

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

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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 1,440 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 ecophysiological 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.

Keywords: community composition, fine scale, plant community, species richness, vegetation cover, wind

1 INTRODUCTION

Recent changes in climate have impacted all aspects of ecological communities, including species richness, total abundance, biomass, cover and species composition (e.g. Kardol et al., 2010; Liu et al., 2018; Menéndez et al., 2006). 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 & Johansson, 2011; Pecl et al., 2017). While some trends, like species range shifts, have been observed fairly consistently (e.g. Freeman et al., 2018; Morueta-Holme et al., 2015), 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 10 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 & 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 Austin & Van Niel, 2011; Bennie et al., 2008; Niittynen & 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 (Bintanja et al., 2014; Combes & Matano, 2018; Watanabe & Hasumi, 2005). It is relatively well-understood how extreme winds (e.g. hurricanes and tornadoes) affect individuals, species and communities (Behie et al., 2014; Mitchell, 2012; Møller, 2013; Xuan & Chang, 2014). However, these extreme conditions are limited in time and space (Lugo, 2008; Nyberg et al., 2007), 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 & 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 (Gardiner et al., 2016; Hadley & Smith, 1983, 1986; de

Langre, 2008), uprooting individuals (Yang et al., 2014), and causing flowers and fruit to be shed (e.g. Lahav & 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 & Anten, 2011). Further, wind can shape the outcome of plant–plant interactions (severity-interaction-relationships; le Roux & McGeoch, 2010). Therefore, wind has the potential to directly affect vegetation patterns, from altering individual species' dominance (Okitsu & Ito, 1984) to impacting the distribution of different plant communities (Williams & Ashton, 1987; Lynch & 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 have considerable potential to drive spatio-temporal variations in plant communities.

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 m × 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 m × 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 m × 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 m × 1 m plots	Wind speed was an important driver of species composition; $R^2 > 0.35$	Vonlanthen, Bühler, et al. (2006)
Distribution of vegetation types	North America, the Alps, European subarctic	Alpine	Review	Wind determines the tree line position in three different ecosystems and can override the role of heat deficiency	Holtmeier and Broll (2010)
	Swedish Scandes	Alpine	10 m × 10 m plots	Wind determines the birch tree line and increasing wind circulation constrains upslope tree line expansion in response to warming temperatures	Kullman and Loyer (2005)
	Five mountain regions from three continents	Alpine	50 m ² plots	Wind exposure was the main determinant of the number of seedlings present at the tree line, with increased wind exposure correlated with fewer tree seedlings	McIntire et al. (2016)
	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 and 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)

Wind stresses and disturbances may vary greatly over short distances (Chiras, 2017; Katsaprakakis & Christakis, 2012), 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, 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 & 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 interspecific 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 & 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 & Ribal, 2019; Zeng et al., 2019), and current predictions suggesting that this trend will continue in the long term (Jeong & 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 (a) vascular plant species richness, (b) species cover and (c) species composition in a wind-exposed environment, after accounting for other potentially ecophysiological important variables (Mod et al., 2016).

2 MATERIALS AND METHODS

2.1 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 (le Roux, 2008; Pendlebury & Barnes-Keoghan, 2007). 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 1,240 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 (le Roux, 2008; Pendlebury & Barnes-Keoghan, 2007) 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). The mean daily maximum and minimum temperatures are 8.7 and 3.2°C, respectively, and the mean annual precipitation is c. 1,800 mm (recorded at the island's meteorological station which is ~1 km away from the study site; average from 2008 to 2018).

