchzerioides.* d) All other species; *A. selago* = *Azorella selago*, *S. procumbens* = *Sagina procumbens*, *A. magellanica* = *Acaena magellanica*, *C. fontanum* = *Cerastium fontanum*.

**Table 2** Comparison of the magnitude of deviance explained for the occurrence of each species and the significance of wind stress in a GAM model which only included wind stress as a predictor (univariate model) and a GAM model that included all eight predictor variables, of which wind stress was one (multivariate model). The mean deviance explained for univariate models was 10.24 %, while for multivariate models then mean deviance explained was 34.59 %. Alien species are preceded by *.

| **Species** | **Deviance explained (%)** | | **p-value of wind stress variable** | |
|---|---|---|---|---|
| | **Univariate model** | **Multivariate model** | **Univariate model** | **Multivariate model** |
| *Acaena magellanica* | 11.2 | 47.8 | < 0.05 | < 0.05 |
| **Agrostis stolonifera* | 6.21 | 72.0 | 0.10 | 0.34 |
| *Austroblechnum penna-marina* | 18.8 | 38.7 | < 0.05 | 0.06 |
| *Azorella selago* | 0.08 | 29.4 | 0.23 | < 0.05 |
| *Carex dikei* | 2.78 | 38.1 | < 0.05 | <0.05 |
| **Cerastium fontanum* | 11.4 | 34.7 | < 0.05 | < 0.05 |
| *Hymenophyllum peltatum* | 23.4 | 40.7 | < 0.05 | < 0.05 |
| *Juncus scheuchzerioides* | 25.4 | 46.3 | < 0.05 | < 0.05 |
| *Lycopodium magellanicum* | 9.57 | 27.9 | < 0.05 | 0.07 |
| *Notogrammitis crassior* | 14.6 | 51.7 | < 0.05 | < 0.05 |
| *Phlegmariurus saururus* | 6.68 | 25.1 | < 0.05 | 0.64 |
| **Poa annua* | 22.6 | 46.7 | < 0.05 | < 0.05 |
| *Poa cookii* | 1.16 | 24.1 | < 0.05 | <0.05 |
| *Polypogon magellanicus* | 4.21 | 25.7 | < 0.05 | < 0.05 |
| *Ranunculus biternatus* | 2.52 | 17.0 | < 0.05 | <0.05 |
| **Sagina procumbens* | 3.23 | 16.7 | < 0.05 | < 0.05 |

**Table 3** Relative variable importance (%) for each predictor variable based on the full GAM model for species occurrence. Variables with > 20 % variable importance are in bold. Alien species are preceded by *.

| | **Wind stress: maximum** | **PDIR** | **Soil depth** | **Rock cover** | **Temperature: winter** | **Temperature: summer** | **Soil moisture** | **pH** |
|---|---|---|---|---|---|---|---|---|
| *Acaena magellanica* | 8.41 | 10.19 | 4.60 | 2.26 | **37.16** | 3.79 | 13.90 | **19.69** |
| **Agrostis stolonifera* | 2.25 | **20.11** | 2.84 | 5.95 | **24.63** | 14.16 | 1.89 | **28.17** |
| *Austroblechnum penna-marina* | 12.99 | 1.28 | 7.68 | 17.03 | 3.28 | 16.49 | 5.44 | **35.79** |
| *Azorella selago* | 5.46 | 6.38 | 7.04 | **22.61** | 6.03 | 2.03 | 10.95 | **39.52** |
| *Carex dikei* | 3.71 | 10.74 | 8.43 | 5.98 | 5.36 | 0.37 | **55.84** | 9.58 |
| **Cerastium fontanum* | **24.99** | 16.97 | 2.85 | **33.74** | 4.31 | 7.38 | 3.33 | 6.43 |
| *Hymenophyllum peltatum* | **30.72** | 1.86 | **34.47** | 10.33 | 0.48 | 0.18 | 8.38 | 13.58 |
| *Juncus scheuchzerioides* | **42.60** | 7.96 | 3.36 | 18.27 | 0.24 | 1.49 | **21.62** | 4.47 |
| *Lycopodium magellanicum* | **23.54** | 0.46 | 8.74 | 0.03 | **35.72** | 0.28 | 13.56 | 17.67 |
| *Notogrammitis crassior* | **20.86** | 0.06 | 11.71 | **41.41** | < 0.01 | 0.08 | 8.45 | 17.42 |
| *Phlegmariurus saururus* | 0.97 | 0.70 | **33.72** | **35.11** | 3.42 | 0.92 | 3.23 | **21.93** |
| **Poa annua* | **40.18** | 3.70 | 6.10 | 11.64 | 16.62 | 0.59 | 11.62 | 9.54 |
| *Poa cookii* | 9.33 | 7.86 | 14.28 | 0.58 | 14.49 | 2.99 | **23.58** | **26.90** |
| *Polypogon magellanicus* | 16.02 | 7.64 | 7.14 | 2.32 | 17.52 | 0.11 | **22.12** | **27.12** |
| *Ranunculus biternatus* | **23.35** | 11.48 | **27.53** | 3.92 | 7.71 | 2.81 | 14.11 | 9.10 |
| **Sagina procumbens* | 14.36 | 8.59 | **21.13** | 6.62 | 13.50 | 14.42 | 6.07 | 15.31 |

Seven out of the twelve native species distributions were strongly driven by wind stress. Wind stress was the most important driver of species occurrence for *Juncus scheuzerioides*, and the second most important predictor of the presence of *Ranunculus biternatus*. These two species are characteristic of mire habitats, and they occur more frequently in moist environments (Smith and Steenkamp, 2001). Wind has a desiccating effect on both soil and plants' leaves , and, therefore, affects moisture availability (Bertiller et al., 1996; Gardiner et al., 2016). In the high arctic, vascular plant species show a preference for microsites with lower wind speed, greater moisture, and higher temperature, likely reflecting how these three variables are intrinsically linked in some environments (Sohlberg and Bliss, 1984). Likewise, all but one of the pteridophtes, *Phlegmariurus saururus,* responded strongly to wind. The three fern species all showed generally lower probability of occurrence under higher wind stress conditions. The lycophyte species, *Lycopodium magellanicum*, had a low probability of occurrence under low wind stress (in contrast to the ferns), but also showed a decline in occurrence after reaching a peak at intermediate wind stress. Fern and lycophyte stomata are highly sensitive to drought and there is a very small margin of leaf water potential between stomatal closure due to drought stress and permanent leaf death (McAdam and Brodribb, 2013). This may be particularly important for species with an affinity for high-moisture environments under the current climatic changes taking place on Marion Island, where annual precipitation has declined by a third between 1950 and 2000, and the number of days between rainfall events has increased (le Roux and McGeoch, 2008; Hedding and Greve, 2018).

Contrary to the patterns exhibited by the other mire and fern species, the cover and occurrence of *Carex dikei* (also characteristic of wet environments) and *Phlegmarius saururus* (a lycophyte) were not strongly correlated to wind stress. *Phlegmariurus saururus* is characteristically found in rock crevices (Crouch et al., 2011), in agreement with rock cover being the most important variable in determining its occurrence in this study. Rock crevices may be less susceptible to drying from wind due to the sheltered nature of the habitat (Haussmann et al., 2010), which could be why *P. saururus* seems to be unaffected by both soil moisture and wind stress. *Carex dikei* (previously *Uncinia dikei*) is native only to Marion Island and the neighbouring Prince Edward Island (Global Carex Group, 2015). This species (and the entire genus *Uncinia*) likely evolved in the Antarctic (Nelmes, 1951), an environment of high and chronic wind stress. Further, the present pattern of distribution for the genus *Carex* is suggested to be due to cooling temperatures during the late Tertiary being the driver for diversification in this genus (Escudero et al., 2012). Therefore, the species has evolved under cold temperatures, which may also be linked to windy habitats in this region.

Leaf nitrogen and wind stress variable importance were significantly related for species occurrence in the GLM model, with a marginally significant relationship for importance from the GAM model. The positive relationship between these variables indicates that wind stress is more important for species with higher leaf nitrogen. *Poa annua* and *Cerastium fontanum*, the two species with the highest leaf nitrogen content (with much higher values than any of the other species), both show a peak in occurrence at intermediate wind stress. Higher leaf nitrogen content relates to plants having greater photosynthetic ability (Osone and Tateno, 2005). Since plants may close their stomata under very windy conditions to reduce water loss, thereby affecting photosynthesis (de Langre, 2008), those species with higher leaf nitrogen content will reach higher rates of photosynthesis during the period when conditions are favourable enough (i.e. low or intermediate wind speeds) for stomata to remain open. Other plant functional traits were not related to how strongly wind stress affects species distributions. That plant height did not have a significant relationship with the importance of wind stress was an unexpected result, which may reflect that the species on Marion Island are all short in stature (mean height ranging between 0.01 and 0.32 m), thereby not showing enough variation in plant height to capture any differences that may be related to this trait (and suggesting that wind stress may be an abiotic filter that acts on plant height). Wind may further have an effect on species occurrence or cover through mechanical damage or moisture loss through the leaves (Hadley and Smith, 1983; Gardiner et al., 2016), and these impacts would not be reflected in the plant functional traits investigated here. Traits reflecting the strength of leaves (e.g. force to tear) and leaf water potential may be worth investigating to test whether a relationship exists with wind stress (see e.g. Onoda and Anten, 2011).

In this study we have sampled the majority of the vascular plant species occurring in this system, and have used accurate field-collected data from a large number of plots, providing a robust test of our hypotheses. There are, however, several other aspects that should still be investigated to provide a more complete understanding of the impacts of chronic wind. For example, wind may have impacts on plant functional traits that were not considered here, including specifically stem density and flexibility (Saiz et al., 2021) and root characteristics (Zhang et al., 2021). The dispersal of propagules through wind could also have an impact on species occurrences at the fine scale (as demonstrated at coarser scales; e.g. Engler et al. 2009). In our study system, rocks and nurse plants may trap seeds, affecting fine-scale abundance and occurrence patterns (Haussmann et al., 2010; although see also Gouws et al., 2021). As a result, an explicit incorporation of seed dispersal, particularly via wind, is still necessary when modelling species occurrence patterns. These nurse plants could potentially also act as facilitator species by providing shelter from wind (Körner, 2003).

Here, wind stress emerges as an important driver of species' distributions and cover for the majority of species, suggesting that the inclusion of wind can improve the accuracy of models of plant distributions. Global forecast data for future climate projections often lack projections for wind characteristics (Fick and Hijmans, 2017). Therefore, when predicting how species will react to climatic changes, it is potentially problematic that information on both future wind speed and dominant wind direction may be less frequently available than forecasts for temperature and precipitation, particularly since wind conditions are currently changing and these changes are predicted to continue into the future (Jeong and Sushama, 2019; Zeng et al., 2019; Abell et al., 2021). Further, while the effect of mean wind stress was considered here, other wind characteristics should be investigated to determine their importance, for example turbulence and maximum gust speed (which are, for example, influential in seed dispersal models; Caplat et al., 2012; Heydel et al., 2014). Broadly, this further highlights the need to incorporate more biologically-meaningful environmental predictors in species distribution models (Mod et al., 2016; Barton, 2017), and at suitable spatial scales (Guisan et al., 2007).

On average, global wind speeds have increased over the last three decades (1985 - 2018; Young and Ribal, 2019). Based on evidence from past climates, under continued warming westerly winds in both hemispheres are predicted to shift poleward (Perren et al., 2020; Abell et al., 2021). Predicting how these changes will affect plant species in particular will be a challenge, due to the fact that wind not only directly affects plants through physiological responses, but also has an indirect effect on flora through changes in seed dispersal (Tackenberg and Stöcklin, 2008), pollination probability due to impacts on insect activity (e.g. Chown et al., 2004), and changes to the substrate in which plants grow (e.g. through dessication; Fitzgerald and Kirkpatrick, 2017). Therefore, future studies should incorporate wind as a climatic driver of biogeography to generate more accurate predictions of both current and future species distributions.

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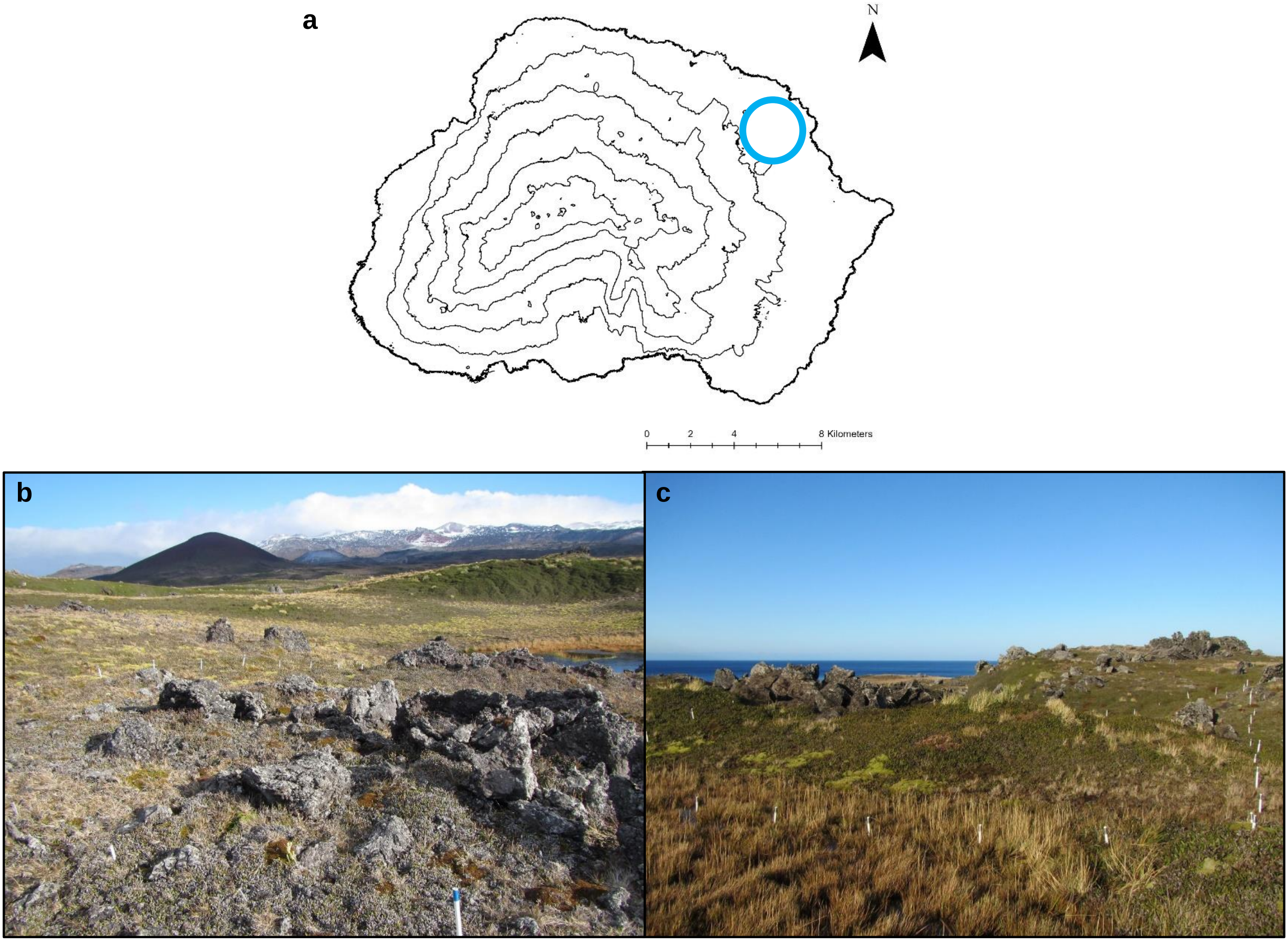
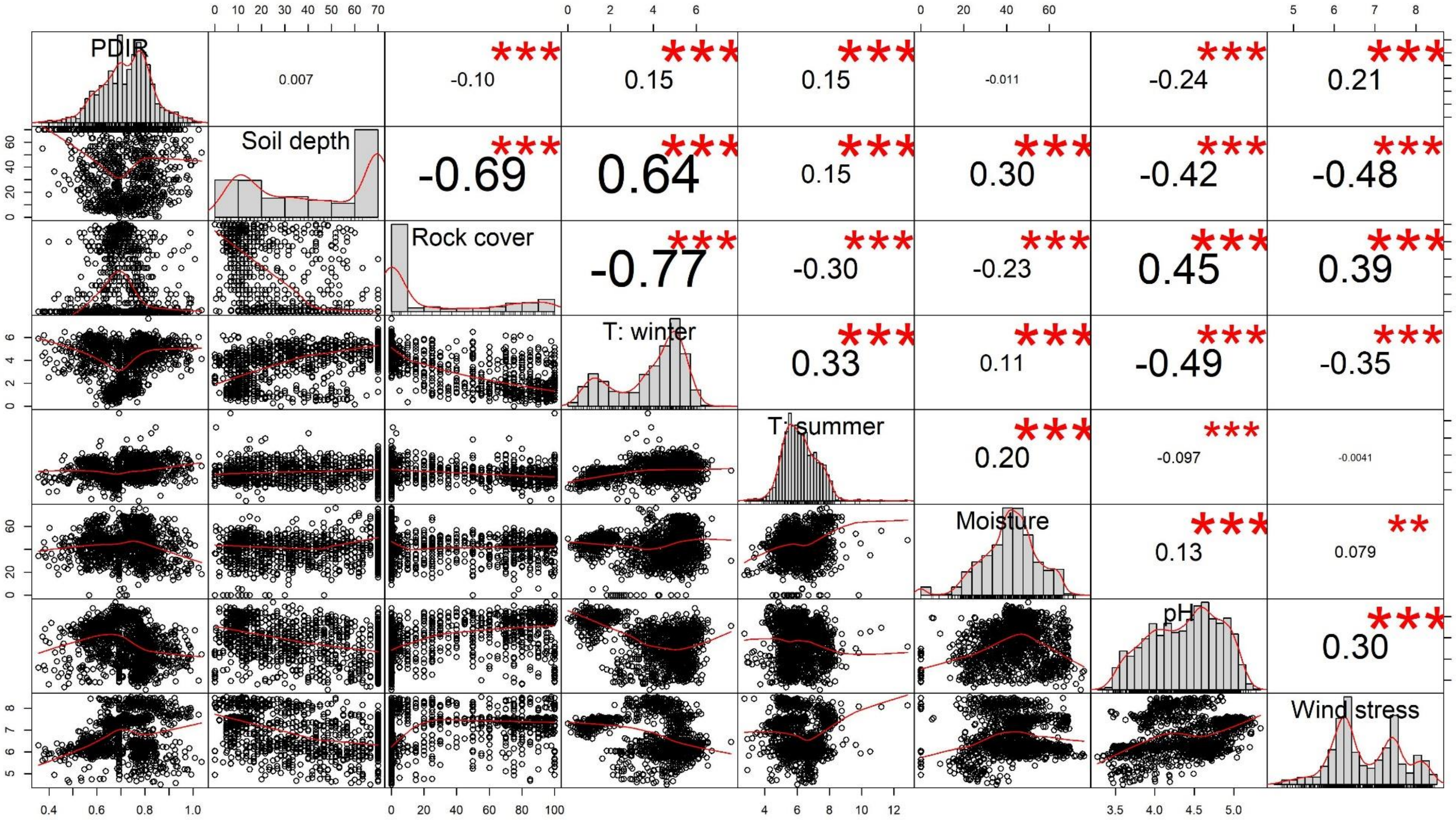
# Appendix

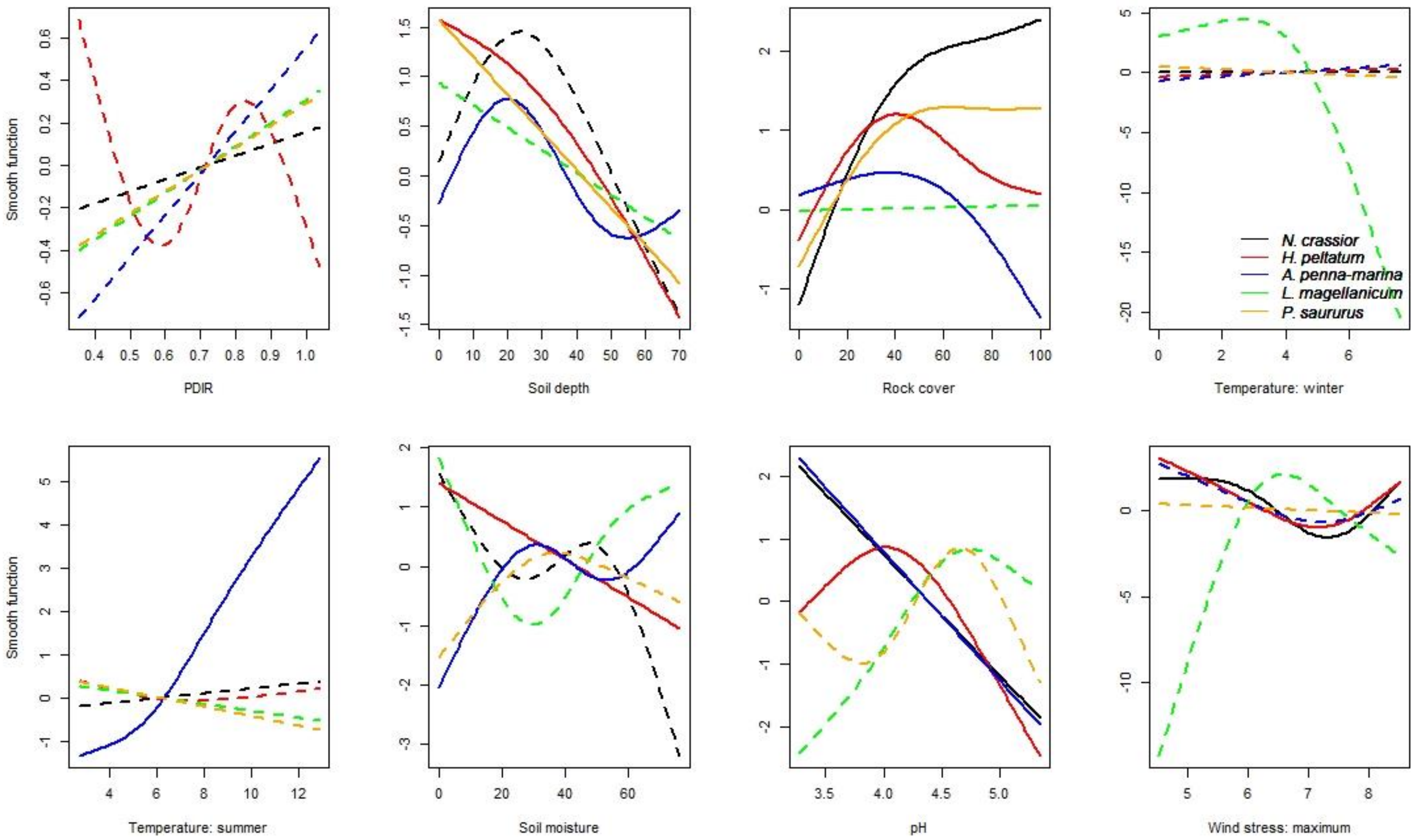


**Appendix S1.** a) Map of Marion Island with the study site location indicated by a blue circle, and photographs of the study site, illustrating b) the grid with the highest mean wind stress, and c) the grid with the lowest mean wind stress.

