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

Running title: Species differ in responses to wind

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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 ecophysiologicaly-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.

Keywords: climatic drivers, community dynamics, fine-scale, species distributions, wind

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 ecophysiologicaly-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

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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 (Momborg 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.

Materials and 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 km²). 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 m² 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 m² 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 \pm 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.

Table 1 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 (%)
<i>Acaena magellanica</i> (Lam.) Vahl	Angiosperm	Rosaceae	0.09	11.97	3619.63	2.47	0.22	37.8	3.20
* <i>Agrostis stolonifera</i> L.	Angiosperm	Poaceae	0.17	47.31	272.19	2.83	0.35	1.0	0.31
<i>Austroblechnum pennamarina</i> (Poir.) Gasper & V.A.O.Dittrich	Pteridophyte	Blechnaceae	0.18	13.08	1535.93	1.53	0.19	89.9	27.52
<i>Azorella selago</i> Hook.f.	Angiosperm	Apiaceae	0.14	8.71	63.75	1.67	0.18	65.8	7.19
<i>Carex dikei</i> (Nelmes) K.L.Wilson	Angiosperm	Cyperaceae	0.08	9.94	793.72	1.62	0.16	30.3	5.17
* <i>Cerastium fontanum</i> Baumg.	Angiosperm	Caryophyllaceae	0.20	20.07	133.33	4.37	0.68	2.0	0.01
<i>Hymenophyllum peltatum</i> (Poir.) Desv.	Pteridophyte	Hymenophyllaceae	0.01▲	NA	NA	NA	NA	8.5	0.35
<i>Juncus scheuchzerioides</i>	Angiosperm	Juncaceae	0.03	14.48	62.17	1.95	0.17	12.9	1.07

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

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 bitermatus* 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 Table A9 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).

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). Pteridophyte species had generally 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 ($r=0.55$, $p=0.04$).