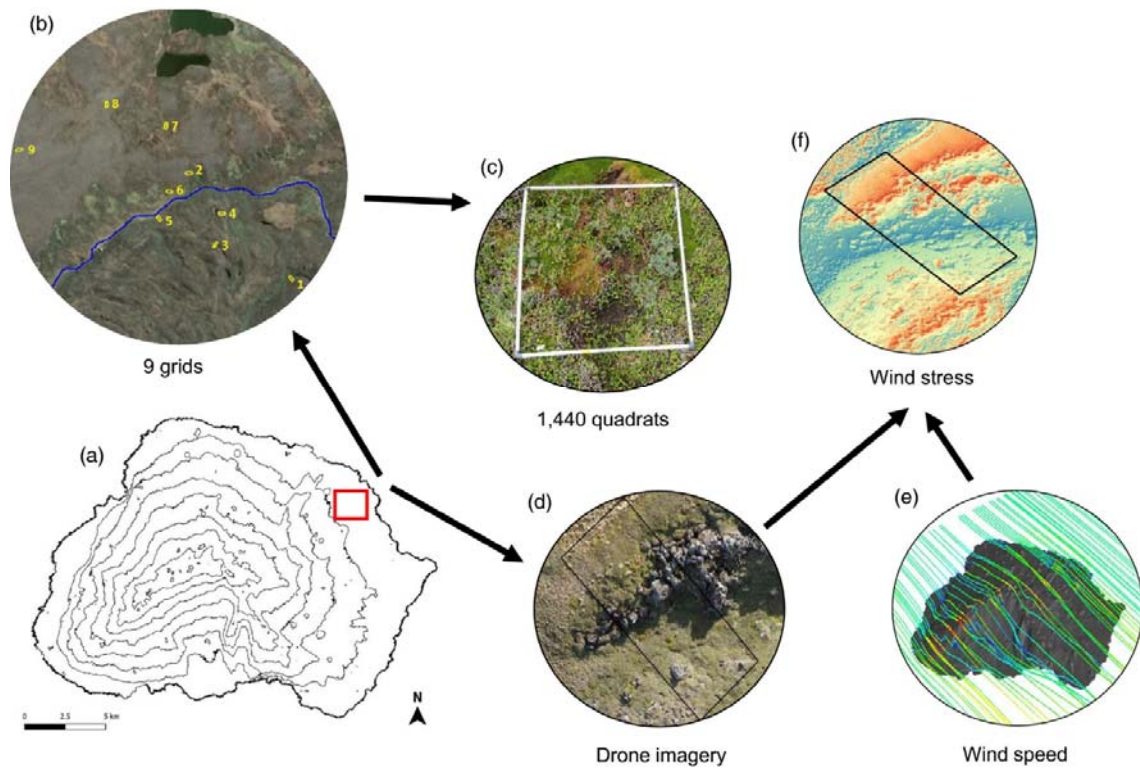


FIGURE 1. Study site location on Marion Island and study design. (a) Marion Island, with contour intervals of 150 m and study location indicated by the red block; (b) the location of all nine study grids (each 8 m × 20 m; the distance from grid 1 to grid 9 is ~900 m; Google Earth imagery), with the Van den Boogaard river indicated in blue; (c) biotic and abiotic data were sampled from 160 quadrats within each grid, resulting in a total of 1,440 quadrats (each 1 m × 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

2.2 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 heterogeneous 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; Figure 1). A survey approach was used that has previously been applied in other high-altitude and high-latitude systems (e.g. Kemppinen et al., 2019; Niittynen et al., 2020a; le Roux, Lenoir, et al., 2013), 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 m × 20 m were sampled, each comprising 160 contiguous quadrats of 1 m² (resulting in 1,440 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.

TABLE 2. Vegetation and abiotic characteristics of each grid. See Figure 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

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, 2007; McCune & Keon, 2002). Soil samples were taken from 16 to 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 hr since the last rainfall event. Volumetric soil moisture content was measured using a handheld time-domain soil moisture metre (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 three to nine 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, Aalto, et al., 2013).

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 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 resolution, with measurement accuracy of 2% (at 12 m/s). Wind speed and direction were sampled at 0.5 Hz, with mean direction and speed logged every 10 min using a CR300 data logger (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 to 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 were recorded between 260° and 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° to 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 & Antonić, 2009). To account for differences in coarser-scale wind stress between grids (since some grids were more wind-exposed than others; Figure 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 & 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 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.

2.3 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 (GLMs; Müller, 2012), generalized additive models (GAMs; Wood & Augustin, 2002) and generalized boosted regression models (GBMs; Friedman, 2001; Friedman et al., 2000). 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 GLMs included quadratic terms for all predictor variables to allow for nonlinear 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 1,000. To determine whether the addition of wind stress improved the performance of the models, each pair of simple and full models from GAMs and GLMs 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 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 & Luoto, 2018). The calculations of variable importance were calculated 10 times and the mean importance value reported.

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 & 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.