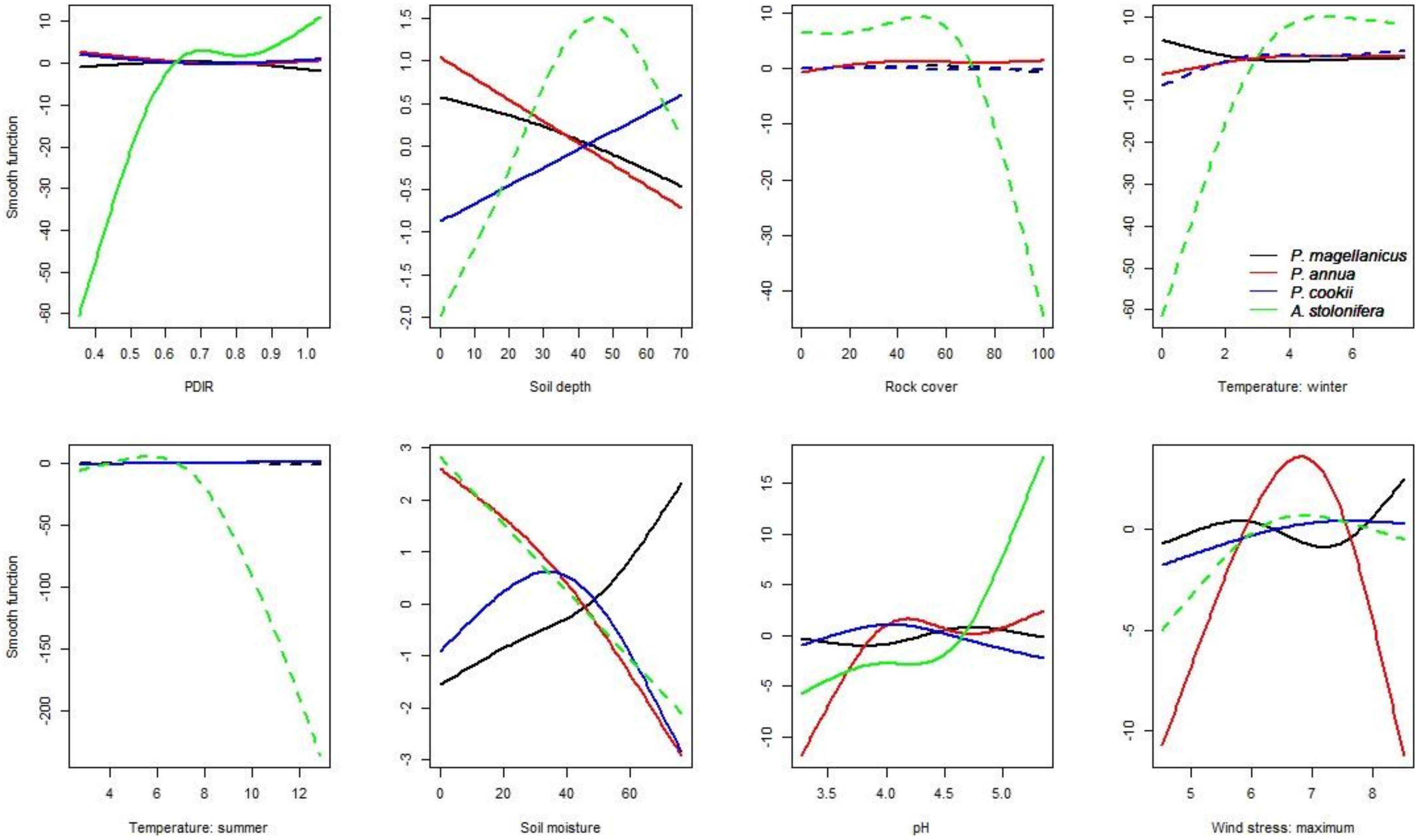
**Appendix S2.** Photographs of a selection of species: a) *Austroblechnum penna-marina*, b) *Ranunculus biternatus* (photo by Elsa van Ginkel), c) *Azorella selago*, with *Polypogon magellanicus* growing on top of it, d) *Phlegmarius saururus* (photo by Peter C. le Roux).



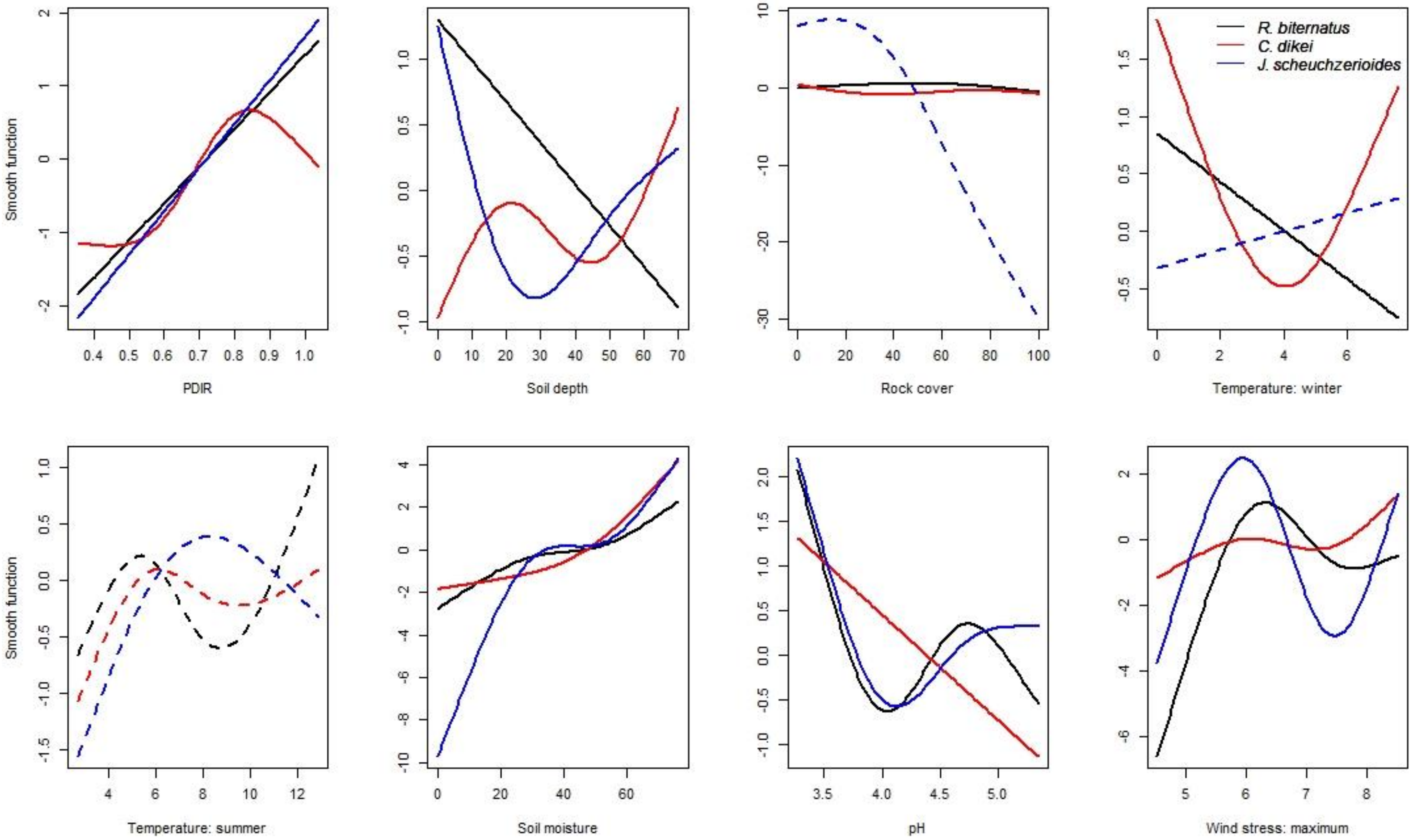
**Appendix S3.** Correlation matrix of all predictor variables. Histograms on the diagonal show the distribution of each variable. Values above the diagonal indicate Pearson correlation values between predictors, with significant correlations indicated by * (**= $p<0.01$, ***= $p<0.05$). Below the diagonal are bivariate scatterplots with a fitted line. PDIR = potential direct incident radiation; T = temperature.



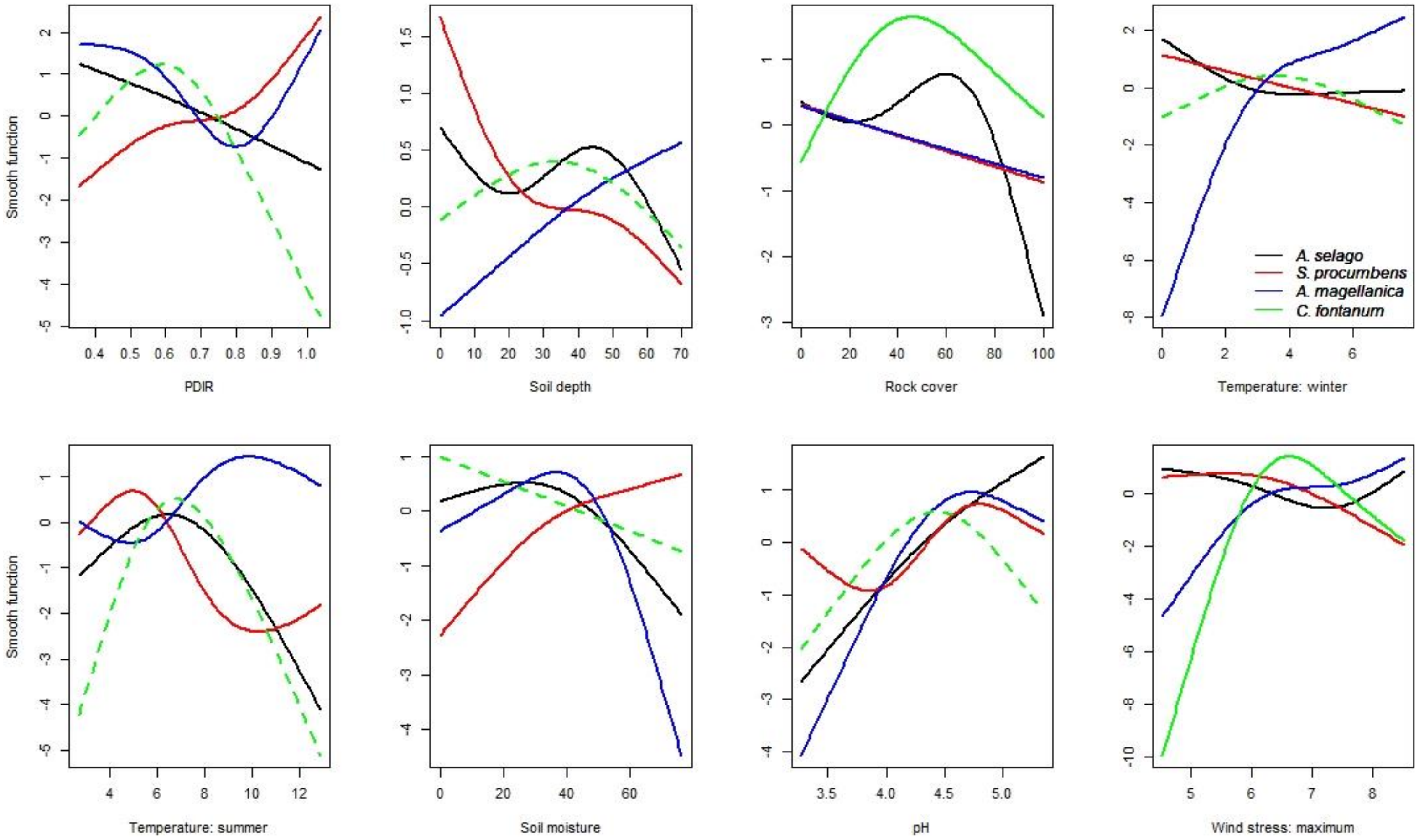
**Appendix S4.** Response curves from the full GAM of the occurrence of all pteridophytes in response to the eight predictor variables. *N. crassior = Notogrammitis crassior, H. peltatum = Hymenophyllum peltatum, A. penna-marina = Austroblechnum penna-marina, L. magellanicum = Lycopodium magellanicum, P. saururus = Phlegmariurus saururus.* Dashed lines represent relationships that were not significant, while solid lines illustrate significant relationships.



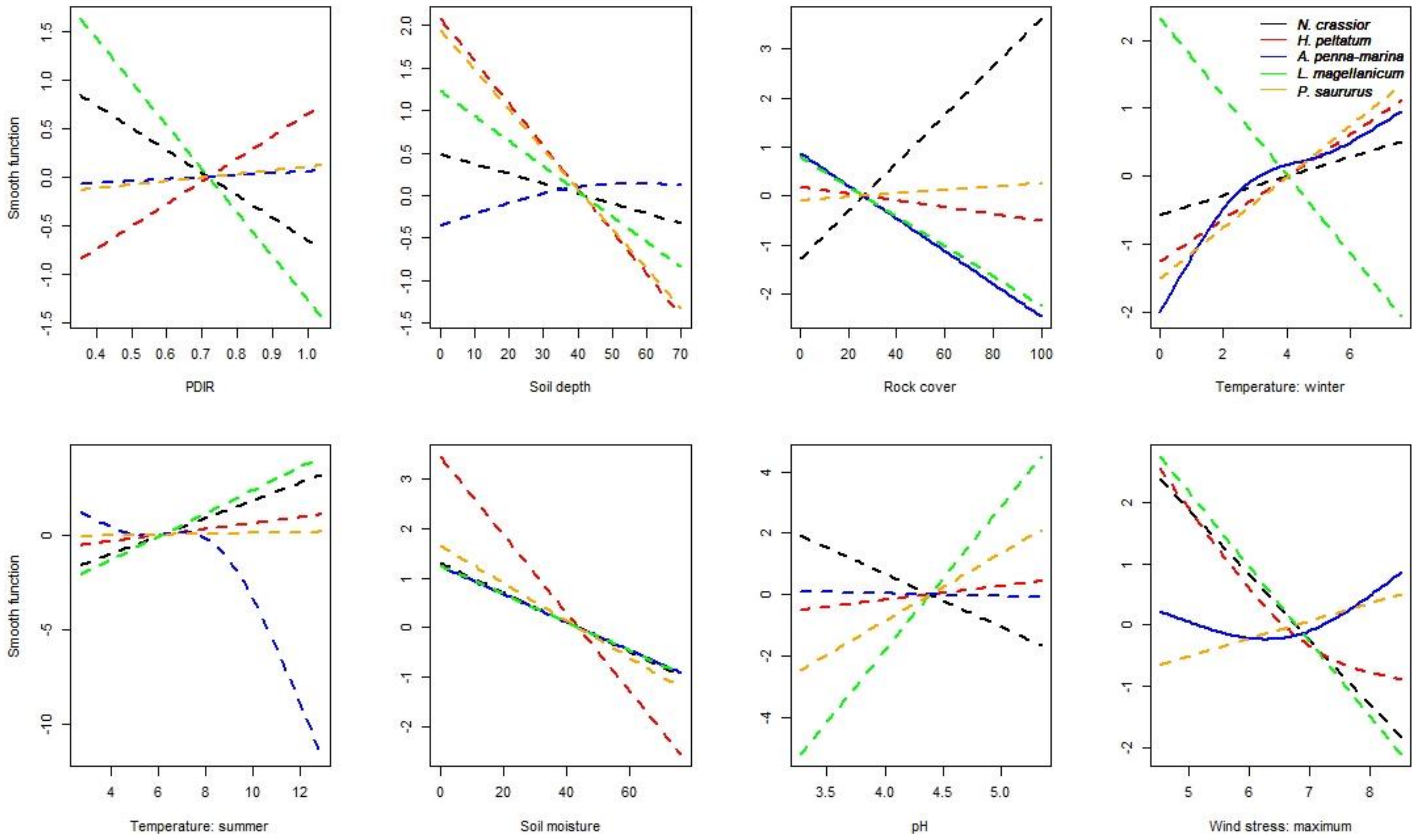
**Appendix S5.** Response curves from the full GAM of the occurrence of all Poaceae (grasses) in response to the eight predictor variables. *P. magellanicus = Polypogon magellanicus, P. annua = Poa annua, P. cookii = Poa cookii, A. stolonifera = Agrostis stolonifera.* Dashed lines represent relationships that were not significant, while solid lines illustrate significant relationships.



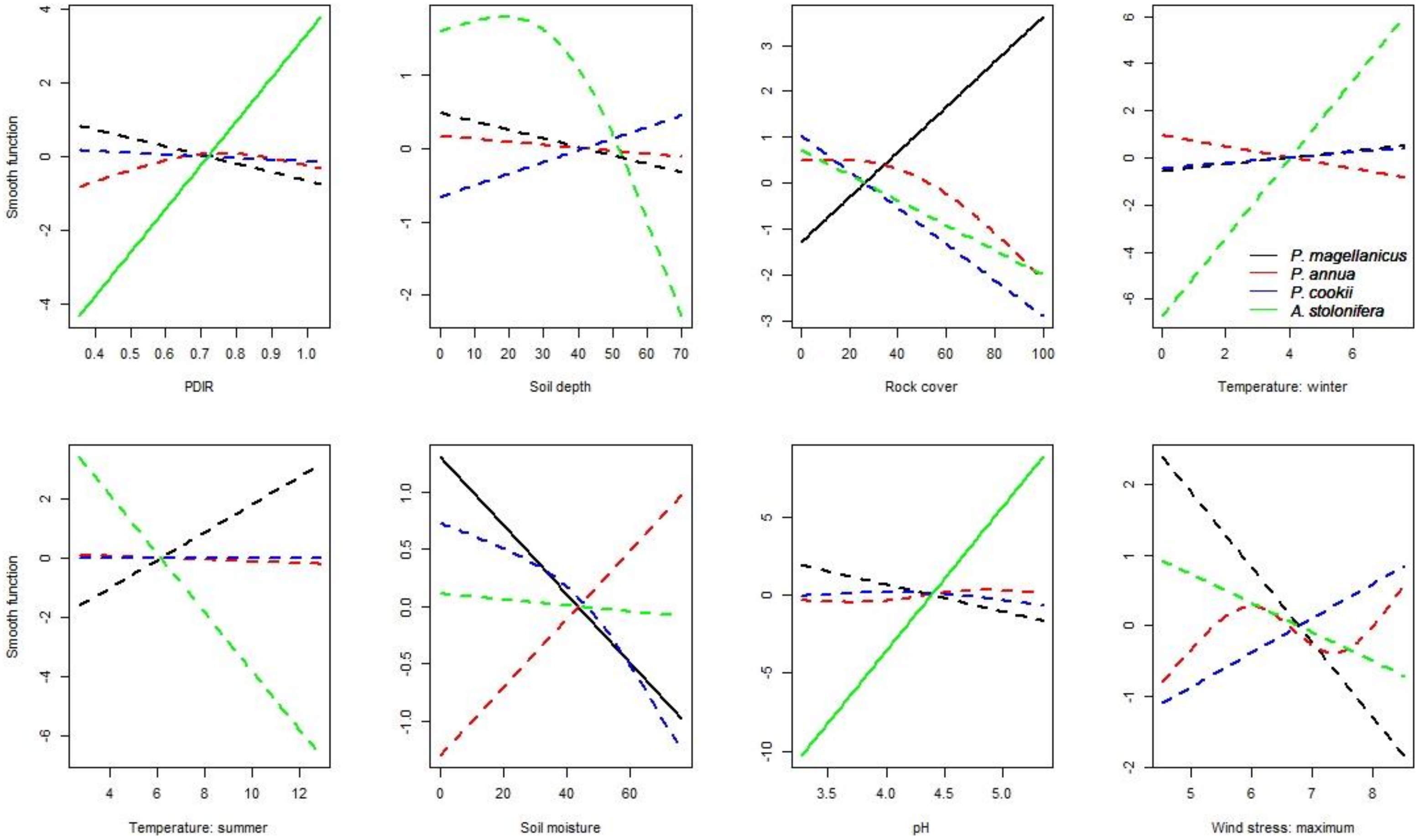
**Appendix S6.** Response curves from the full GAM of the occurrence of mire species in response to the eight predictor variables. *R. biternatus* = *Ranunculus biternatus*, *C. dikei* = *Carex dikei*, *J. scheuchzerioides* = *Juncus scheuchzerioides*. Dashed lines represent relationships that were not significant, while solid lines illustrate significant relationships.