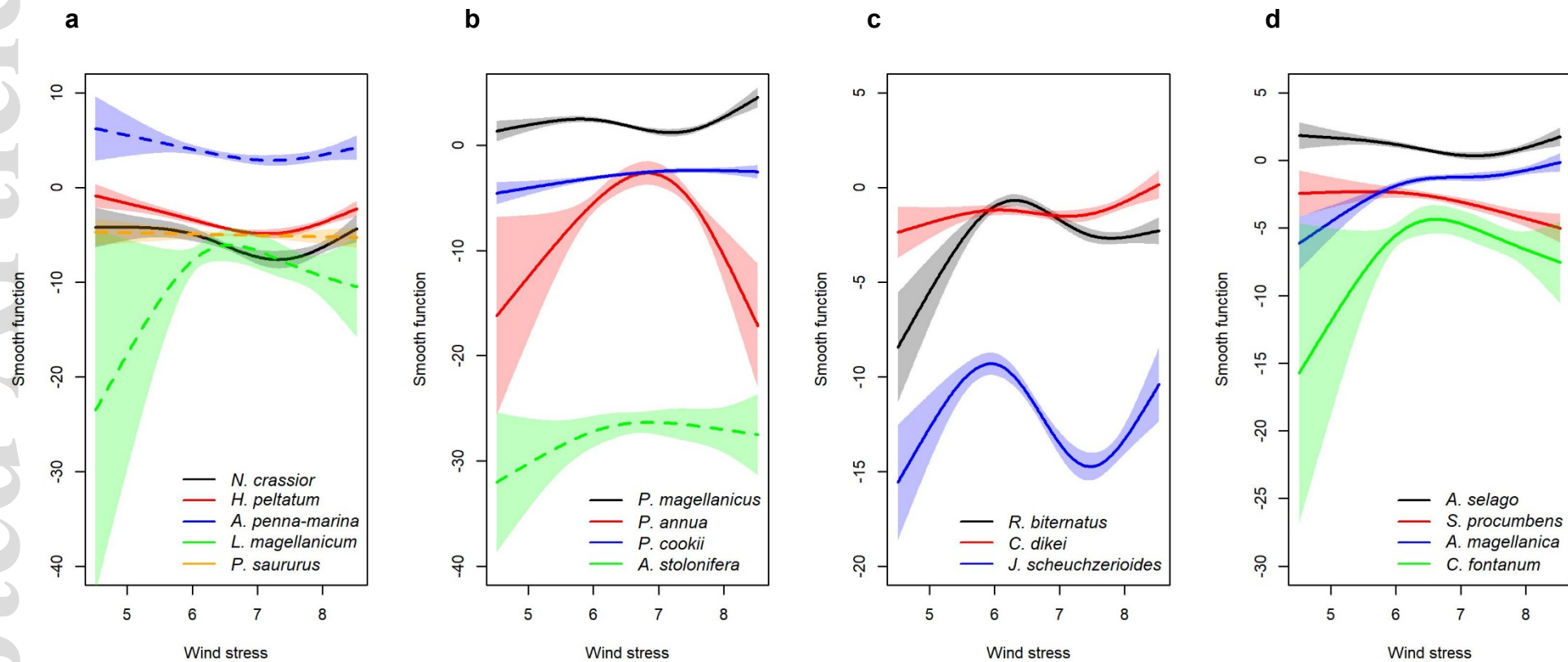


Figure 1 Response curves from the full GAM of the occurrence of all species in response to wind stress. Dashed lines represent models where wind stress was not a significant predictor of species occurrence in the multivariate models. a) Pteridophytes; *N. crassior* = *Notogrammitis crassior*, *H. peltatum* = *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 %.

Species	Deviance explained (%)		p-value of wind stress variable	
	Univariate model	Multivariate model	Univariate model	Multivariate model
<i>Acaena magellanica</i>	11.2	47.8	< 0.05	< 0.05
* <i>Agrostis stolonifera</i>	6.21	72.0	0.10	0.34
<i>Austroblechnum penna-marina</i>	18.8	38.7	< 0.05	0.06
<i>Azorella selago</i>	0.08	29.4	0.23	< 0.05
<i>Carex dikei</i>	2.78	38.1	< 0.05	<0.05
* <i>Cerastium fontanum</i>	11.4	34.7	< 0.05	< 0.05
<i>Hymenophyllum peltatum</i>	23.4	40.7	< 0.05	< 0.05

<i>Juncus scheuchzerioides</i>	25.4	46.3	< 0.05	< 0.05
<i>Lycopodium magellanicum</i>	9.57	27.9	< 0.05	0.07
<i>Notogrammitis crassior</i>	14.6	51.7	< 0.05	< 0.05
<i>Phlegmariurus saururus</i>	6.68	25.1	< 0.05	0.64
* <i>Poa annua</i>	22.6	46.7	< 0.05	< 0.05
<i>Poa cookii</i>	1.16	24.1	< 0.05	<0.05
<i>Polypogon magellanicus</i>	4.21	25.7	< 0.05	< 0.05
<i>Ranunculus biternatus</i>	2.52	17.0	< 0.05	<0.05
* <i>Sagina procumbens</i>	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. * = invasive species

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

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.

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 pteridophytes, *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 *Phlegmariurus 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 (Hausmann 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 (Osoné 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 (Hausmann 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.

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 desiccation; 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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Author contributions

P.C.I.R., M.L. and M.M. conceived the ideas and designed the methodology; M.M., P.C.I.R. and D.W.H. collected and processed the data; M.M. and P.C.I.R. analysed the data, with inputs from D.W.H. and M.L.; M.M. led the writing of the manuscript. All the authors contributed critically to the drafts and gave final approval for publication.

Data availability statement

The data that support the findings of this study are available from the corresponding author upon reasonable request at <https://doi.org/10.5281/zenodo.5639635>.

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Supporting information

Appendix S1. Map and photographs of study site.

Appendix S2. Photographs of a selection of species.

Appendix S3. Correlation matrix of all predictor variables.

Appendix S4. Response curves from the full GAM of the occurrence of all pteridophytes in response to the eight predictor variables.

Appendix S5. Response curves from the full GAM of the occurrence of all Poaceae (grasses) in response to the eight predictor variables.

Appendix S6. Response curves from the full GAM of the occurrence of mire species in response to the eight predictor variables.

Appendix S7. Response curves from the full GAM of the occurrence of all other angiosperms in response to the eight predictor variables.

Appendix S8. Response curves from the full GAM of the cover of all pteridophytes in response to the eight predictor variables.

Appendix S9. Response curves from the full GAM of the cover of all Poaceae (grasses) in response to the eight predictor variables.

Appendix S10. Response curves from the full GAM of the cover of mire species in response to the eight predictor variables.

Appendix S11. Response curves from the full GAM of the cover of all other angiosperms in response to the eight predictor variables.

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 and a GLM that included all eight predictors.

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 and a GAM that included all eight predictors.

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 and a GLM that included all eight predictors.

Appendix S15. Percentage variable importance for each predictor variable based on the full GLM model for species occurrence.

Appendix S16. Percentage variable importance for each predictor variable based on the full GBM model for species occurrence.

Appendix S17. Percentage variable importance for each predictor variable based on the full GAM model for species cover.

Appendix S18. Percentage variable importance for each predictor variable based on the full GLM model for species cover.

Appendix S19. Percentage variable importance for each predictor variable based on the full GBM model for species cover.

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.

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).