3 RESULTS

Wind stress ranged from 4.5 to 8.5, with grid 1 experiencing the overall lowest wind stress, and grid 4 the highest wind stress (Figure 2). Species richness varied between zero and eight species per 1-m² quadrat, and between nine and 15 species per grid (Figure 3), while vascular plant cover varied between a minimum of zero and a maximum of 100% (Figure A5).

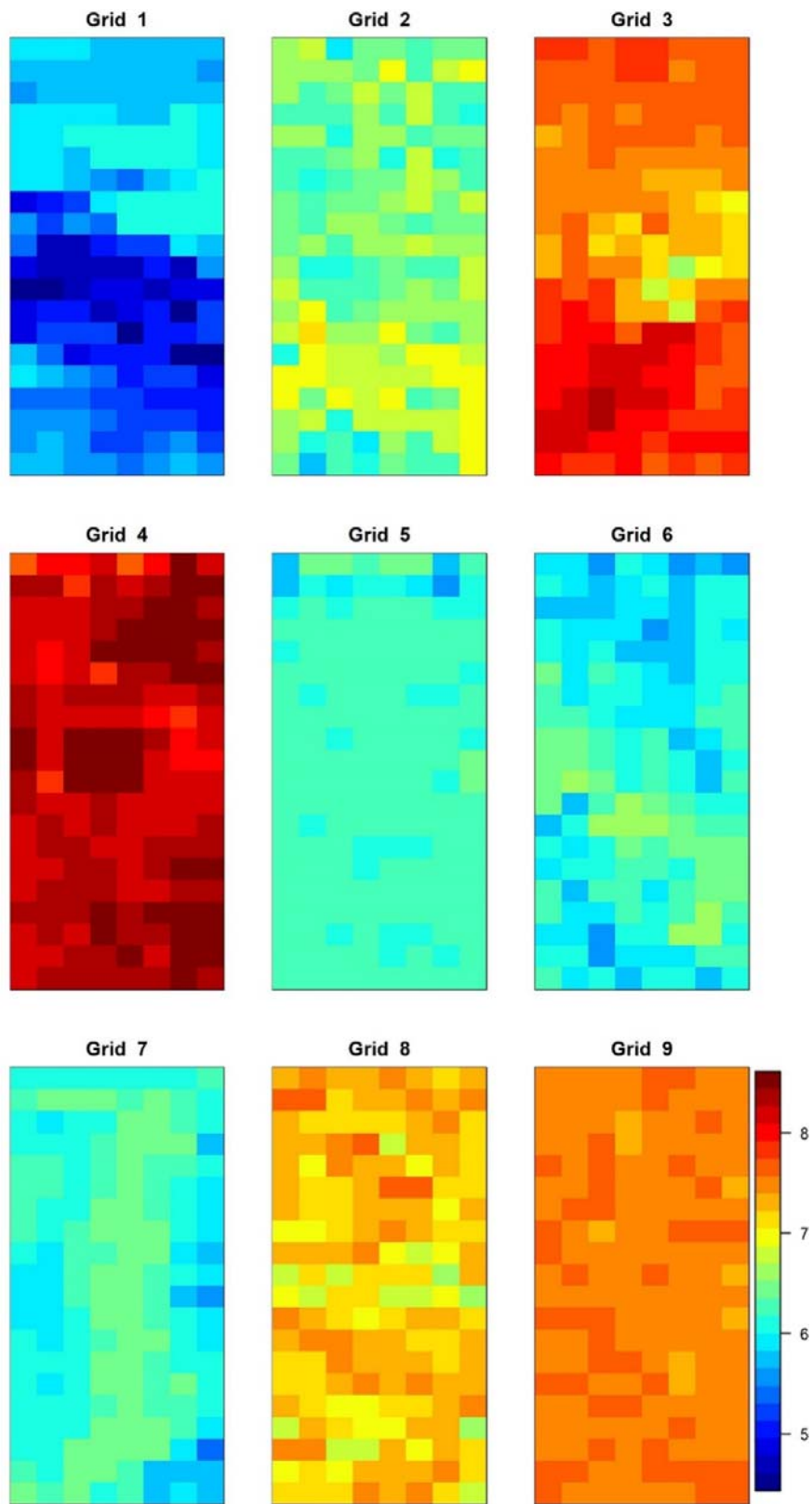


FIGURE 2. Variation in maximum wind stress in all nine study grids (see Figure 1 for location of the grids) indicated for each 1-m² quadrat. Cooler colours indicate low wind stress and warmer colours indicate higher wind stress