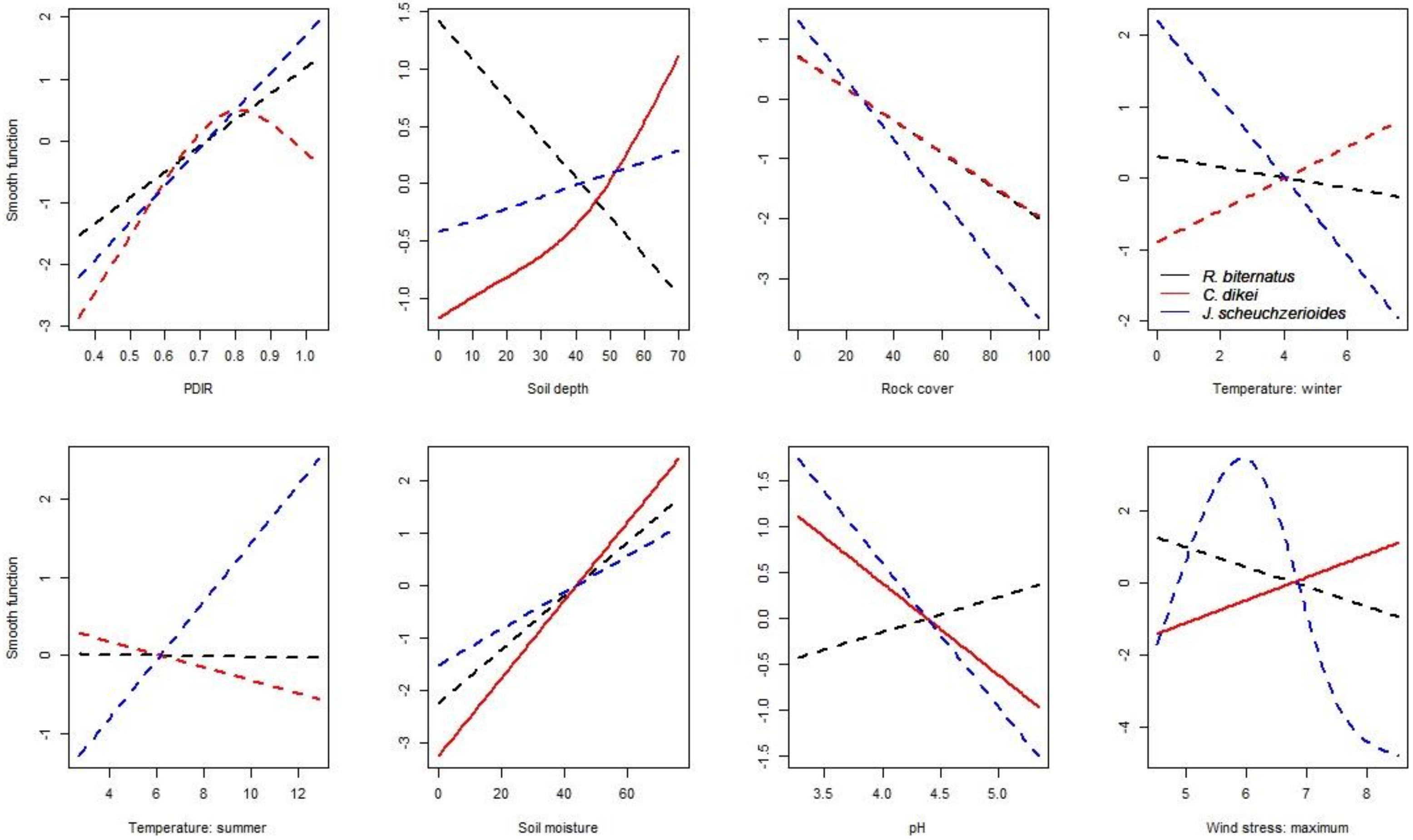
**Appendix S7.** Response curves from the full GAM of the occurrence of all other angiosperms in response to the eight predictor variables. *A. selago* = *Azorella selago*, *S. procumbens* = *Sagina procumbens*, *A. magellanica* = *Acaena magellanica*, *C. fontanum* = *Cerastium fontanum*. Dashed lines represent relationships that were not significant, while solid lines illustrate significant relationships.



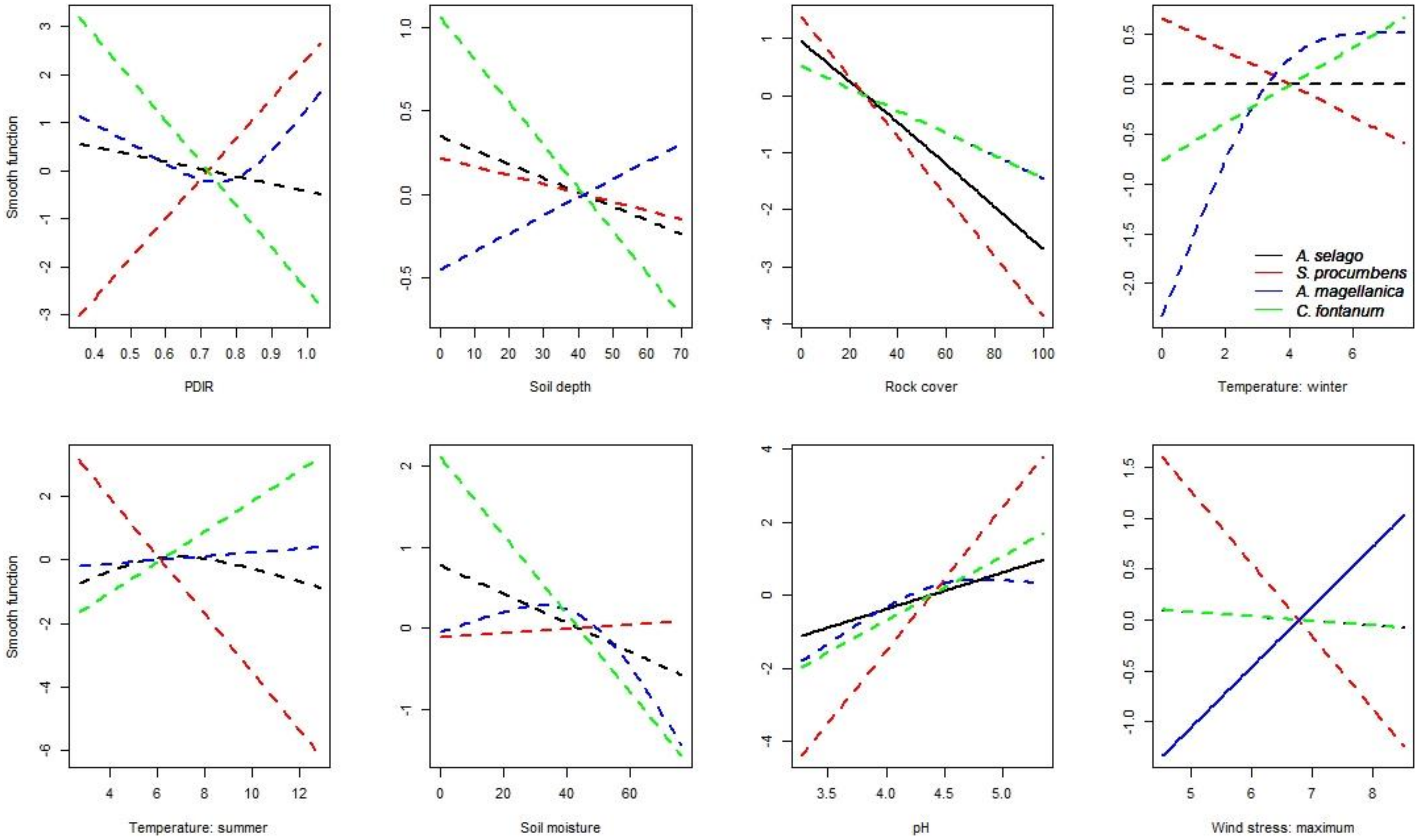
**Appendix S8.** Response curves from the full GAM of the cover of all pteridophytes in response to the eight predictor variables. *N. crassior* = *Notogrammitis crassior*, *H. peltatum* = *Hymenophyllum peltatum*, *A. penna-marina* = *Austroblechnum penna-marina*, *L. magellanicum* = *Lycopodium magellanicum*, *P. saururus* = *Phlegmariurus saururus*. Dashed lines represent relationships that were not significant, while solid lines illustrate significant relationships.



**Appendix S9.** Response curves from the full GAM of the cover of all Poaceae (grasses) in response to the eight predictor variables. *P. magellanicus* = *Polypogon magellanicus*, *P. annua* = *Poa annua*, *P. cookii* = *Poa cookii*, *A. stolonifera* = *Agrostis stolonifera*. Dashed lines represent relationships that were not significant, while solid lines illustrate significant relationships.



**Appendix S10.** Response curves from the full GAM of the cover of mire species in response to the eight predictor variables. *R. biternatus* = *Ranunculus biternatus*, *C. dikei* = *Carex dikei*, *J. scheuchzerioides* = *Juncus scheuchzerioides*. Dashed lines represent relationships that were not significant, while solid lines illustrate significant relationships.



**Appendix S11.** Response curves from the full GAM of the cover of all other angiosperms in response to the eight predictor variables. *A. selago* = *Azorella selago*, *S. procumbens* = *Sagina procumbens*, *A. magellanica* = *Acaena magellanica*, *C. fontanum* = *Cerastium fontanum*. Dashed lines represent relationships that were not significant, while solid lines illustrate significant relationships.

**Appendix S12.** Comparison of the magnitude of deviance explained for the occurrence of each species and the significance of wind stress in a GLM model which only included wind stress as a predictor (univariate model) and a GLM model that included all eight predictor variables, of which wind stress was one (multivariate model). The mean deviance explained for univariate models was 1.75 %, while for multivariate models then mean deviance explained was 25.55 %. Alien species are preceded by *.

| **Species** | **Deviance explained (%)** | | **p-value of wind stress variable** | |
|---|---|---|---|---|
| | **Univariate model** | **Multivariate model** | **Univariate model** | **Multivariate model** |
| *Acaena magellanica* | 0.16 | 35.61 | 0.08 | < 0.05 |
| **Agrostis stolonifera* | 3.21 | 47.68 | < 0.05 | 0.12 |
| *Austroblechnum penna-marina* | 3.11 | 34.47 | < 0.05 | 0.71 |
| *Azorella selago* | 0.08 | 21.30 | 0.23 | 0.10 |
| *Carex dikei* | 0.39 | 33.41 | < 0.05 | 0.09 |
| **Cerastium fontanum* | 0.15 | 16.42 | 0.52 | 0.36 |
| *Hymenophyllum peltatum* | 0.58 | 28.52 | < 0.05 | 0.74 |
| *Juncus scheuchzerioides* | 10.18 | 33.98 | < 0.05 | < 0.05 |
| *Lycopodium magellanicum* | 1.24 | 18.71 | 0.11 | 0.26 |
| *Notogrammitis crassior* | 1.40 | 42.02 | < 0.05 | 0.14 |
| *Phlegmariurus saururus* | 3.96 | 19.93 | < 0.05 | 0.79 |
| **Poa annua* | 0.34 | 21.39 | 0.16 | 0.15 |
| *Poa cookii* | 0.02 | 15.15 | 0.64 | < 0.05 |
| *Polypogon magellanicus* | 3.01 | 18.95 | < 0.05 | 0.79 |
| *Ranunculus biternatus* | 0.19 | 8.97 | 0.09 | < 0.05 |
| **Sagina procumbens* | 0.01 | 12.32 | 0.75 | < 0.05 |

**Appendix S13.** Comparison of the magnitude of deviance explained for the cover of each species and the significance of wind stress in a GAM model which only included wind stress as a predictor (univariate model) and a GAM model that included all eight predictor variables, of which wind stress was one (multivariate model). The mean deviance explained for univariate models was 8.6 %, while for multivariate models then mean deviance explained was 43.4 %. Alien species are preceded by *.

| **Species** | **Deviance explained (%)** | | **p-value of wind stress variable** | |
|---|---|---|---|---|
| | **Univariate model** | **Multivariate model** | **Univariate model** | **Multivariate model** |
| *Acaena magellanica* | 5.04 | 38.1 | 0.13 | < 0.05 |
| **Agrostis stolonifera* | 9.28 | 73.5 | 0.43 | 0.72 |
| *Austroblechnum penna-marina* | 13.6 | 60.1 | < 0.05 | < 0.05 |
| *Azorella selago* | 6.84 | 28.6 | < 0.05 | 0.78 |
| *Carex dikei* | 3.70 | 72.9 | < 0.05 | < 0.05 |
| **Cerastium fontanum* | 1.03 | 21.3 | 0.90 | 0.99 |
| *Hymenophyllum peltatum* | 33.40 | 56.8 | 0.08 | 0.18 |
| *Juncus scheuchzerioides* | 34.90 | 66.7 | 0.38 | 0.40 |
| *Lycopodium magellanicum* | 0.27 | 26.5 | 0.95 | 0.86 |
| *Notogrammitis crassior* | 15.30 | 74.9 | 0.11 | 0.32 |
| *Phlegmariurus saururus* | 4.87 | 20.1 | 0.77 | 0.93 |
| **Poa annua* | 0.74 | 32.8 | 0.78 | 0.65 |
| *Poa cookii* | 0.05 | 21.1 | 0.85 | 0.18 |
| *Polypogon magellanicus* | 5.22 | 34.5 | 0.12 | 0.24 |
| *Ranunculus biternatus* | 0.50 | 22.7 | 0.79 | 0.48 |
| **Sagina procumbens* | 3.01 | 43.4 | 0.45 | 0.53 |

**Appendix S14.** Comparison of the magnitude of deviance explained for the cover of each species and the significance of wind stress in a GLM model which only included wind stress as a predictor (univariate model) and a GLM model that included all eight predictor variables, of which wind stress was one (multivariate model). The mean deviance explained for univariate models was 4.1 %, while for multivariate models then mean deviance explained was 39.3 %. Alien species are preceded by *.

| **Species** | **Deviance explained (%)** | | **p-value of wind stress variable** | |
|---|---|---|---|---|
| | **Univariate model** | **Multivariate model** | **Univariate model** | **Multivariate model** |
| *Acaena magellanica* | 0.29 | 26.22 | 0.52 | < 0.05 |
| **Agrostis stolonifera* | 3.35 | 68.86 | 0.23 | 0.52 |
| *Austroblechnum penna-marina* | 4.09 | 55.66 | < 0.05 | < 0.05 |
| *Azorella selago* | 3.05 | 27.92 | < 0.05 | 0.67 |
| *Carex dikei* | 0.02 | 70.74 | 0.80 | < 0.05 |
| **Cerastium fontanum* | 1.03 | 21.32 | 0.90 | 0.99 |
| *Hymenophyllum peltatum* | 13.01 | 54.21 | < 0.05 | 0.16 |
| *Juncus scheuchzerioides* | 15.54 | 54.47 | < 0.05 | < 0.05 |
| *Lycopodium magellanicum* | 0.27 | 26.46 | 0.95 | 0.86 |
| *Notogrammitis crassior* | 15.28 | 74.93 | 0.11 | 0.32 |
| *Phlegmariurus saururus* | 4.86 | 20.10 | 0.77 | 0.93 |
| **Poa annua* | 0.70 | 19.65 | 0.78 | 0.99 |
| *Poa cookii* | 0.05 | 19.24 | 0.85 | 0.13 |
| *Polypogon magellanicus* | 0.00 | 23.41 | 0.94 | 0.86 |
| *Ranunculus biternatus* | 0.49 | 22.70 | 0.79 | 0.48 |
| **Sagina procumbens* | 3.00 | 43.44 | 0.45 | 0.53 |

**Appendix S15.** Percentage variable importance for each predictor variable based on the full GLM model for species occurrence. Variables with > 20 % variable importance are highlighted in bold. * = alien species.

| | **Wind stress: maximum** | **PDIR** | **Soil depth** | **Rock cover** | **Temperature: winter** | **Temperature: summer** | **Soil moisture** | **pH** |
|---|---|---|---|---|---|---|---|---|
| *Acaena magellanica* | 7.37 | 8.60 | 3.71 | 1.56 | **40.37** | 2.53 | 13.22 | **22.63** |
| **Agrostis stolonifera* | 2.61 | 19.39 | 4.38 | 2.79 | **26.09** | 12.29 | 4.95 | **27.51** |
| *Austroblechnum penna-marina* | 15.49 | 2.18 | 3.58 | 11.37 | 10.40 | 18.99 | 4.80 | **33.19** |
| *Azorella selago* | 4.89 | 8.76 | 5.40 | 19.31 | 4.20 | 3.12 | 14.27 | **40.04** |
| *Carex dikei* | 2.89 | 8.64 | 5.76 | 6.42 | 3.79 | 1.01 | **61.05** | 10.45 |
| **Cerastium fontanum* | 13.85 | 17.76 | 4.86 | **32.05** | 10.11 | 8.49 | 2.34 | 10.54 |
| *Hymenophyllum peltatum* | **21.88** | 0.58 | **36.74** | 8.36 | 2.18 | 2.36 | 10.27 | 17.62 |
| *Juncus scheuchzerioides* | **31.35** | 7.02 | 3.68 | **20.83** | 0.09 | 2.48 | **25.40** | 9.15 |
| *Lycopodium magellanicum* | 16.39 | 5.55 | 7.14 | 4.89 | **32.01** | 0.41 | 13.20 | **20.41** |
| *Notogrammitis crassior* | 5.28 | 0.70 | 19.40 | **35.81** | 0.95 | 1.25 | 10.19 | **26.41** |
| *Phlegmariurus saururus* | 6.25 | 0.01 | **26.60** | **31.01** | 6.42 | 5.33 | 6.94 | 17.44 |
| **Poa annua* | **44.15** | 3.09 | 3.52 | 14.12 | **20.58** | 0.78 | 13.06 | 0.71 |
| *Poa cookii* | 10.39 | 10.12 | 13.55 | 0.60 | 6.18 | 3.91 | **25.77** | **29.49** |
| *Polypogon magellanicus* | 2.28 | 15.78 | 15.08 | 2.29 | 3.34 | 2.97 | **26.79** | **31.46** |
| *Ranunculus biternatus* | **20.27** | 7.36 | **40.53** | 7.63 | 1.50 | 5.21 | 16.99 | 0.51 |
| **Sagina procumbens* | 17.99 | 6.78 | **23.78** | 6.10 | 16.44 | 13.40 | 6.02 | 9.49 |

**Appendix S16.** Percentage variable importance for each predictor variable based on the full GBM model for species occurrence. Variables with > 20 % variable importance are highlighted in bold. * = alien species.

| | **Wind stress: maximum** | **PDIR** | **Soil depth** | **Rock cover** | **Temperature: winter** | **Temperature: summer** | **Soil moisture** | **pH** |
|---|---|---|---|---|---|---|---|---|
| *Acaena magellanica* | 3.91 | 6.08 | 0.21 | 0.09 | **60.68** | 0.01 | 1.71 | **27.30** |
| **Agrostis stolonifera* | 6.66 | **55.74** | 0.22 | 0.97 | 1.01 | 9.47 | 0.64 | **25.29** |
| *Austroblechnum penna-marina* | 0.72 | 1.06 | 1.46 | 5.90 | **72.68** | 8.78 | 0.06 | 9.33 |
| *Azorella selago* | 0.25 | 6.95 | 2.40 | 7.64 | 0.01 | 3.41 | **20.48** | **58.85** |
| *Carex dikei* | 0.08 | 16.19 | 14.79 | 0.89 | 0.17 | 0.96 | **66.58** | 0.33 |
| **Cerastium fontanum* | 2.57 | **56.98** | 8.23 | 16.15 | 0.85 | 13.64 | 0.21 | 1.37 |
| *Hymenophyllum peltatum* | **64.42** | 0.01 | 9.00 | 2.79 | 0.01 | 0.68 | **23.03** | 0.06 |
| *Juncus scheuchzerioides* | **53.90** | 6.04 | 1.65 | 0.00 | 0.02 | 0.03 | **37.89** | 0.46 |
| *Lycopodium magellanicum* | 12.82 | 0.32 | 5.33 | 0.09 | **49.15** | 0.17 | 11.89 | **20.23** |
| *Notogrammitis crassior* | **27.85** | 0.99 | 0.00 | **49.49** | 0.37 | 0.13 | **47.91** | 3.26 |
| *Phlegmariurus saururus* | 0.33 | 3.48 | **20.29** | **41.01** | 10.32 | 0.27 | 6.81 | 17.50 |
| **Poa annua* | 19.29 | **36.69** | 9.20 | 0.97 | 0.69 | 1.99 | **21.72** | 9.45 |
| *Poa cookii* | 8.99 | **21.32** | 6.72 | 2.56 | 4.02 | 0.24 | **23.20** | **32.95** |
| *Polypogon magellanicus* | 8.09 | 8.03 | 2.09 | 0.00 | 0.05 | 0.08 | 16.30 | **65.35** |
| *Ranunculus biternatus* | 4.10 | 1.69 | **51.69** | 4.08 | 0.12 | 0.17 | 8.20 | **29.94** |
| **Sagina procumbens* | 4.70 | **23.42** | 2.75 | 0.46 | **25.07** | 8.12 | 0.09 | **35.38** |

**Appendix S17.** Percentage variable importance for each predictor variable based on the full GAM model for species cover. Variables with > 20 % variable importance are highlighted in bold. * = alien species.

| | **Wind stress: maximum** | **PDIR** | **Soil depth** | **Rock cover** | **Temperature: winter** | **Temperature: summer** | **Soil moisture** | **pH** |
|---|---|---|---|---|---|---|---|---|
| *Acaena magellanica* | **20.82** | 14.82 | 6.70 | 18.67 | 13.61 | 0.45 | 9.68 | 15.24 |
| **Agrostis stolonifera* | 0.87 | 12.17 | 19.77 | 4.25 | **24.14** | 9.48 | 0.01 | **29.31** |
| *Austroblechnum penna-marina* | 7.92 | 0.05 | 1.73 | **59.22** | 12.90 | 3.30 | 14.71 | 0.17 |
| *Azorella selago* | 0.15 | 4.35 | 4.71 | **63.12** | 0.00 | 1.12 | 6.45 | **20.10** |
| *Carex dikei* | 10.68 | 7.36 | **22.19** | 11.39 | 3.28 | 0.37 | **35.78** | 8.95 |
| **Cerastium fontanum* | 0.05 | **28.35** | 13.33 | 12.80 | 2.41 | 13.03 | 15.07 | 14.95 |
| *Hymenophyllum peltatum* | **24.74** | 2.06 | **25.82** | 2.96 | 6.68 | 0.95 | **35.61** | 1.18 |
| *Juncus scheuchzerioides* | **30.41** | 6.71 | 1.36 | 10.74 | 17.84 | 6.43 | 9.19 | 17.32 |
| *Lycopodium magellanicum* | 14.86 | 5.86 | 9.16 | 16.35 | 13.64 | 13.58 | 3.06 | **23.48** |
| *Notogrammitis crassior* | **23.39** | 1.43 | 2.55 | **42.98** | 1.06 | 7.29 | 7.05 | 14.25 |
| *Phlegmariurus saururus* | 4.04 | 0.08 | **34.07** | 1.07 | 14.96 | 0.04 | 17.87 | **27.86** |
| **Poa annua* | 18.39 | 16.11 | 14.12 | 8.63 | 14.58 | 1.17 | **24.67** | 2.33 |
| *Poa cookii* | **20.94** | 0.46 | 15.84 | **37.69** | 2.73 | 0.00 | 19.03 | 3.32 |
| *Polypogon magellanicus* | 9.78 | 2.14 | 1.63 | **40.93** | 15.36 | 0.15 | 17.34 | 12.67 |
| *Ranunculus biternatus* | 12.17 | 11.19 | **28.24** | **23.94** | 0.67 | 0.00 | **21.74** | 2.06 |
| **Sagina procumbens* | 6.21 | **20.41** | 0.44 | **25.73** | 1.21 | 17.93 | 0.03 | **28.04** |

**Appendix S18.** Percentage variable importance for each predictor variable based on the full GLM model for species cover. Variables with > 20 % variable importance are highlighted in bold. * = alien species.

| | Wind stress: maximum | PDIR | Soil depth | Rock cover | Temperature: winter | Temperature: summer | Soil moisture | pH |
|---|---|---|---|---|---|---|---|---|
| *Acaena magellanica* | 15.55 | 17.57 | 8.23 | 11.63 | 15.40 | 1.60 | 12.39 | 17.64 |
| **Agrostis stolonifera* | 2.30 | 15.60 | 13.28 | 2.49 | **22.88** | 16.41 | 1.39 | **25.66** |
| *Austroblechnum penna-marina* | 10.55 | 0.32 | 3.73 | **58.19** | 11.54 | 0.20 | 15.16 | 0.31 |
| *Azorella selago* | 1.86 | 5.82 | 2.94 | **61.57** | 1.62 | 3.68 | 5.29 | 17.21 |
| *Carex dikei* | 8.90 | 10.06 | 19.50 | 11.16 | 8.79 | 0.56 | **32.93** | 8.09 |
| **Cerastium fontanum* | **21.52** | 12.22 | 10.04 | 17.89 | 5.89 | 7.93 | **22.49** | 2.03 |
| *Hymenophyllum peltatum* | **33.42** | 0.44 | **23.34** | 0.71 | 6.33 | 0.70 | **32.76** | 2.30 |
| *Juncus scheuchzerioides* | **31.69** | 8.08 | 9.25 | 11.80 | 8.41 | 7.31 | 9.84 | 13.64 |
| *Lycopodium magellanicum* | **21.11** | 7.33 | 7.74 | 3.46 | 17.77 | 11.42 | 12.74 | 18.43 |
| *Notogrammitis crassior* | 17.88 | 1.21 | 12.90 | **30.18** | 6.95 | 3.04 | 13.71 | 14.14 |
| *Phlegmariurus saururus* | **26.60** | 5.30 | 9.76 | 19.82 | 1.02 | 6.34 | 7.17 | **23.99** |
| **Poa annua* | **31.24** | 9.14 | 10.19 | 18.63 | 11.31 | 1.01 | 12.17 | 6.30 |
| *Poa cookii* | 9.81 | 7.42 | 11.85 | **28.50** | 2.42 | 3.69 | 16.08 | **20.22** |
| *Polypogon magellanicus* | 2.65 | 5.37 | 6.48 | **48.03** | 6.48 | 1.36 | 16.37 | 13.27 |
| *Ranunculus biternatus* | 13.45 | 12.09 | **33.37** | **24.93** | 0.24 | 4.38 | 10.00 | 1.53 |
| **Sagina procumbens* | 8.78 | **28.25** | 3.07 | **27.78** | 5.34 | 7.61 | 1.08 | 18.08 |

**Appendix S19.** Percentage variable importance for each predictor variable based on the full GBM model for species cover. Variables with > 20 % variable importance are highlighted in bold. * = alien species.

| | **Wind stress: maximum** | **PDIR** | **Soil depth** | **Rock cover** | **Temperature: winter** | **Temperature: summer** | **Soil moisture** | **pH** |
|---|---|---|---|---|---|---|---|---|
| *Acaena magellanica* | 12.18 | **42.79** | 0.04 | **26.84** | 2.75 | 0.38 | 1.33 | 13.69 |
| **Agrostis stolonifera* | **24.72** | **23.91** | 1.86 | 1.04 | 8.32 | 3.58 | 3.58 | **33.00** |
| *Austroblechnum penna-marina* | 2.27 | 0.03 | 0.05 | **83.23** | 0.60 | 0.03 | 13.30 | 0.50 |
| *Azorella selago* | 0.23 | 4.84 | 0.00 | **67.52** | 0.19 | 0.28 | 6.23 | **20.71** |
| *Carex dikei* | 4.07 | 1.71 | 8.89 | 0.00 | 0.08 | 2.24 | **76.33** | 6.68 |
| **Cerastium fontanum* | 4.29 | **68.96** | 0.34 | 9.99 | 2.37 | 12.70 | 1.30 | 0.06 |
| *Hymenophyllum peltatum* | **47.05** | 0.01 | 2.61 | 0.00 | 0.04 | 0.36 | **47.30** | 2.63 |
| *Juncus scheuchzerioides* | 3.83 | 0.10 | 0.01 | 0.00 | 2.23 | 5.95 | **27.21** | **60.66** |
| *Lycopodium magellanicum* | **27.53** | 0.84 | 3.19 | 0.01 | **27.96** | 2.47 | 0.67 | **37.33** |
| *Notogrammitis crassior* | **28.36** | 0.06 | 0.62 | 0.85 | 0.18 | 0.73 | **68.83** | 0.36 |
| *Phlegmariurus saururus* | **47.30** | 4.62 | 0.99 | **28.25** | 1.29 | 1.22 | 0.27 | 16.07 |
| **Poa annua* | **29.21** | **49.92** | 0.41 | 7.38 | 2.76 | 7.52 | 2.68 | 0.12 |
| *Poa cookii* | 8.05 | **25.15** | 0.27 | **28.99** | **23.79** | 2.45 | 3.26 | 8.04 |
| *Polypogon magellanicus* | 0.44 | 0.06 | 1.27 | **51.81** | 2.05 | 0.02 | **22.71** | **21.65** |
| *Ranunculus biternatus* | 3.33 | **27.58** | **37.99** | 0.59 | 0.06 | 1.26 | **27.22** | 1.97 |
| **Sagina procumbens* | 3.68 | **61.19** | 0.00 | 0.06 | 0.07 | 2.28 | 0.00 | **32.71** |

**Appendix S20.** Area under the receiver operating characteristic curve (AUC) and true skill statistic (TSS) values for the simple validation model and the full validation models of each species' occurrence. Generalized additive model (GAM), generalized linear model (GLM), and boosted regression trees (GBM). Bold values indicate where the full model had a higher score than the simple model.

| | **AUC** | | | | | | **TSS** | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | **GAM** | | **GLM** | | **GBM** | | **GAM** | | **GLM** | | **GBM** | |
| | **Simple** | **Full** | **Simple** | **Full** | **Simple** | **Full** | **Simple** | **Full** | **Simple** | **Full** | **Simple** | **Full** |
| *Acaena magellanica* | 0.832 | 0.787 | 0.829 | 0.801 | 0.790 | 0.774 | 0.547 | 0.521 | 0.531 | 0.519 | 0.459 | **0.476** |
| **Agrostis stolonifera* | 0.523 | **0.539** | 0.791 | **0.869** | 0.528 | **0.659** | -0.047 | - | -0.052 | - | 0.036 | - |
| *Austroblechnum penna-* | 0.831 | 0.801 | 0.815 | 0.779 | 0.835 | **0.836** | 0.590 | 0.554 | 0.562 | 0.514 | 0.640 | 0.635 |
| *Azorella selago* | 0.706 | 0.654 | 0.704 | 0.689 | 0.703 | 0.662 | 0.312 | 0.245 | 0.333 | 0.276 | 0.328 | 0.276 |
| *Carex dikei* | 0.767 | 0.729 | 0.768 | 0.714 | 0.754 | 0.729 | 0.449 | 0.410 | 0.466 | 0.407 | 0.455 | 0.425 |
| **Cerastium fontanum* | 0.553 | 0.517 | 0.675 | **0.717** | 0.648 | **0.696** | 0.144 | **0.164** | 0.283 | **0.378** | 0.020 | - |
| *Hymenophyllum peltatum* | 0.757 | 0.642 | 0.769 | 0.640 | 0.643 | 0.636 | 0.442 | 0.200 | 0.409 | 0.097 | 0.311 | 0.095 |
| *Juncus scheuchzerioides* | 0.640 | **0.732** | 0.639 | **0.672** | 0.634 | **0.746** | 0.076 | **0.245** | 0.075 | **0.153** | 0.141 | **0.284** |
| *Lycopodium magellanicum* | 0.684 | 0.669 | 0.678 | **0.735** | 0.734 | 0.665 | 0.176 | **0.190** | 0.175 | -0.10 | 0.096 | **0.113** |
| *Notogrammitis crassior* | 0.860 | 0.644 | 0.888 | 0.828 | 0.800 | 0.709 | 0.627 | 0.090 | 0.626 | 0.420 | 0.433 | 0.422 |
| *Phlegmariurus saururus* | 0.812 | 0.807 | 0.836 | 0.812 | 0.811 | **0.813** | 0.494 | 0.486 | 0.598 | 0.487 | 0.441 | 0.323 |
| **Poa annua* | 0.872 | 0.646 | 0.848 | 0.727 | 0.900 | 0.888 | -0.219 | **0.058** | -0.231 | **-** | -0.217 | **-** |
| *Poa cookii* | 0.700 | 0.695 | 0.707 | 0.700 | 0.682 | 0.669 | 0.277 | **0.324** | 0.342 | 0.333 | 0.263 | 0.220 |
| *Polypogon magellanicus* | 0.688 | 0.614 | 0.693 | 0.538 | 0.696 | 0.606 | 0.329 | 0.163 | 0.310 | 0.052 | 0.350 | 0.171 |
| *Ranunculus biternatus* | 0.526 | **0.576** | 0.531 | 0.517 | 0.534 | 0.523 | 0.089 | **0.140** | -0.051 | **0.001** | 0.093 | 0.076 |

| | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Sagina procumbens* | 0.568 | 0.563 | 0.529 | **0.539** | 0.601 | 0.560 | 0.149 | 0.130 | 0.065 | **0.080** | 0.229 | 0.217 |

**Appendix S21.** Spearman correlation values between the predicted and observed values of species cover for the simple (excluding wind stress) and full validation models (including wind stress). Generalized additive model (GAM), generalized linear model (GLM), and boosted regression trees (GBM). NA* = number of occurrences for this species were too small for GBM analysis. Bold values indicate where the full model had a higher score than the simple model.

| | **Spearman correlation** | | | | | |
|---|---|---|---|---|---|---|
| | **GAM** | | **GLM** | | **GBM** | |
| | **Simple** | **Full** | **Simple** | **Full** | **Simple** | **Full** |
| *Acaena magellanica* | 0.369 | 0.353 | 0.442 | 0.397 | 0.414 | 0.326 |
| **Agrostis stolonifera* | -0.033 | -0.106 | -0.084 | -0.112 | NA | NA |
| *Austroblechnum penna-marina* | 0.625 | 0.591 | 0.603 | 0.596 | 0.653 | 0.637 |
| *Azorella selago* | 0.362 | 0.327 | 0.359 | 0.326 | 0.295 | 0.272 |
| *Carex dikei* | 0.515 | **0.524** | 0.487 | 0.477 | 0.494 | 0.452 |
| **Cerastium fontanum* | -0.077 | -0.088 | 0.054 | 0.020 | -0.128 | **-0.125** |
| *Hymenophyllum peltatum* | 0.220 | -0.241 | 0.171 | 0.041 | 0.038 | **0.181** |
| *Juncus scheuchzerioides* | 0.154 | **0.332** | 0.164 | **0.332** | 0.227 | **0.331** |
| *Lycopodium magellanicum* | 0.055 | **0.069** | 0.063 | **0.096** | -0.017 | -0.050 |
| *Notogrammitis crassior* | 0.209 | -0.069 | 0.192 | **0.215** | 0.188 | 0.138 |
| *Phlegmariurus saururus* | 0.163 | 0.150 | 0.181 | 0.164 | 0.091 | -0.029 |
| **Poa annua* | -0.306 | **-0.300** | -0.296 | **-0.291** | -0.219 | -0.228 |
| *Poa cookii* | 0.141 | **0.172** | 0.197 | 0.197 | 0.104 | **0.134** |

| | | | | | | |
|---|---|---|---|---|---|---|
| *Polypogon magellanicus* | 0.314 | 0.201 | 0.325 | 0.135 | 0.343 | 0.305 |
| *Ranunculus biternatus* | -0.029 | **-0.006** | -0.062 | **-0.020** | -0.120 | -0.138 |
| **Sagina procumbens* | 0.019 | **0.032** | 0.018 | **0.043** | -0.030 | -0.099 |

# Chapter 5:

# Factors determining nest-site selection of surface-nesting seabirds: A case study on the world's largest pelagic bird, the Wandering Albatross *Diomedea exulans*

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**Authors' contributions:** MM and PCLR conceived the ideas; MM, PCLR, DWH and PGR designed the methodology; PGR, JS, KJC and KAG collected and processed the data; MM and PCLR analysed the data; MM led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

## Abstract

Several factors may drive bird nest-site selection, including predation risk, resource availability, weather conditions, and interaction with other individuals. Other potentially important factors, and some groups of birds, however, have not been investigated with regards to nest-site selection. Understanding the drivers affecting where birds nest is important for conservation planning, especially where environmental change may alter the distribution of suitable nest sites. This study investigates which environmental variables affect nest-site selection by the Wandering Albatross *Diomedea exulans*, the world's largest pelagic bird. For the first time, wind characteristics are quantitatively investigated as a driver of nest-site selection in surface nesting birds, in addition to several topographical variables, vegetation, and geological characteristics. Nest locations from three different breeding seasons on sub-Antarctic Marion Island were modelled to assess which environmental factors affect nest-site selection. Elevation was the most important determinant of nest-site selection, with Wandering Albatrosses only nesting at low elevations. Distance from the coast and terrain ruggedness were also important predictors, with nests more generally found close to the coast and in flatter terrain, followed by wind velocity, which showed a hump-shaped relationship with the probability of nest occurrence. Nests occurred more frequently on coastal vegetation types, and were absent from polar desert vegetation (generally above ~ 500 m elevation). Of the variables that influence Wandering Albatross nest location, both vegetation type and wind characteristics are likely to be influenced by climate change, and have already changed over the last 50 years. As a result, the availability of suitable nest sites needs to be considered in light of future climatic change, in addition to the impacts that these changes will have on foraging patterns and prey distribution. More broadly, these results provide insights into how a wide range of environmental variables, including wind, can affect nest-site selection of surface nesting seabirds.

## Introduction

Nest-site selection by birds may be driven by a variety of environmental factors, including habitat conditions related to predator avoidance, trophic and non-trophic resource availability, exposure to weather conditions, and interactions with conspecifics (Jones, 2001). It is well understood, for example, that many ground-nesting birds choose sites based on topography that allows them to either detect predators from afar (e.g., open areas) or those that provide protection from predators (e.g., less accessible sites within wetlands; Colwell et al., 2011; Miller et al., 2014; Cunningham et al., 2016; Korne et al., 2020). Vegetation is also regularly linked to the avoidance or detection of predators (Muir and Colwell, 2010), and is often important in determining where nests are constructed (Flemming et al., 2019). Food availability is another key factor that is often linked to vegetation, and which can influence nest site selection by bird species (McCollin, 1998). Social cues, both inter- and intra-specific, can also affect the choice of breeding sites in songbirds (Betts et al., 2008). Temperature tends to be an important driver of nest-site selection, particularly in systems that experience high levels of solar radiation, with nests typically located in cooler microsites within hot environments (With and Webb, 1993; Kauffman et al., 2021), and probably in buffered microsites in cold environments. Quantifying and understanding these factors is important in order to preserve environments that will be suitable for nesting in the future, and to understand how populations will be affected under environmental change.

Wind conditions may affect where birds choose to nest, but the influence of wind has been poorly studied (see e.g., Cunningham et al., 2016). Wind has been hypothesized to be important for nest location in certain specific scenarios, where, for example, nests are constructed downwind from taller vegetation which may act as a windbreak (Holmes et al., 2020). Similarly, microscale tundra features in the Arctic may be important factors influencing shorebird nest-site location, because these landforms provide windbreaks (Cunningham et al., 2016). In other systems, the windward sides of nests have trampled vegetation where the birds enter the nest (Miller et al., 2014). Wind is increasingly being recognized as an important factor for seabirds, affecting their movement (Weimerskirch et al., 2000; Clay et al., 2020), foraging ecology (Cornioley et al., 2016), and even life-history (Weimerskirch et al., 2012). Large seabirds breeding on sub-Antarctic islands are an ideal system in which to study the influence of wind on the nest-site selection of surface-nesting species. In these environments, natural predators are absent, proximity to food should not be a factor since these birds typically cover extremely large distances to forage (Gaston, 2004), winds are constant and strong, and, therefore, environmental effects can be studied without the interference of predator risk or resource availability, which affect bird nesting sites strongly in other systems.

The Procellariiformes is a large order of seabirds, including the bird with the largest wingspan, the Wandering Albatross *Diomedea exulans* (Diomedeidae). Wandering Albatrosses breed in loose colonies, where nests tend to be in open, flat areas. They build large raised mound nest structures from surrounding vegetation and peat (Tickell, 2000), having large, but very localized, impacts on the terrestrial ecosystem where they nest (Joly et al., 1987). While not tested, it has been hypothesised that differences in breeding success on islands could be linked to environmental conditions, in particular shelter from westerly winds (Rackete et al., 2021).

While several threats to Wandering Albatross populations (globally listed as vulnerable) are well documented and understood (see e.g., Jones and Ryan, 2010; Pardo et al., 2017; Jones et al., 2019), factors affecting nest-site selection, and what this would mean for the distribution and availability of future breeding sites, have not been investigated. Wandering Albatross' foraging patterns, breeding success, and survival is affected by wind in different ways (Weimerskirch et al., 2000; Weimerskirch et al., 2012; Cornioley et al., 2016; Pardo et al., 2017). Due to their large wingspan and heavy weight, energy expenditure is largest for these birds when they take off (Weimerskirch et al., 2000). Wandering Albatrosses take off into strong headwinds, and larger albatrosses, which have a higher wing loading and require faster wind speeds for gliding flight, are more strongly influenced by favourable wind conditions when making flight decisions (Clay et al., 2020).

This study, therefore, investigates which environmental drivers affect the nest-site selection of the Wandering Albatross, and also, for the first time, quantitatively investigates wind as one of these factors. We expect that Wandering Albatross nests will be located in flat areas that have adequate space for the birds to take off into the predominant winds, and which have moderate and predictable wind speeds to facilitate take-off and landing, and in areas with adequate vegetation cover to build their nests. Moreover, we test these patterns using data from three different breeding seasons to determine their generality.

## Methods

### *Study area and study species*

This study was conducted on sub-Antarctic Marion Island (46°54′ S, 37°45′ E), in the Prince Edward Islands group, southeast of Africa. Marion Island is situated in the "roaring forties", a band of strong westerly winds in the Southern Ocean, where strong winds blow on most days of the year, with winds predominantly coming from the west (le Roux, 2008). The island has a hyper-oceanic climate, where the Southern Ocean moderates daily and seasonal temperature variation (mean annual temperature of 6°C, mean daily temperature range of 1.9°C). The island receives around 1800 mm of precipitation annually, with rain or snow falling on >290 days per year (1960-2018; unpublished data, South African Weather Service; le Roux, 2008; le Roux and McGeoch, 2008a). Vegetation on Marion Island can broadly be described as tundra, with similarities to the tundra systems in the Northern Hemisphere (Kemppinen et al., 2021).

The Wandering Albatross is an oceanic nomad that only visits land to breed, and nests exclusively on the islands in the Southern Ocean (ACAP, 2009). It has the largest wingspan of any living bird in the world, and can live up to at least 42 years (Cooper et al., 2003), with breeding pairs exhibiting high fidelity rates, and with birds almost always returning to the same colony (Gauthier et al., 2010). Approximately 44% of the world's breeding population of Wandering Albatrosses breed on the Prince Edward Islands (Birdlife International, 2018), with 22% of the global population breeding on Marion Island (Jones and Ryan, 2010). Unfortunately, the global population of Wandering Albatross is declining, mainly as a result of bycatch in longline fishing, and the species is currently listed as Vulnerable (Poncet et al., 2017; Birdlife International, 2018).

### *Data collection*

The geographic coordinates of 1928 of 1960 active Wandering Albatross nests on Marion Island (98.4% of all active nests in the 2016/17 breeding season; Fig. 1, after removing 4 outliers at elevations higher than 100 m a.s.l., representing <0.003 % of nests, and records that included errors in locations or lacked of coverage by the digital surface model) were collected using a handheld GPS device (following the methods of Nel et al., 2002) in January 2017. The active nests from the 2006 (1711 nests), and

2018 (2139 nests) breeding seasons were used to confirm the generality of results across years. This provides a test of the generality of observed patterns, with data more than 10 years apart, and data from a subsequent breeding season representing the nesting preferences of different individual birds (since Wandering Albatross generally breed every second year, although due to the longevity of this species not all records are entirely independent).