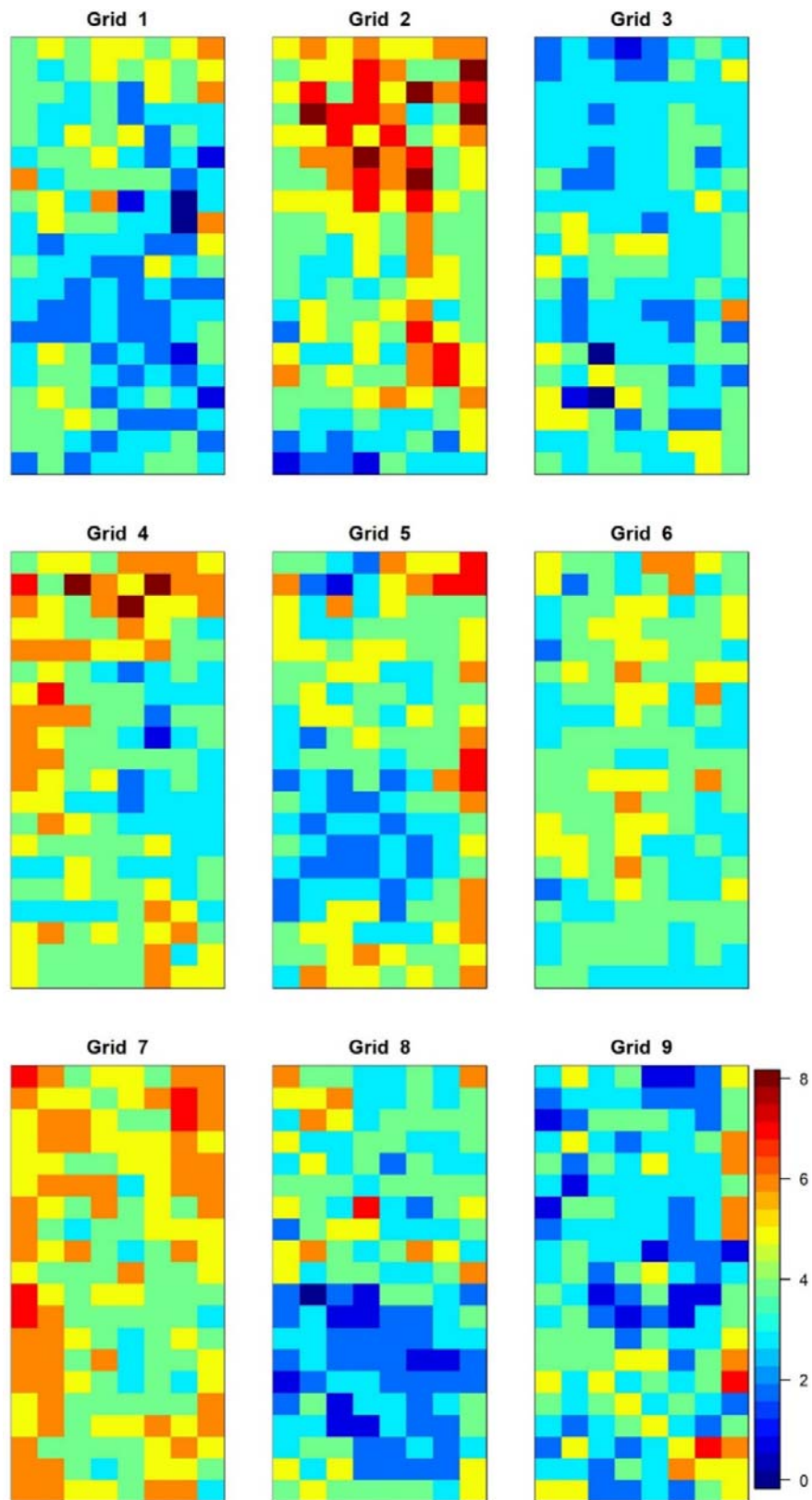


FIGURE 3. Species richness across all nine study grids (see Figure 1 for location of the grids), with vascular plant species richness indicated for each 1-m² quadrat. Cooler colours indicate low species richness and warmer colours indicate higher richness

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 GLM. For vegetation cover the full model performed significantly better in both statistical approaches (GLM 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 GLM 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 GLM and by 1.4% for the GAM (Table A1).