*Data processing*

Absences (n=10,000) were randomly generated in ArcGIS Pro, with a minimum distance of 30 m between absence points and between nest locations. The island is surveyed intensively, so all locations that were recorded as not having a nest represent true absences (see e.g., Guillera-Arroita et al., 2015). Since models using pseudo-absences sampled from environments that are dissimilar to environments in which presences occur may be positively biased (Hazen et al., 2021), absences were *a priori* generated in areas that were deemed biologically-suitable based on initial observations of where nests occur. The following factors were considered when choosing where to generate absences: nests occurred at elevations lower than 100 m a.s.l., and the species does not nest on cliffs, due to their lack of agility when landing. Marion Island has over 130 scoria (cinder) cones (Boelhouwers et al., 2008) comprising loose unconsolidated rock resulting from explosive volcanic events (Verwoerd, 1971; Rudolph et al., 2021). This geology type typically supports little to no vegetation and scoria cones are also generally very steep (see e.g., Holness, 2004, with measurements of up to 35°), and Wandering Albatrosses have not been observed to nest on these cones. Since scoria (cinder) cone vegetation was represented by only one nest in the dataset, this vegetation type was lumped with polar desert since both of these vegetation types represent abiotically extreme environments. Therefore, absences were not generated from areas with an altitude greater than 100 m a.s.l., slopes > 45°, scoria cones, or lakes.

The elevation for each presence and absence point was extracted from a 1-m resolution digital surface model (DSM; Fig. 1; DRDLR, 2019). Temperature and elevation show strong collinearity on Marion Island (Leihy et al., 2018), and therefore temperature was not included as a predictor. The DSM was subsequently resampled to 10 m resolution, before calculating and extracting the terrain ruggedness index (TRI) and slope angle. The terrain ruggedness index represents the elevation difference between a cell and the eight cells surrounding it, and was used as a proxy for the flatness of the space around each point. This indicated the available space which the birds would be able to use for take-off and landing (Fig. 1).

Distance to the coast was calculated since salt spray from the ocean might affect nest-site selection, and salt spray can travel as far as 300 m inland on Marion Island (Smith, 1978c). The vegetation type at each point was determined from the latest vegetation classification for Marion Island, which mapped five broad vegetation types: coastal vegetation, mire-slope vegetation, fellfield, scoria (cinder) cones, and polar desert (Smith and Mucina, 2006). Geology for each point was determined from Rudolph et al. (2021), and then simplified to two categories, namely flows from before the last glacial maximum (pre-glacial flows), which represent a smooth substrate, and post-glacial flows that are more rugged.

The weighted mean wind velocity and wind turbulence intensity were extracted from a computational fluid dynamics (CFD) model of Marion Island (30 m resolution; Goddard, 2021). These mean values were weighted by the observed frequency of wind recordings from 16 wind directions. The CFD model uses the full DSM of Marion Island and simulates air flow over the topography by iteratively solving a set of partial differential equations (Reynolds-Averaged Navier Stokes Equations: Versteeg and Malalasekera, 2007; Cindori et al., 2018). Sixteen wind directions (at intervals of 22.5°) were used as the free-stream condition, with a reference speed of 8.22 $m \cdot s^{-1}$ at 1.5 m above ground. The model included considerations for the atmospheric boundary layer and the effect of the Coriolis force (Breedt et al., 2018; Goddard, 2021), and generated estimates of wind velocity and turbulence for 30 x 30 m cells across Marion Island (with mean errors of 26.9% for velocity and 32.6% for turbulence; Goddard 2021). From these analyses, we extracted wind characteristics at 1 m above the ground as we considered this relevant to adult albatrosses when on the ground and chicks on nests. Outliers for wind turbulence, representing values greater than the value of the 99th percentile, were set to the value of the 99th percentile.

*Statistical analyses*

The terrain ruggedness index and wind turbulence values were logarithmically transformed prior to analyses to reduce the leverage of a few large values. Slope and ruggedness were strongly correlated (Pearson $r = 0.86$, $p < 0.001$), and therefore slope was excluded from the analyses because ruggedness was considered to be more biologically relevant in terms of quantifying the available flat space around a point for take-off and landing. None of the remaining predictor variables had a generalised variance inflation factor (GVIF) > 2.5, or were strongly correlated with another variable (Pearson $r < |0.7|$; Fig. A7). Wind velocity, turbulence, vegetation type, elevation, geology, terrain ruggedness, and distance from the coast were investigated as predictors of nest presence or absence using generalised additive models (GAM) and generalised linear models (GLM; including quadratic terms of continuous predictors), implementing a binomial distribution. Variable importance for GAMs and GLMs was calculated by comparing the Pearson correlation between predictions made on the original data and predictions made on the data where the predictor variable of interest has been randomly shuffled (following Niittynen and Luoto, 2018). The calculations of variable importance were calculated 10 times and the mean importance value rescaled to percentage is reported.

All statistical analyses were performed in R version 4.1.0 (R Core Team, 2021), using additional functions from the mgcv (Wood and Augustin, 2002), ggplot2 (Wickham, 2016), voxel (Garcia de la Garza et al., 2018), ggpubr (Kassambara, 2020), and scico (Pedersen and Crameri, 2020) libraries. All figures were produced using the scientific colour scheme “batlow” (Crameri, 2018), to prevent visual distortion of the data and to be accessible to readers with colour-vision deficiency (Crameri et al., 2020).

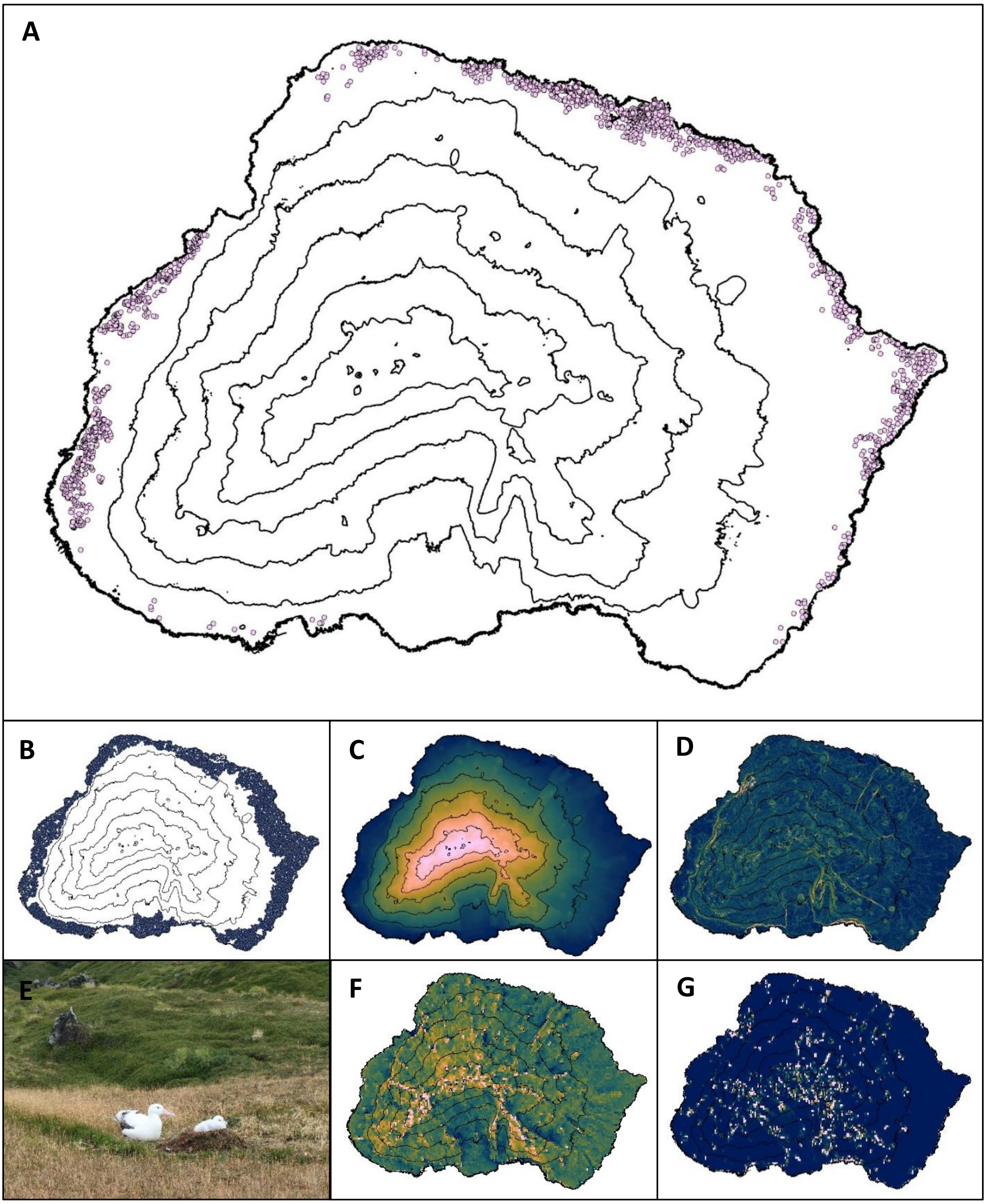

**Figure 1** A) Map of Marion Island with 200 m contour lines and the 1928 georeferenced Wandering Albatross nests recorded in January 2017 (light pink points); B) 10,000 randomly generated absences (dark blue); C) Digital Surface Model; D) Terrain ruggedness index; E) Wandering Albatross parent and chick on nest; F) Wind velocity ($m \cdot s^{-1}$); G) Wind turbulence. For all maps, lighter colours indicate higher values and darker colours indicate lower values. See Appendix Figs A1 - A6 for larger images, including legends and scales.

## Results

Results presented here are from the 2017 breeding season. Similar results were obtained from the 2006 and 2018 breeding seasons, with predictors consistently ranked in the same order of importance and with response curves showing similar shapes across all three datasets (see Appendix Figures A8 - A9 and Tables A1 - A2 for results from these additional years). The GAM explained of 32.8% of deviance in the nest distribution data, while the GLM explained 31.1% of the deviance.

Five of the six continuous predictors contributed significantly to explaining nest-site suitability in both the GAM and GLM models, while wind turbulence did not significantly affect the nest-site suitability in either of the two models (Table 1). For both statistical approaches, elevation was the most important predictor, followed by distance from the coast, vegetation type, terrain ruggedness, and wind velocity (Table 1). Most nests were located in coastal or mire-slope vegetation types, with a small proportion in fellfield, while no nests were recorded in polar desert (Fig. 2). Pre-glacial flows made up a significantly larger proportion of the underlying geology on which nests were found than expected by chance, with a similar proportion of pre- to post-glacial flows observed for absences (Fig. 2). Response curves from the GAMs showed that there was a higher probability of a nest occurring in areas close to the coast and at low elevation (Fig. 3). The more rugged the terrain, the lower the probability of a site being used to build a nest. Wind velocity had a hump-shaped relationship with nest occurrence, with the highest probability of a nest in areas with intermediate wind velocities. Areas with higher wind turbulence generally had a smaller probability of containing a nest as areas with lower turbulence, although this relationship was not significant (Fig. 3).

**Table 1** Significance and variable importance for all predictor variables when modelling the occurrence (i.e. presence or absence) of Wandering Albatross nests, listed in order of decreasing variable importance. GAM, generalized additive model; GLM, generalized linear model. Since an overall p-value for categorical predictors is not reported from a GAM, the ranking of the levels is reported. Post = post-glacial flows, Pre = pre-glacial flows, P = sub-Antarctic polar desert, F = sub-Antarctic fellfield, M = sub-Antarctic mire-slope vegetation, C = sub-Antarctic coastal vegetation.

| **Predictor** | **GAM** | | **GLM** | |
|---|---|---|---|---|
| | p-value | Relative importance (%) | p-value | Relative importance (%) |
| Elevation | < 0.01 | 46.05 | 0.04* | 42.23 |
| Distance to coast | < 0.01 | 23.80 | < 0.01* | 23.83 |
| Vegetation type | P<F<M<C | 16.02 | P<F<M<C | 15.65 |
| Terrain ruggedness | < 0.01 | 6.80 | < 0.01* | 9.29 |
| Wind velocity | < 0.01 | 6.62 | < 0.01* | 8.40 |
| Geology type | Post<Pre | 0.44 | Post<Pre | 0.25 |
| Wind turbulence | 0.10 | 0.28 | 0.51 | 0.35 |

*quadratic term of that variable was significant in the GLM

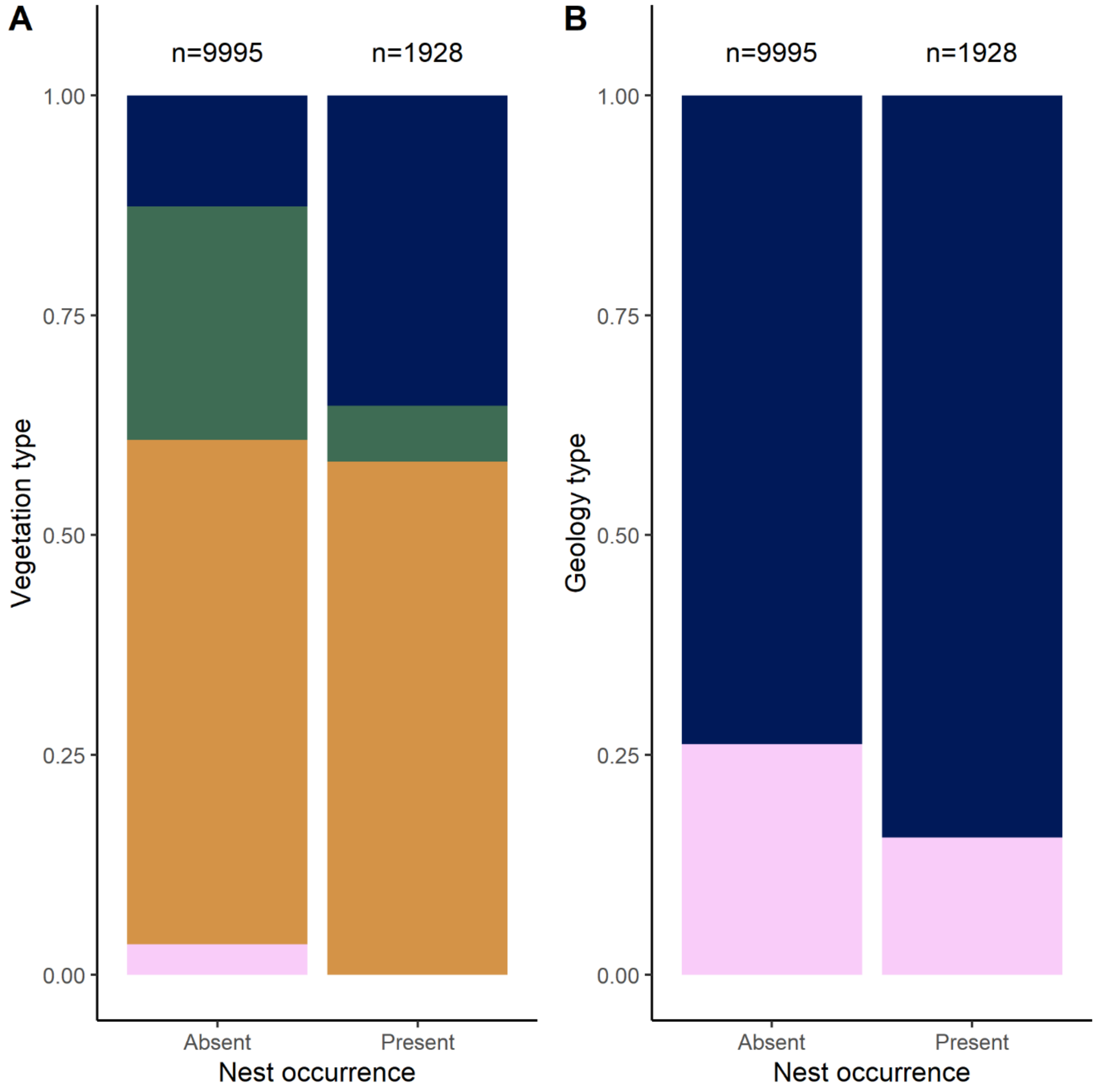

**Figure 2** Stacked bar charts showing the proportion of nest presences and absences in each A) vegetation type, and B) geology type. A) sub-Antarctic coastal vegetation = dark blue, sub-Antarctic fellfield = olive green, sub-Antarctic mire-slope vegetation = orange, sub-Antarctic polar desert = light pink. B) Post-glacial flows = dark blue, pre-glacial flows = light pink.

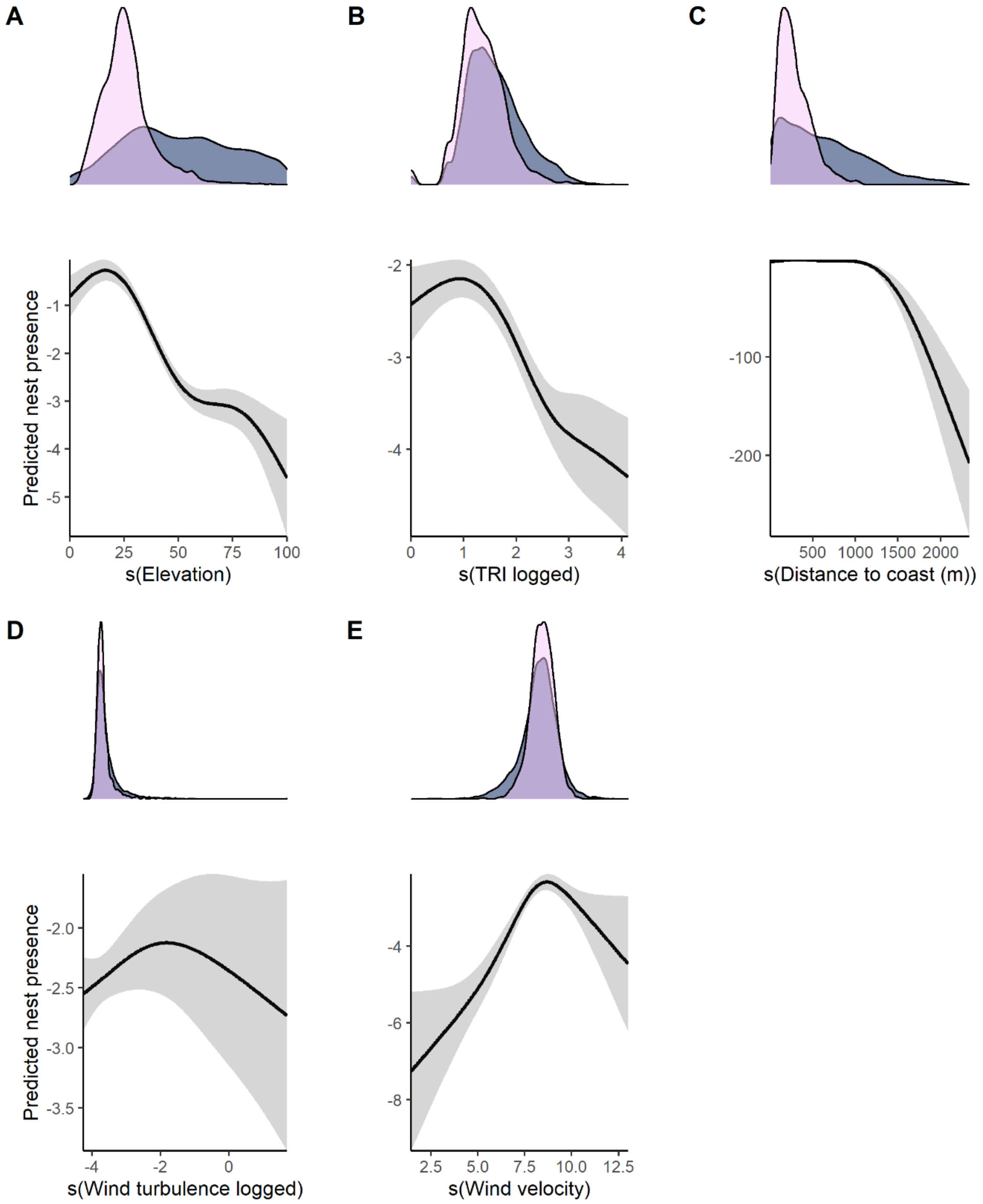

**Figure 3** Density plots of the raw data and GAM response curves for the occurrence of Wandering Albatross nests for the 2017 breeding season, for A) Elevation, B) Terrain Ruggedness Index (logged), C) Distance to the coast, D) Wind turbulence (logged), and E) Wind velocity ($m \cdot s^{-1}$). Light pink density plots represent data from presences and dark blue density plots data from absences. In the response curves, larger values on the y-axis represent a higher probability of occurrence.

## Discussion

Predictor variables representing topographic, vegetation, geological and wind velocity characteristics were significantly related to Wandering Albatross nest locations in the tundra landscape of Marion Island, although the relative importance of these predictors varied strongly. The strong consistency between results across three different years indicates a clear generality in these findings (i.e. across different individuals and different time periods). Elevation was the most important predictor of Wandering Albatross nests, with the probability of encountering a nest decreasing rapidly above c. 25 m a.s.l. Similar results have been seen for surface-nesting species in the Arctic, where low elevation areas are important for 33 species of tundra breeding birds (Hawkshaw et al., 2021). Further, due to the strong negative correlation between elevation and temperature on the island (Leihy et al., 2018), lower elevations also present warmer sites where the chicks are not as exposed to very cold temperatures (although Wandering Albatross chicks are likely well insulated against cold temperatures; Cooper and Lutjeharms, 1992). Similarly, the probability of nests being present declined with distance from the coast. This result is comparable to several studies on Arctic birds, where higher numbers of birds are present in coastal habitats, likely due to the higher amounts of suitable habitat (e.g., wetlands or tidal habitats) available in these areas (Conkin and Alisauskas, 2013; Saalfeld et al., 2013; Hawkshaw et al., 2021).

Vegetation type was the third most important predictor, and co-varies with elevation and the distance from the coast, since some vegetation types are limited to areas receiving salt-spray (i.e., coastal vegetation) and others are limited to high altitudes (e.g. polar desert; Smith, 1978b). High vegetation productivity (which on Marion Island declines with increasing elevation; Smith, 2008) has previously also been linked to tundra bird abundance, as some birds utilise the vegetation cover for nesting, and others for foraging (Hawkshaw et al., 2021). The composition of vegetation surrounding the nest was also an important determinant of nesting site choice for several Arctic-breeding shorebirds, likely due to predator protection and invertebrate food sources (Cunningham et al., 2016), and adequate vegetation is needed to construct nests. Wandering Albatross likely prefer low elevation, coastal areas for nesting because these areas are warmer, and there is ample vegetation available with which to construct their nests.

Terrain ruggedness was also significantly related to nest occurrence, with areas that have a higher ruggedness having a lower chance of containing a Wandering Albatross nest, in line with our hypothesis. Terrain ruggedness has been shown to be an important driver of nest-site selection in other systems, where birds prefer to nest in areas with low terrain ruggedness in order to provide individuals with a greater field of view to detect predators (Korne et al., 2020). Since Wandering Albatrosses have a high visibility in the landscape (due to being taller than almost all vegetation on the island), the mechanism through which this terrain ruggedness affects nest-site selection is likely different (although predation by invasive house mice has been recorded in recent years; Jones and Ryan, 2010; Jones et al., 2019). Wandering Albatrosses need adequate flat space (i.e. low terrain ruggedness) during take-off and landing, due to their large size requiring longer “runways” to achieve adequate speed before taking flight and to land safely (Warham, 1977). For some other surface-nesting species, (micro-) relief can provide wind shelter for nesting birds, helping them to avoid excessive heat loss in windy conditions in the Arctic (Cunningham et al., 2016). However, for species that have chicks which stay on the nest throughout winter, these microsites could also allow for greater snow accumulation, which might offset the benefits that these sites provide in terms of wind shelter. This is likely also true for Northern Giant Petrels *Macronectes halli*, which nest adjacent to rocks or on the leeward side of vegetation, where they are sheltered from wind (Marchant et al., 1990) . Here, however, we observe the opposite pattern for Wandering Albatross, where it appears that shelter is not as important as potential runway area. Topography and wind may be strongly linked at certain spatial scales, and while there is not a strong correlation between terrain ruggedness and wind velocity in this study, this relationship may change when investigated at different spatial scales. Therefore, this result may not be universal and may depend on site-specific characteristics and/or spatial scale.

Wind velocity can affect birds and their nests in several ways. High wind speeds can greatly decrease nest temperatures (Heenan and Seymour, 2012; Gray and Deeming, 2017), and also affect the chick’s body temperature, potentially reducing their growth rate (Sauve et al., 2021). Protection from wind in general, or from the strongest winds at a site, have been theorized to impact where birds construct their nests based on the topographic and vegetative protection seen at these sites (Cunningham et al., 2016; Holmes et al., 2020). This study presents the first quantitative results for wind impacting bird nest-site selection, and shows that for the Wandering Albatross, nests were most likely to be constructed in areas of intermediate wind speeds. This is likely because this species needs high enough wind speeds to take-off and land (i.e., making very wind-sheltered locations unsuitable), but also benefits from protection from the strongest wind speeds, both for thermoregulation, and for chicks not to be blown off their nests.

Wind turbulence and geology had weak impacts on the probability of a nest occurring at a site. Wind turbulence could have a limited effect on nest site locations because these birds only nest just above ground level, and wind speed is lower at ground level, implying that wind turbulence, or ‘gusting’ occurs from a low underlying speed value. Nonetheless, the observed negative trend between turbulence and nest occurrence fits our expectation that Wandering Albatrosses would avoid areas of turbulent wind flow, since these areas may increase the risks of crashing during take-off or landing (although the influence of wind conditions on landing may need to be considered at broader scales due to the large distances, spanning different heights above the ground, required for landing). In terms of geology, pre-glacial deposits tend to be flatter and smoother, and, therefore, meet the requirements for long, flat “runways” more closely than post-glacial flows. However, many of the post-glacial flows at low altitudes are vegetated and often occur under peat deposits, which evens out the underlying ruggedness, and leads to less biologically relevant differences for the Wandering Albatrosses between geology types. Pre-glacial deposits tend to have relatively less vegetation, but include in depressions that are filled with peat. These areas with peat deposits (regardless of the underlying geology) provide sufficient vegetation for Wandering Albatrosses to build their nests, suggesting that surface substrate may be more important than underlying geology in influencing nest site selecting in this species.

Due to their influence on terrestrial systems, Wandering Albatrosses are important in maintaining the functioning of these ecosystems, and act as ecosystem engineers (Haupt et al., 2016). Disturbance around their nests decreases bryophyte species richness and changes in vascular plant composition, depending on distance from the nest (Joly et al., 1987), while the increased nitrogen and phosphorous content due to manuring close to the nest leads to increased vitality of vascular plants (Smith, 1978a). Similar impacts are seen on diatom and testacean communities (Vincke et al., 2007; Moravcová et al., 2010). Active nests exhibit higher temperatures than surrounding areas, which benefit the caterpillars of the endemic flightless moth (*Pringleophaga marioni*) on Marion Island (Sinclair and Chown, 2006; Haupt et al., 2016).

Predicting how nest-site availability might change under future conditions would likely be most dependent on vegetation and wind characteristics (wind speed, and possibly wind direction and wind turbulence), both of which are currently being affected by anthropogenic-driven climate change. Changes to vegetation in relation to climatic changes have already been documented, with some species in the sub-Antarctic showing strong upslope range expansion, leading to community reorganization in some areas (le Roux and McGeoch, 2008b), and others showing decreased survival due to warming temperatures and lower precipitation (Le Roux et al., 2005). These changes will affect the distribution of entire vegetation types and may, for example, increase the availability of vegetation for nest building at higher altitudes (improving the suitability of more inland areas as nesting sites). Wind speeds have increased globally over the past three decades, with the strongest increases observed in the Southern Ocean (Young et al., 2011; Young and Ribal, 2019). Since nest-site selection is influenced by wind velocity, anthropogenic-driven shifts in climate could potentially affect the total suitable nesting area and, consequently, potentially the population's total breeding success via changes in wind characteristics. A factor that has not been quantified here, but could potentially also have large impacts on suitable nest-sites and breeding success, is changes to the frequency of extreme wind events which can, for example, blow chicks off their nests.

Since elevation and temperature are strongly correlated on Marion Island (Leihy et al., 2018), and elevation had the strongest influence on nest occurrence, it is possible that changes to temperature could have a large effect on suitable nest locations. The sub-Antarctic islands, where Wandering Albatrosses and many other pelagic seabirds breed, have already experienced rapid climatic changes (le Roux, 2008). Temperature has increased at more than double the global average warming rate over the past 50 years, and annual precipitation has declined on several islands (le Roux, 2008; le Roux and McGeoch, 2008a). This change in temperature, specifically, might lead to Wandering Albatrosses experiencing heat stress, which could alter where they nest in future. Altitudinal shifts in nesting sites could be a possibility, both as a result of increasing temperatures and the shift in vegetation due to temperature changes.

Other surface-nesting seabirds that breed in the sub-Antarctic, like giant petrels (Ryan and Bester, 2008), are likely to show similar patterns and experience analogous changes to suitable nesting locations in future. More generally, several other seabird species, like skuas, shags, gulls and terns (among other seabirds) all construct nests on the ground surface and occur in environments where wind speeds are relatively high (due to being close to the open ocean, Possner and Caldeira, 2017). Therefore, these results could provide insights into where surface-nesting seabirds nest in general, and how the availability of these sites will be affected by future climatic changes. More broadly, this work provides insights into wind as an underexplored climatic component of nest-site selection for surface-nesting seabirds, and is important for improving our predictions for climate change impacts on nesting habitat for pelagic species.

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## Appendix

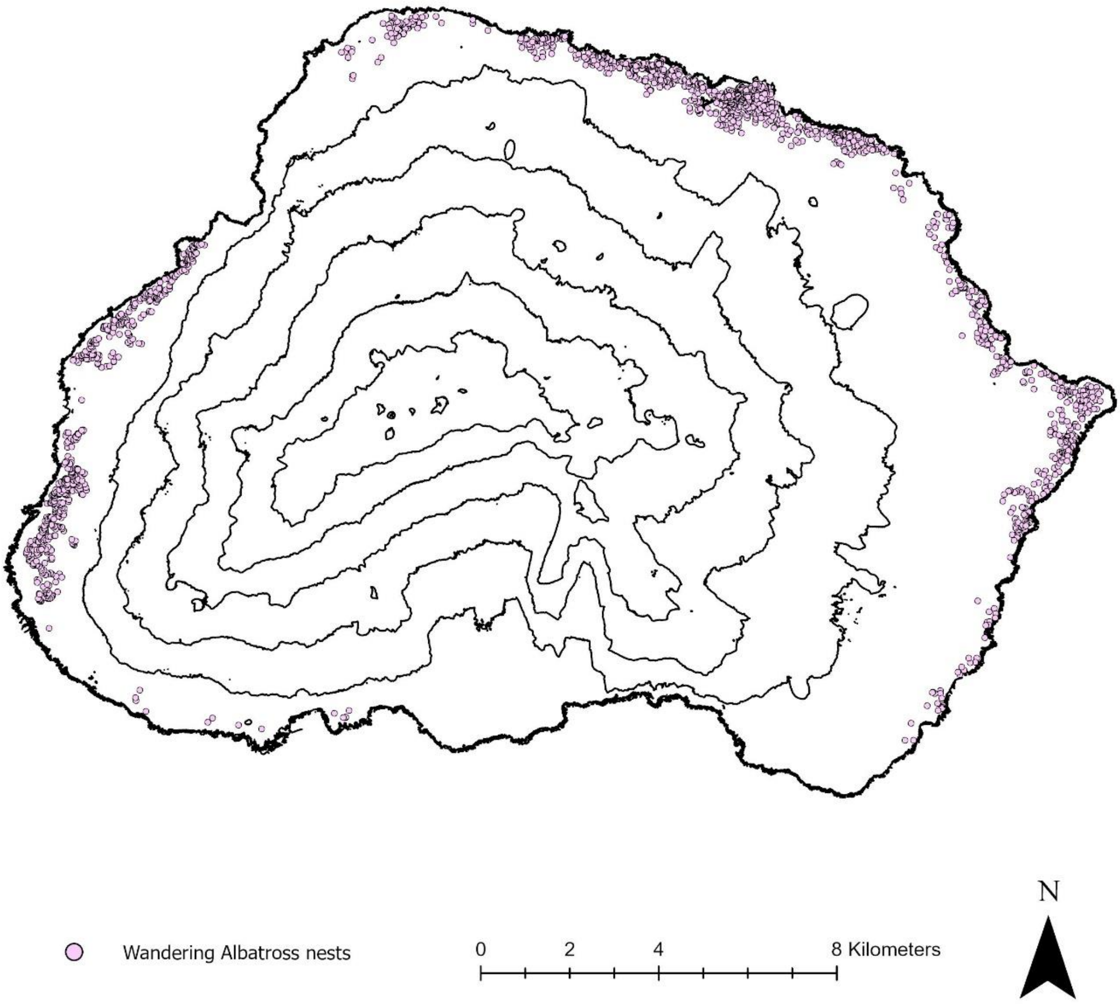

**Figure A1** Locations of Wandering Albatross nests on Marion Island in January 2017. Contours are plotted at 200 m intervals.

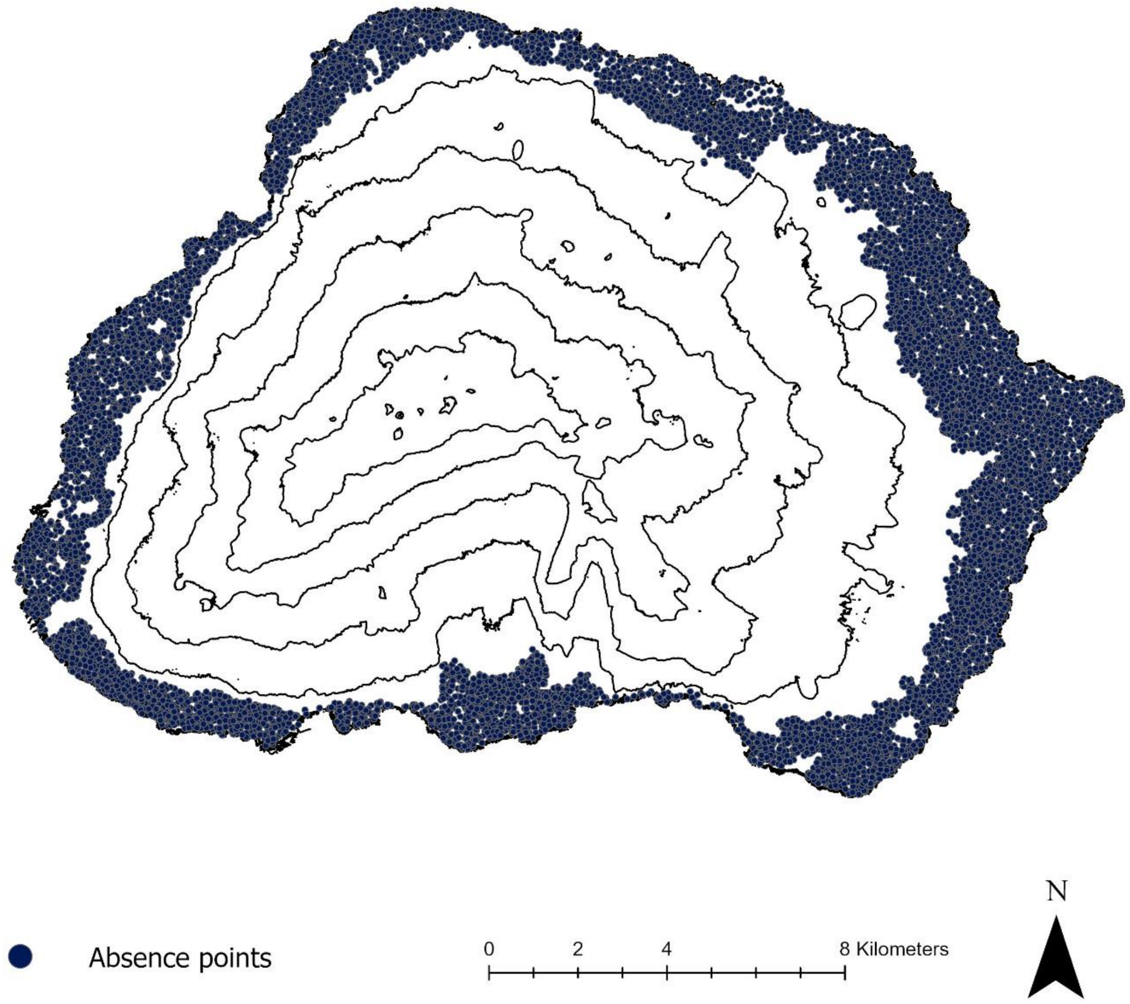

**Figure A2** Locations of absence points generated on Marion Island based on the nest locations from January 2017. All absences were at least 30 m from any Wandering Albatross nest, and a minimum of 30 m from one another. Absences were restricted to areas lower than 100 m in elevation, with a slope less than 45 °, and were exlcuded from areas classified as lakes or with scoria geology. Contours are plotted at 200 m intervals.

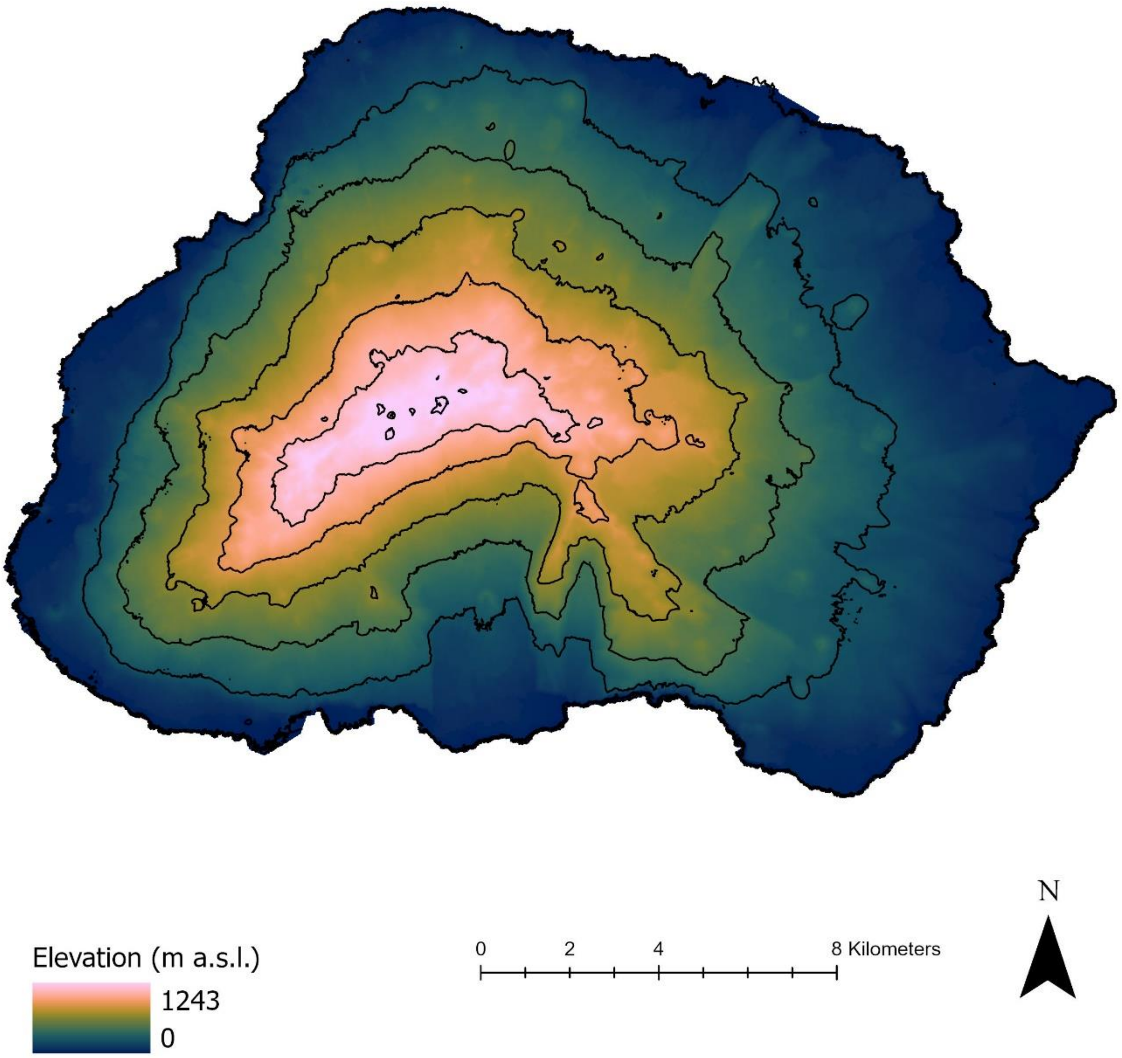

**Figure A3** Digital Surface Model of Marion Island, based on DRDLR (2019). Lighter colours indicate higher elevations, while darker colours indicate lower elevations. Contours are plotted at 200 m intervals.

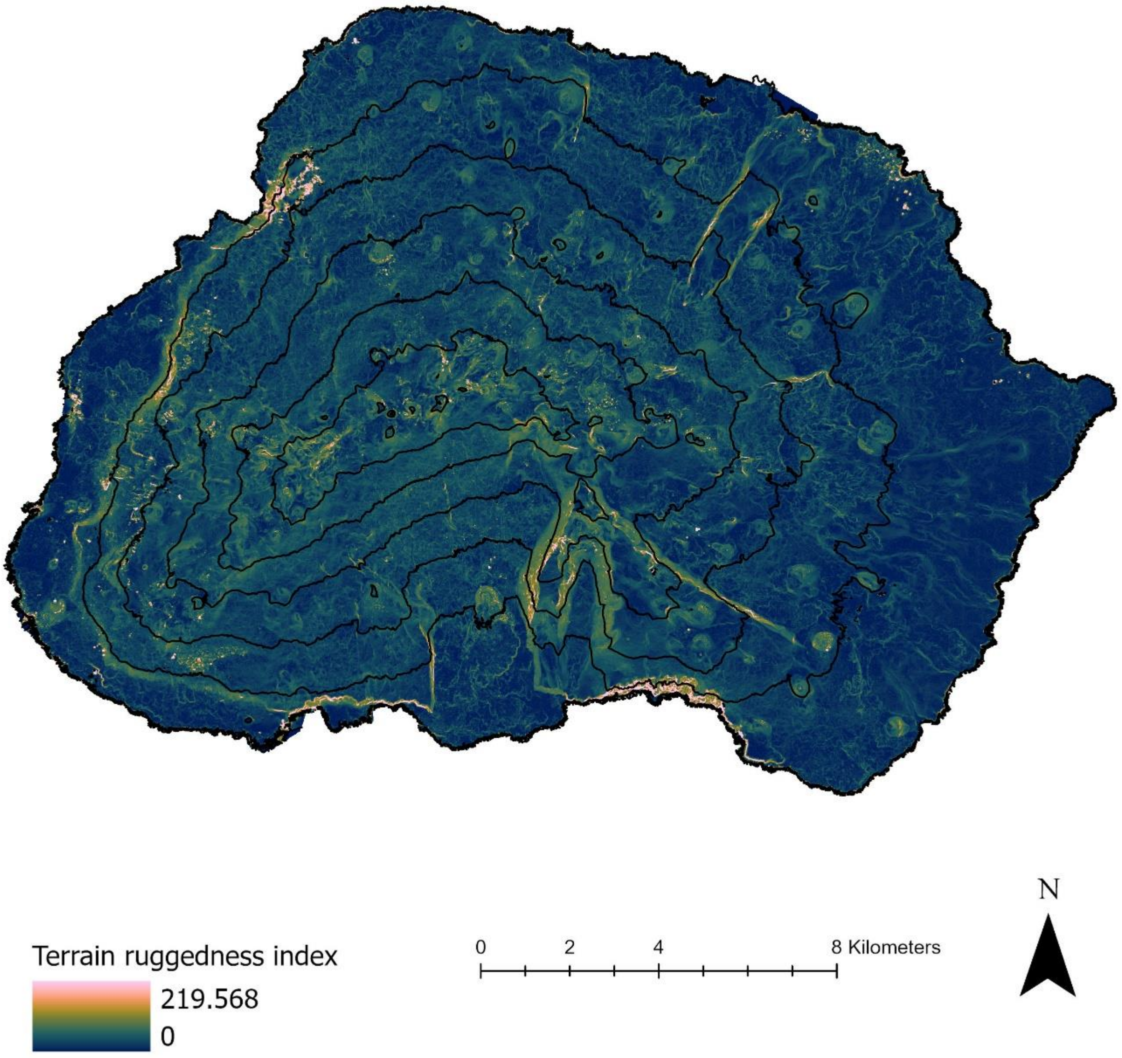

**Figure A4** Terrain Ruggedness Index values across Marion Island. Lighter colours indicate more rugged terrain, while darker colours indicate less rugged terrain. Contours are plotted at 200 m intervals.

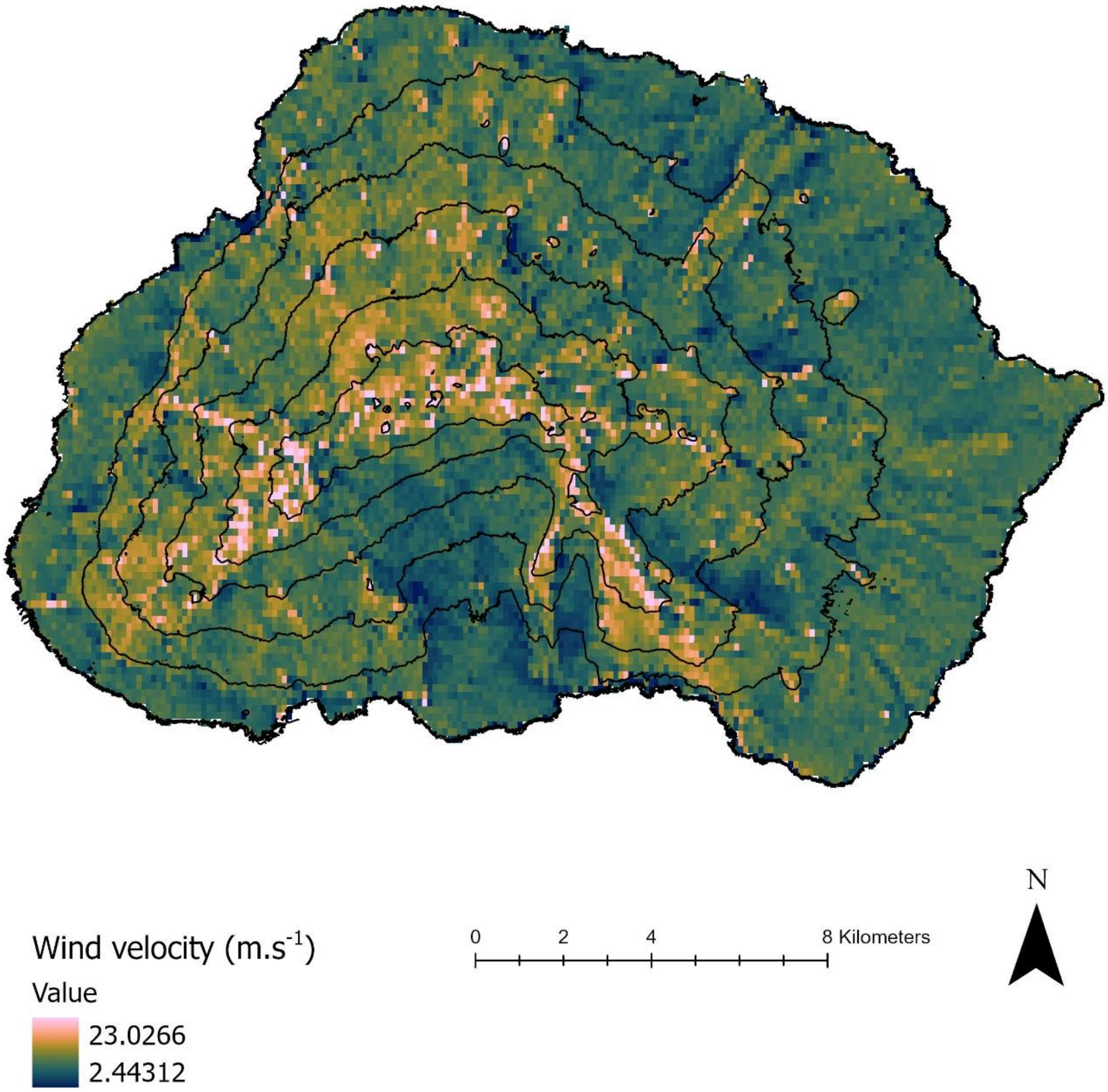

**Figure A5** Wind velocity on Marion Island, based on Goddard (2021). Lighter colours indicate higher wind velocity, while darker colours indicate lower wind velocity. Contours are plotted at 200 m intervals.

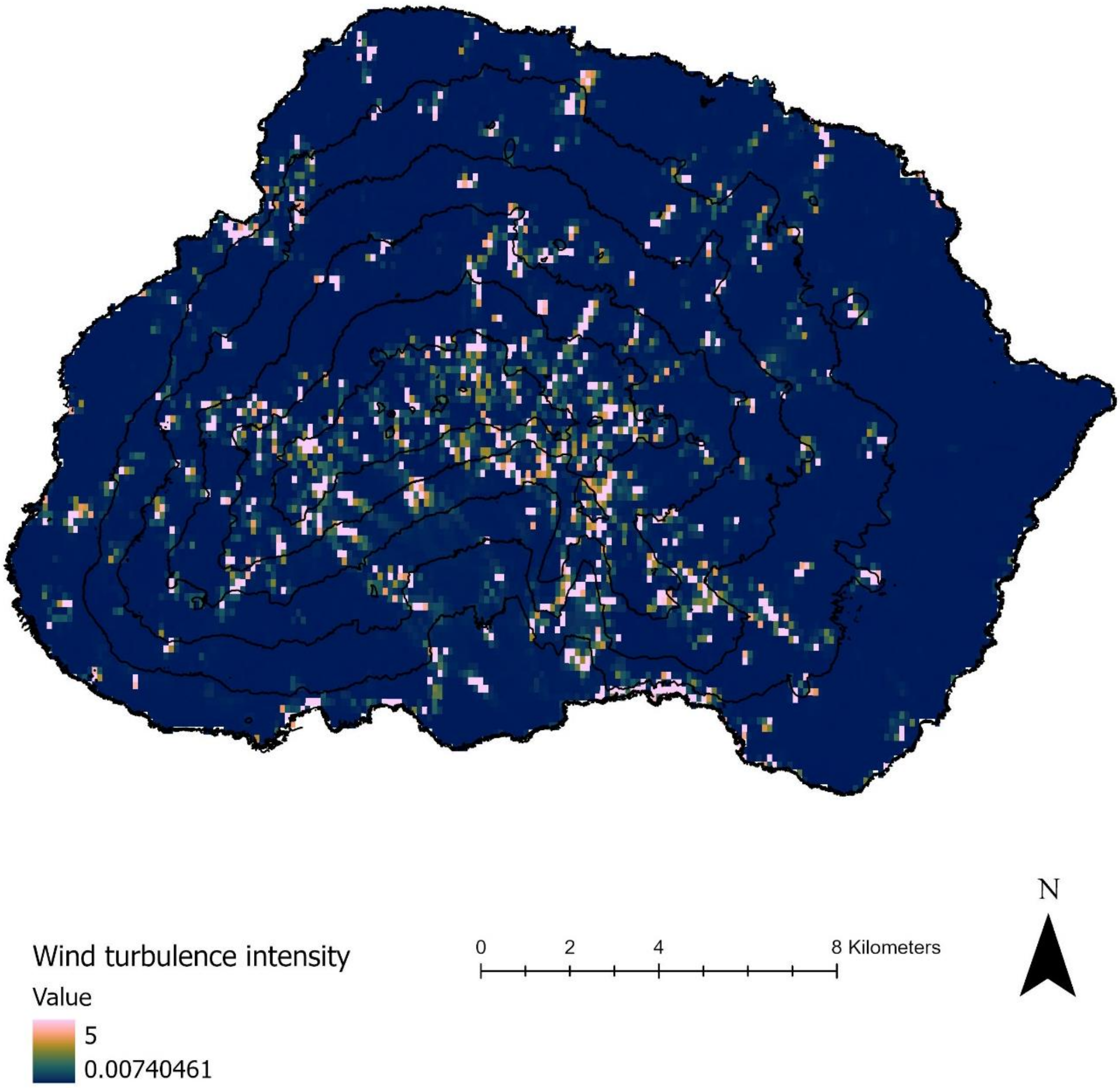

**Figure A6** Wind turbulence intensity on Marion Island, based on Goddard (2021). Lighter colours indicate higher wind turbulence, while darker colours indicate lower wind turbulence. Contours are plotted at 200 m intervals. For island-scale visualisation of wind turbulence, all turbulence values >5 were set to a value of 5 (<0.2% of the dataset).

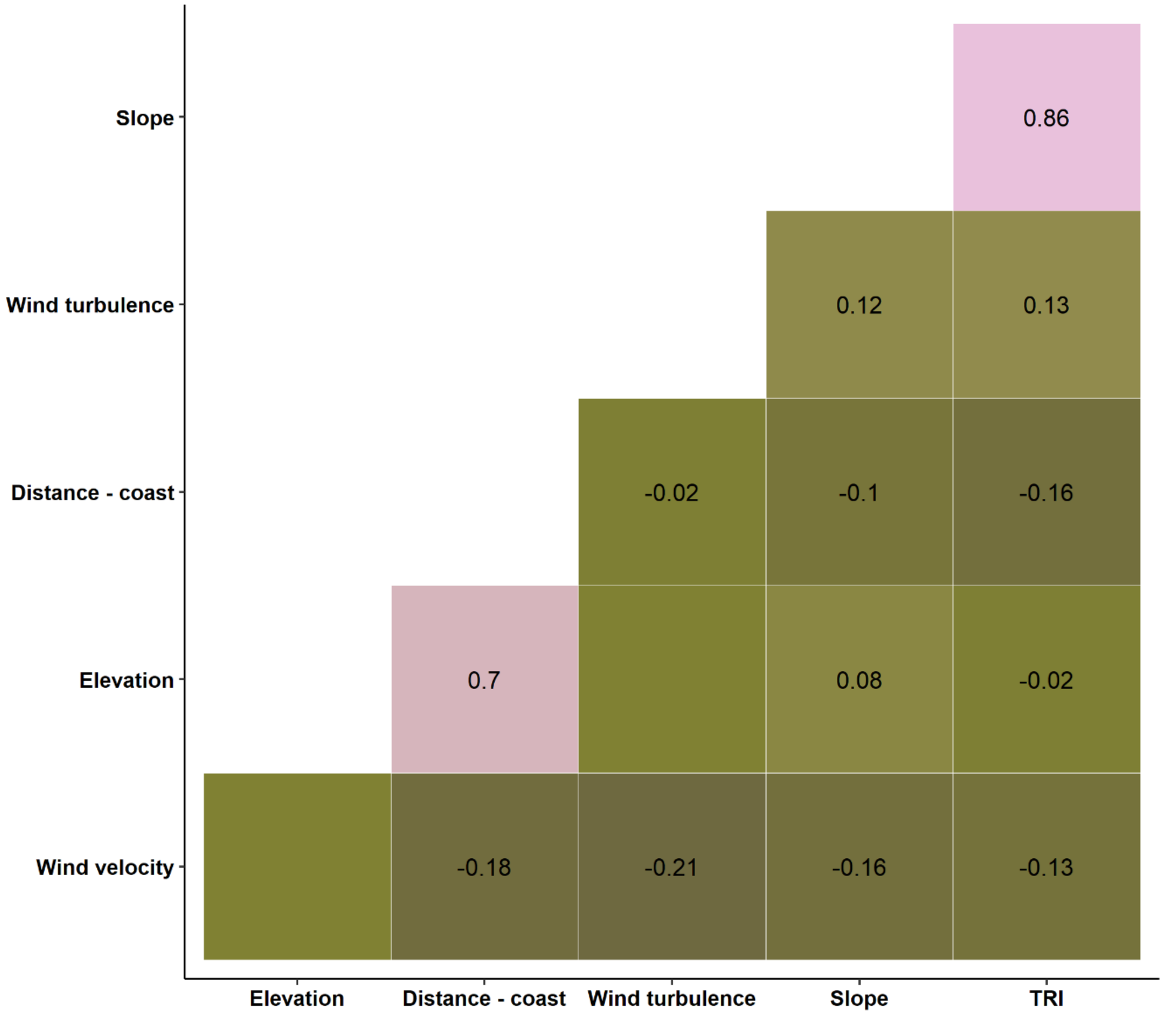

**Figure A7** Correlation matrix showing significant Pearson correlation coefficients between all of the continuous predictor variables initially considered. Cells with no values indicate no significant correlation. TRI = terrain ruggedness index. Distance - coast = shortest distance to the coast line.

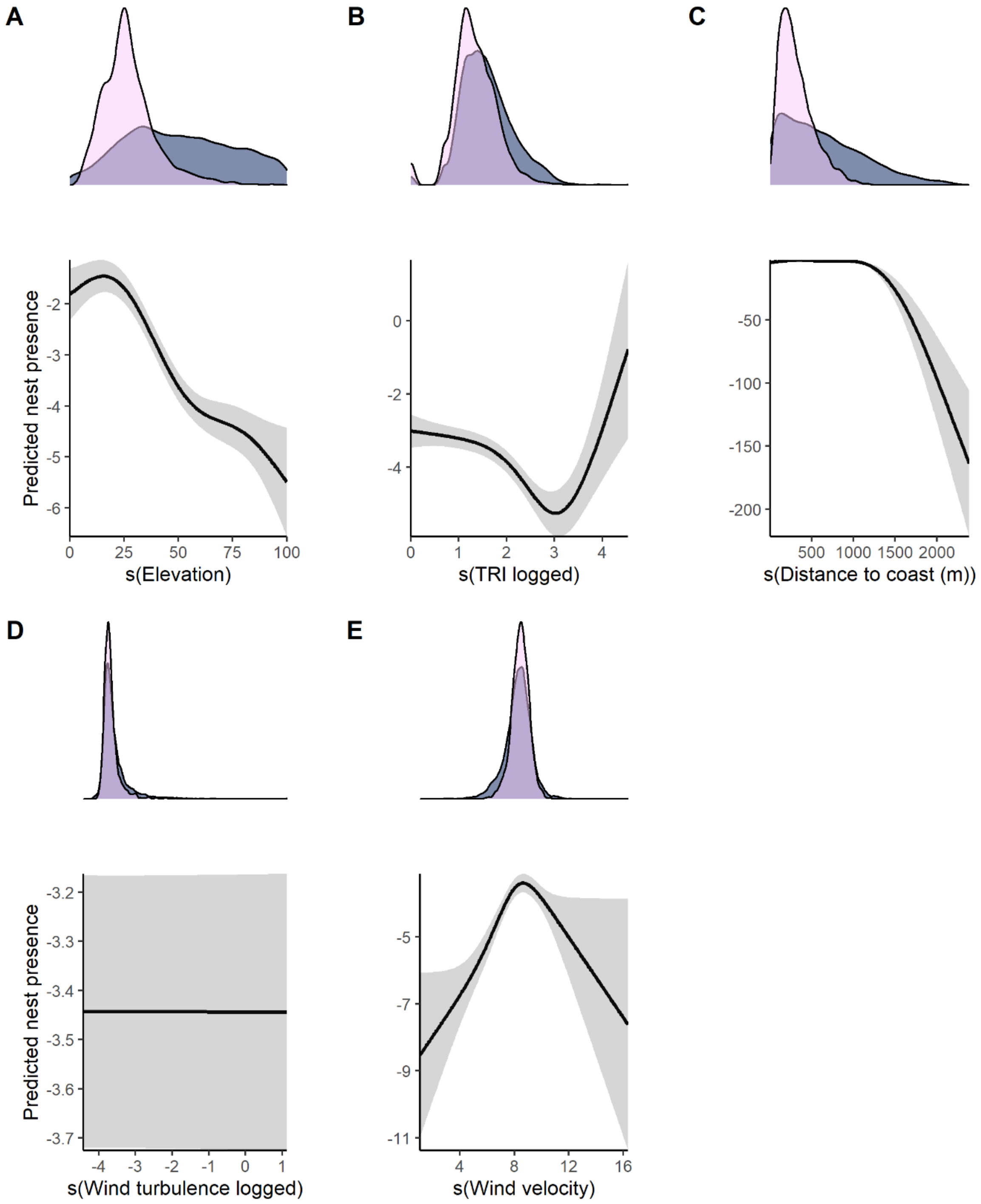

**Figure A8** GAM response curves for the occurrence of Wandering Albatross nests based on data from the 2006 breeding season. A) Elevation, B) Terrain ruggedness index (logged), C) Distance to the coast (m), D) Wind turbulence (logged), E) Wind velocity (m·s$^{-1}$). Light pink density plots represent data from presences and dark blue density plots data from absences. In the response curves, larger values on the y-axis represent a higher probability of occurrence.

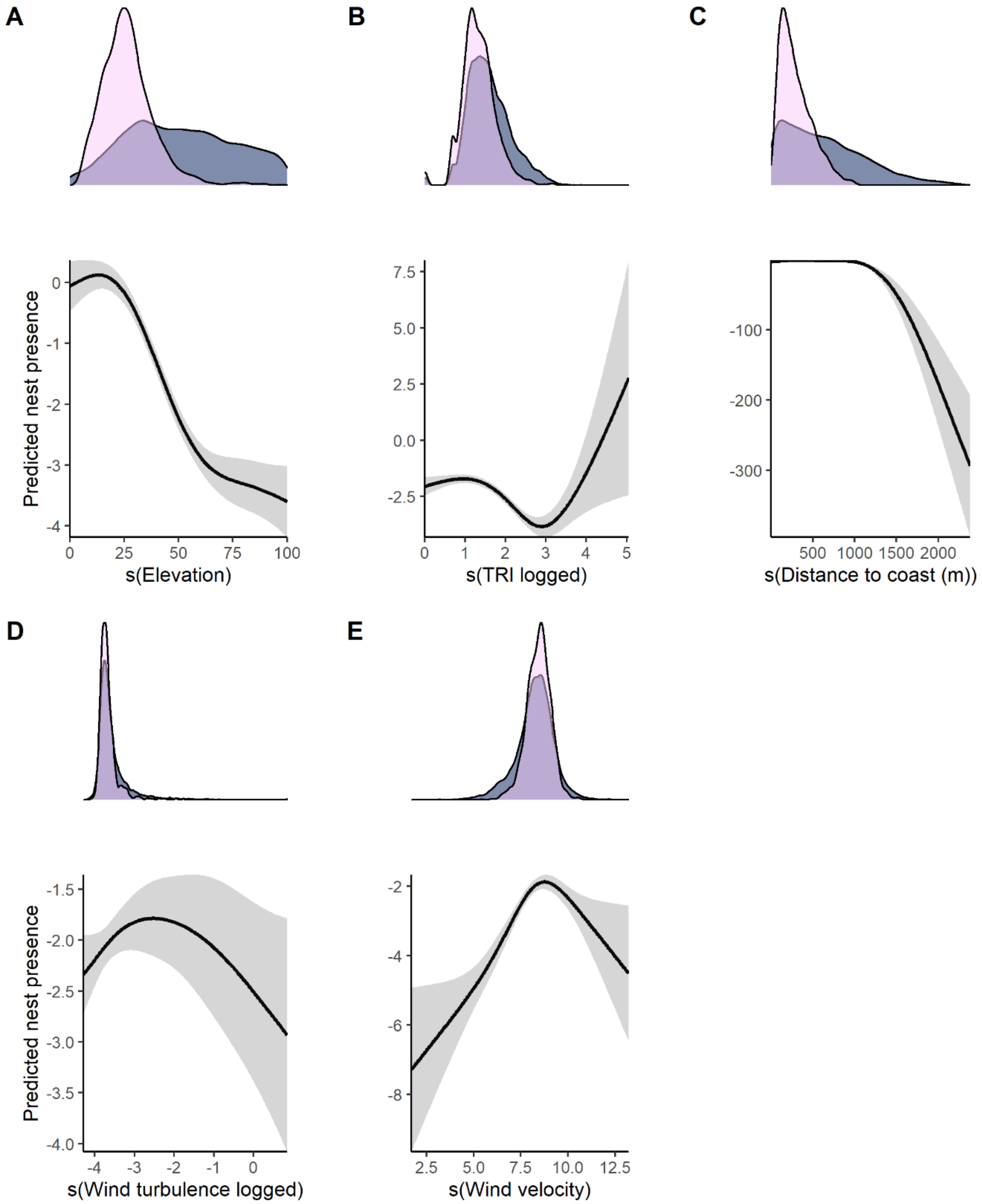

**Figure A9** GAM response curves for the predicted presence of Wandering Albatross nests based on data from the 2018 breeding season. A) Elevation, B) Terrain ruggedness index (logged), C) Distance to the coast (m), D) Wind turbulence (logged), E) Wind velocity (m·s$^{-1}$). Light pink density plots represent data from presences and dark blue density plots data from absences. In the response curves, larger values on the y-axis represent a higher probability of occurrence.

**Table A1** Significance and variable importance for all predictor variables when modelling the presence or absence of Wandering Albatross nests based on data from the 2006 breeding season. GAM, generalized additive model; GLM, generalized linear model. The percent deviance explained was 30.50 % for the GAM, and 29.01 % for the GLM. Since an overall p-value for categorical predictors is not reported from a GAM, the ranking of the levels is reported. Post = post-glacial flows, Pre = pre-glacial flows, P = sub-Antarctic polar desert, F = sub-Antarctic fellfield, M = sub-Antarctic mire-slope vegetation, C = sub-Antarctic coastal vegetation.

| **Predictor** | **GAM** | | **GLM** | |
|---|---|---|---|---|
| | p-value | Relative importance (%) | p-value | Relative importance (%) |
| Elevation | < 0.01 | 47.83 | 0.03* | 43.90 |
| Distance to coast | < 0.01 | 20.92 | < 0.01* | 20.62 |
| Vegetation type | P<F<M<C | 17.63 | P<F<M<C | 17.46 |
| Terrain ruggedness | < 0.01 | 7.69 | 0.55* | 9.35 |
| Wind velocity | < 0.01 | 5.86 | < 0.01* | 8.40 |
| Wind turbulence | 0.44 | 0.06 | 0.28 | 0.24 |
| Geology type | Post<Pre | < 0.01 | Pre<Post | 0.04 |

* quadratic term of that variable was significant in the GLM

**Table A2** Significance and variable importance for all variables when predicting the presence or absence of a Wandering Albatross nest based on data from the 2018 breeding season. GAM, generalized additive model; GLM, generalized linear model. The % deviance explained was 34.00 % for the GAM, and 32.57 % for the GLM. Since an overall p-value for categorical predictors is not reported from a GAM, the ranking of the levels is reported. Post = post-glacial flows, Pre = pre-glacial flows, P = sub-Antarctic polar desert, F = sub-Antarctic fellfield, M = sub-Antarctic mire-slope vegetation, C = sub-Antarctic coastal vegetation.

| **Predictor** | **GAM** | | **GLM** | |
|---|---|---|---|---|
| | p-value | Relative importance (%) | p-value | Relative importance (%) |
| Elevation | < 0.01 | 46.35 | < 0.01* | 44.63 |
| Distance to coast | < 0.01 | 21.12 | < 0.01* | 20.92 |
| Vegetation type | P<F<M<C | 15.07 | P<F<M<C | 14.72 |
| Terrain ruggedness | < 0.01 | 9.31 | 0.01* | 10.03 |
| Wind velocity | < 0.01 | 7.48 | < 0.01* | 9.07 |
| Wind turbulence | 0.08 | 0.35 | 0.12 | 0.39 |
| Geology type | Post<Pre | 0.31 | Post<Pre | 0.24 |

* quadratic term of that variable was significant in the GLM

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# Chapter 6:

# General conclusion

Scientists have been fascinated by the links between abiotic factors and biotic communities from the very beginning of ecological studies (Darwin, 1859). Understanding the effects of climate on biological systems has now become paramount, due to changes in global climate causing shifts in current biological patterns (Parmesan and Yohe, 2003). Traditionally, research examining the impacts of climate change has focussed heavily on temperature and, to a lesser degree, on precipitation (Barton, 2017). While these components of climate are important, relatively little is known about how changes to other climatic variables will affect biological systems. As a result, there have been calls to include other climatic components into ecological research to improve our understanding of what structures natural systems, and how these systems will respond under changing climatic conditions (e.g. Gardner et al., 2019). Wind is an underexplored component of climate (see e.g. Wilson, 1959), with the potential to have large impacts on individual species' performance and community functioning (e.g. Lynch and Kirkpatrick, 1995; Onoda and Anten, 2011).

Although there is some understanding of the ecological impacts of wind in certain scenarios, like how wind may determine the elevation of treelines (e.g. Holtmeier and Broll, 2010), this climatic driver is poorly understood (Sutherland et al., 2017), particularly in areas exposed to chronically windy conditions. The overarching aim of this thesis was to examine the role of wind in shaping biological communities, using the sub-Antarctic as a model system to answer this question. Throughout all four research chapters, wind was found to have an impact on the biota of the windy sub-Antarctic, ranging from individual species to island-scale vegetation patterns. In Chapter 2 I investigated wind speed and wind turbulence as potential drivers of spatial variation in vegetation cover and the distribution of vegetation types across Marion Island. I found that after accounting for elevation, wind velocity had a strong impact on vegetation cover. Wind velocity also significantly affected the occurrence of five out of the six vegetation types. Biotically-influenced vegetation was the only vegetation type where its occurrence that was not significantly affected by wind, likely reflecting that its distribution is driven primarily by manuring and trampling by birds and seals (Smith et al., 2001). The only other predictor affecting the occurrence of as many vegetation types was elevation.

In Chapter 3, I examined the characteristics of plant communities at a finer scale, by quantifying vascular plant species richness, vegetation cover, and species composition in 1 $m^2$ quadrats. Using a novel metric representing wind stress, which incorporates exposure to dominant wind direction and wind speed, the influence of wind on plant communities was quantified. After rock cover, which physically limits vegetation growth, wind stress was the most important driver of vegetation cover, outperforming soil temperature and moisture variables. Species richness was also strongly driven by wind stress, where once again the wind metric explained more of the variation in richness than soil moisture or growing season soil temperature. Including wind stress gave more accurate predictions of plant assemblage attributes, illustrating the relevance of including wind as a metric in biological studies investigating climatic drivers and future climatic change.

In Chapters 4 and 5, I examined how individual species respond to spatial variation in wind. The results indicate that the response of plant species richness and vegetation cover are driven by individual species responses, with the majority of species' occurrence patterns being significantly affected by wind stress after accounting for seven other ecophysiologically-important abiotic variables (Momberg et al., 2021). Wind stress was a more important predictor than any temperature- or precipitation-related variables for six of these species' occurrences, and for five of the species' cover. Fern species and species characteristic of wet mire habitats were particularly strongly affected by wind, likely reflecting a potential sensitivity to wind-driven evapotranspiration causing moisture stress. Furthermore, these results indicate that occurrence of species was more strongly affected by wind than the cover of a species. This has implications for species distributions and community assembly under changing future wind patterns, suggesting that under unfavourable wind stress conditions a species may be completely lost from a site, instead of perhaps just becoming less dominant.

Wind not only impacts on plant species, but also on species that are highly mobile, including the Wandering Albatross (*Diomedea exulans*; Chapter 4). Wind patterns affect flight, foraging, and breeding success in Wandering Albatrosses (Weimerskirch et al., 2000; Weimerskirch et al., 2012; Cornioley et al., 2016; Richardson et al., 2018; Clay et al., 2020), but I examined for the first time how wind affects their nest-site selection. Wind speed had a strong impact on where the world's largest pelagic bird chooses to construct their nests on Marion Island. Elevation, distance from the coast and terrain ruggedness were also important predictors of nest occurrence. The Wandering Albatross needs strong headwinds to allow for take-off and landing due to their large wingspan (Warham, 1977). Therefore, nests located in areas characterized by intermediate wind speeds may allow the birds to reliably land at, and take off from, nesting sites.

Wind is likely also important in affecting other aspects of communities in the sub-Antarctic, and globally, which were not examined here. Although species-level plant traits did not show significant correlations with wind stress (Chapter 4), investigating this question at the intra-specific level could provide new insights. For example, it was noted that individuals of *Crassula moschata* from a wind sheltered site had smaller leaves than those in an exposed site (Huntley, 1971). Further, personal observations in the field showed marked differences in plant height for *C. moschata* growing in areas of different wind exposure (Figure 1). The grass *Polypogon magellanicus* has a lower stature when growing on the cushion plant *Azorella selago* on Marion Island than when growing in the adjacent soil, despite the cushion plant providing a richer and more stable substrate (van der Merwe et al., 2020). This likely reflects that the grasses growing on *A. selago* experience greater wind exposure (since *A. selago* cushions grow to heights of c. 5 – 35 cm in fellfield habitats on Marion Island), with that higher wind stress limiting grass height (van der Merwe et al., 2020). Shorter plants could, however, be protected from the dominant winds through a facilitative mechanism provided by cushion plants (Körner, 2003). The traits of alien plant species in the sub-Antarctic are also affected by wind exposure, which negatively impacts on their plant performance (biomass; Saiz et al., 2021). Therefore, when examining intra-specific trait variation, wind may be an important factor in determining individual plant's morphology and fitness. Directly measuring plant fitness or a close proxy thereof (e.g., number of reproductive structures), or population-level demographics may also provide more clear insights into the direct effects of wind on individuals.

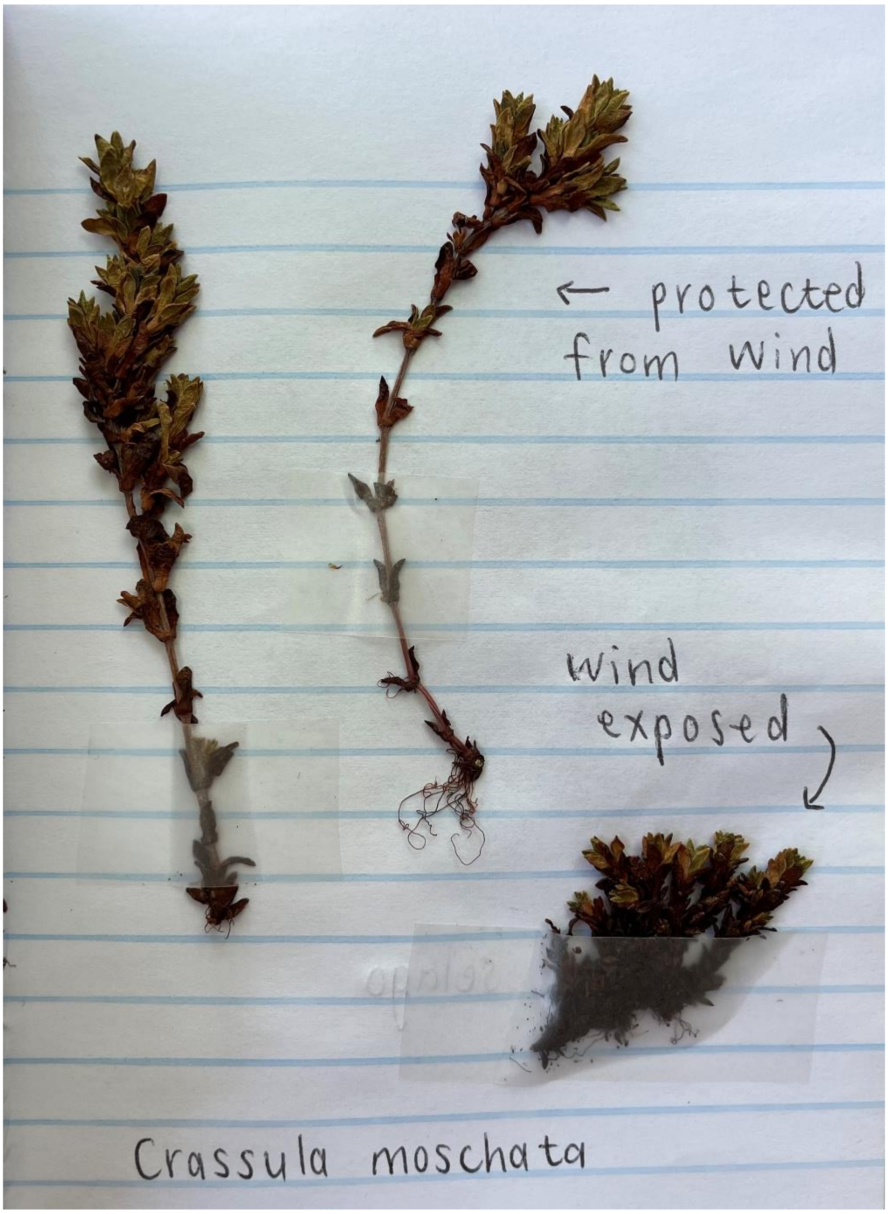

**Figure 1** Differences in plant height of two individuals of *Crassula moschata* growing at different levels of wind exposure (7 May 2019, near Macaroni Bay).

*Azorella* selago is a widespread and keystone species in the sub-Antarctic (le Roux et al., 2005), for which asymmetrical dieback has been noted, likely due to wind scouring as well as seed deposition of *P. magellanicus* on the windward side of plants (Figure 2; Boelhouwers et al., 2003; Combrinck et al., 2020). I hypothesize that the dieback on the windward side of these plants is further affected by wind through desiccation, since previous research has shown that reduced rainfall increases stem mortality disproportionately on the windward side of individuals (le Roux et al., 2005). This same species can also be found growing in vegetation stripes orientated parallel to salt-bearing winds (Huntley, 1971). Since this keystone species is strongly affected by wind, other species should also be investigated to determine whether they show directionality in growth and deaths rates (see e.g. Smith, 1972; Fitzgerald and Kirkpatrick, 2017; Ramírez-Pinero et al., 2019). Micro-scale differences in plant performance linked to the directionality of the wind could explain whether species will be able to survive, or indeed whether individuals will expand or retract in size, under changing wind directions.

**Figure 2** Asymmetrical dieback on the windward side of an individual *Azorella selago* plant. Stems on one side of the plant have died, causing snow to accumulate in this area, while stems on the other side of the plant remain healthy. Wind plays an important role in determining the distribution of snow in the landscape.

My findings show that wind velocity affects the nest-site selection of the world's largest pelagic bird, the Wandering Albatross. Since wind velocity plays a key role in determining where nests are constructed by this species, future work should also investigate whether wind velocity has an impact on the fledgling success rate. Chicks that are exposed to more extreme wind speeds may be blown off the nest or lose body heat more rapidly, which could negatively affect their survival (Cunningham et al., 2016). Other surface-nesting species will likely also be affected by wind conditions. Cliff-nesting birds may show range contractions if wind direction shifts result in these exposed cliff areas becoming more susceptible to strong winds coming from the sea, or increases in wind turbulence through interactions with the topography.

## Which way will the wind blow?

Species distribution models are widely used in the field of ecology to inform management plans. While the need to include more biologically relevant variables into these models has been highlighted (Mod et al., 2016), only recently have a new range of climate variables been considered, including solar radiation, snow cover, and soil moisture (Niittynen and Luoto, 2018; Kemppinen et al., 2019). The results from this thesis highlight the need to also include wind characteristics into species distribution models.

Studies examining links between biological systems and climate are valuable for objectively estimating how ecosystems, species assemblages, and their functioning, may change under shifting climatic conditions. Plants and animals are adapting to climatic changes to temperature and precipitation, but these adaptations are likely inadequate in terms of the magnitude of the climatic shifts forecast to occur in the next 50 years (Gómez-Ruiz and Lacher Jr, 2019; Radchuk et al., 2019). It is possible that plants and animals may also struggle to adapt fast enough to changing wind conditions. Given that changes have already been recorded for global wind patterns over the last three decades (Young and Ribal, 2019), and that wind conditions are predicted to continue to change (Jeong and Sushama, 2019; Zeng et al., 2019), there will be pressure on species and communities to adapt to new wind conditions. Changing wind conditions will also interact with temperature and precipitation regimes. For example, regions experiencing reduced precipitation or increased temperatures will be disproportionately affected by moisture stress if they also experience increased wind speeds. In contrast, increases in maximum temperatures in the future could potentially be mediated by the cooling effect of an increase in average wind speed in an area.

Wind was an important driver of biological patterns across all spatial scales. From this research it appears that wind turbulence at, and near, ground level does not strongly affect biological communities (as assessed for both vegetation and bird responses). Wind turbulence is more difficult to measure than wind speed and wind exposure, requiring a high frequency of measurements, and cannot be derived from remotely-sensed data. This result provides a good indication that future work should focus on including wind exposure and wind speed, given the widespread impacts thereof across different spatial extents. Where possible, both of these components should be incorporated, since microsites could be protected from or exposed to strong wind speeds based on exposure linked to local topography. Interpolated wind speed data is available at a resolution of 1 $km^2$ (Fick and Hijmans, 2017) and wind exposure can be estimated from digital elevation models, and studies with a large enough spatial resolution can therefore easily include speed and exposure among their predictor variables. At a finer scale, at a minimum, wind exposure should be included as a predictor (see e.g. Burke et al., 1989; Fernández-Palacios and Nicolás, 1995), or wind patterns should be simulated where coverage of anemometer readings from weather stations is complete enough.

Globally, there are large areas that experience high mean wind speeds (Figure 3a). Coastal areas typically experience stronger winds than inland regions (Wright and Grab, 2017), with the Arctic (and Greenland in particular), the Sahara and Sahel, and the mountains in north America and Europe being consistently windy. Future research should focus on testing the importance of wind in structuring these chronically windy systems in order to understand the generality of the findings of this thesis. Wind is an important geological and geomorphological force in deserts (Goudie, 1989), and arid systems should also be investigated as high priority areas for wind-related studies, particularly since the interactions between wind, high temperatures and low amounts of soil moisture can also be studied. Areas with thin soils (Figure 3b) are also expected to be more influenced by wind, as these soils will desiccate more easily, affecting soil moisture available to plants (Bertiller et al., 1996; Fitzgerald and Kirkpatrick, 2017). In particular, research in areas that have both high wind speeds and thin soils will be valuable to improve the understanding of how these two factors interact.

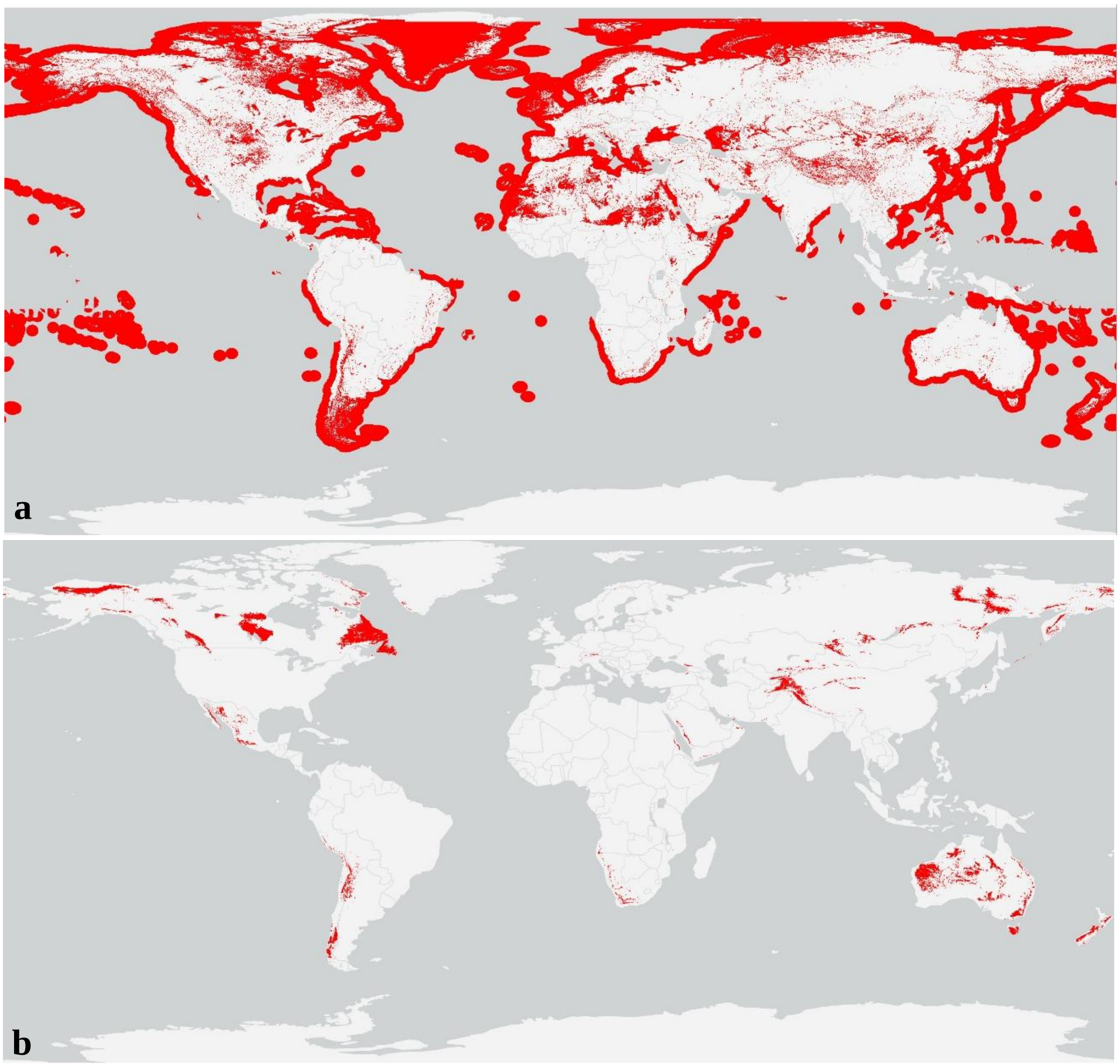

**Figure 3** Terrestrial areas with a) a mean wind speed of greater than 5 m·s$^{-1}$ at a height of 10 m, and b) soil depth to bedrock of less than 20 cm, highlighted in red. Maps created in ArcGIS, using data from Global Wind Atlas 3.0 (2021) and Hengl et al. (2017).

Additionally, wind may also have indirect impacts on biotic communities through affecting other processes. Shifts in wind patterns may affect fine-scale changes in air temperature, where wind directionality will affect whether hot winds increase temperatures or cooler winds can offset temperature increases (Kullman and Loyer, 2005; Ashcroft et al., 2009). Soil temperatures may also be affected through the redistribution of plant litter by wind, where areas with high plant litter deposition remain cooler, as well as having higher nutrient contents (Fahnestock et al., 2000). Soil erosion is also affected by wind, and changes to wind patterns could lead to increased erosion (Nylén et al., 2015; Nylén and Luoto, 2015). Other types of disturbances can also interact with wind, for example, the complex interaction between wind speed and fire intensity which affects the overall magnitude of disturbance (Beer, 1991; Eftekharian et al., 2019). Consequently, wind needs to be considered in climatic models not only for its direct effects on biotic communities, but also to further understand its indirect effects through interaction with other abiotic factors.

In this thesis, I show that wind has a strong effect in shaping the biological communities in the sub-Antarctic, a region which experiences chronic winds. Given the widespread potential ecological impacts of wind, across different taxa, different organizational levels and different spatial scales, wind needs to be examined more widely as a driver of biological communities. Wind-focused studies are important in improving our understanding of poorly studied ecological predictors, and providing better estimates for future predictions of the ecological impacts of changing climatic conditions.

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