Both GLMs and GAMs 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, Table A2). Response curves from the GAM 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 GLM, Figure A8; and for the GBM, Figure 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 nonlinear 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).

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; GLM, generalized linear model. See Table A2 for results from the generalized boosted regression models

	Richness		Cover	
	GAM	GLM	GAM	GLM
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*

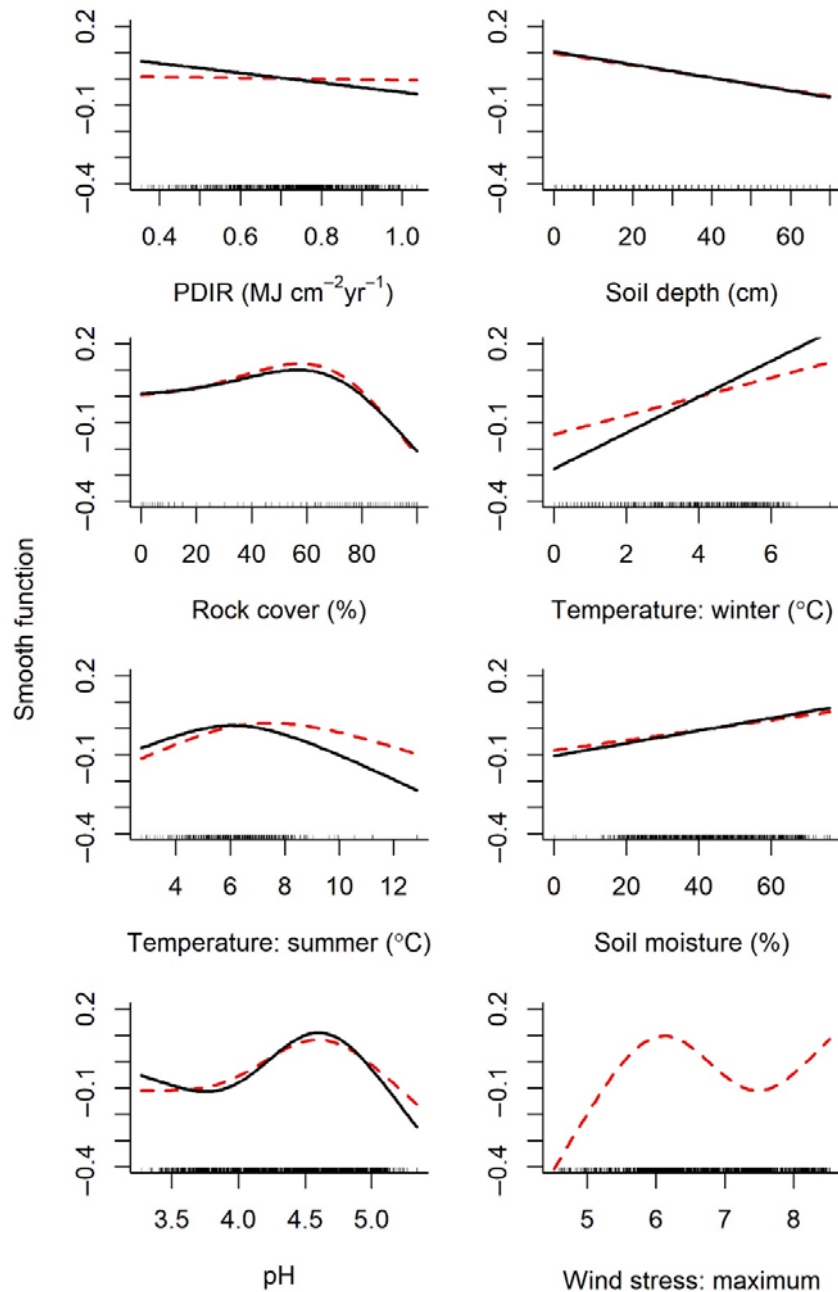


FIGURE 4. Individual predictor variables' response curves for species richness in GAMs. Tick marks on the x-axis indicate observed values. Solid black lines represent the response curves from the simple model (excluding wind stress predictor variables), while dashed red lines represent the response curves from the full model. PDIR = potential direct incident radiation

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 GLM and the GAM (Table 3; and third most important in the GBM, 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 Figures A9 and A11 for GLM 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).

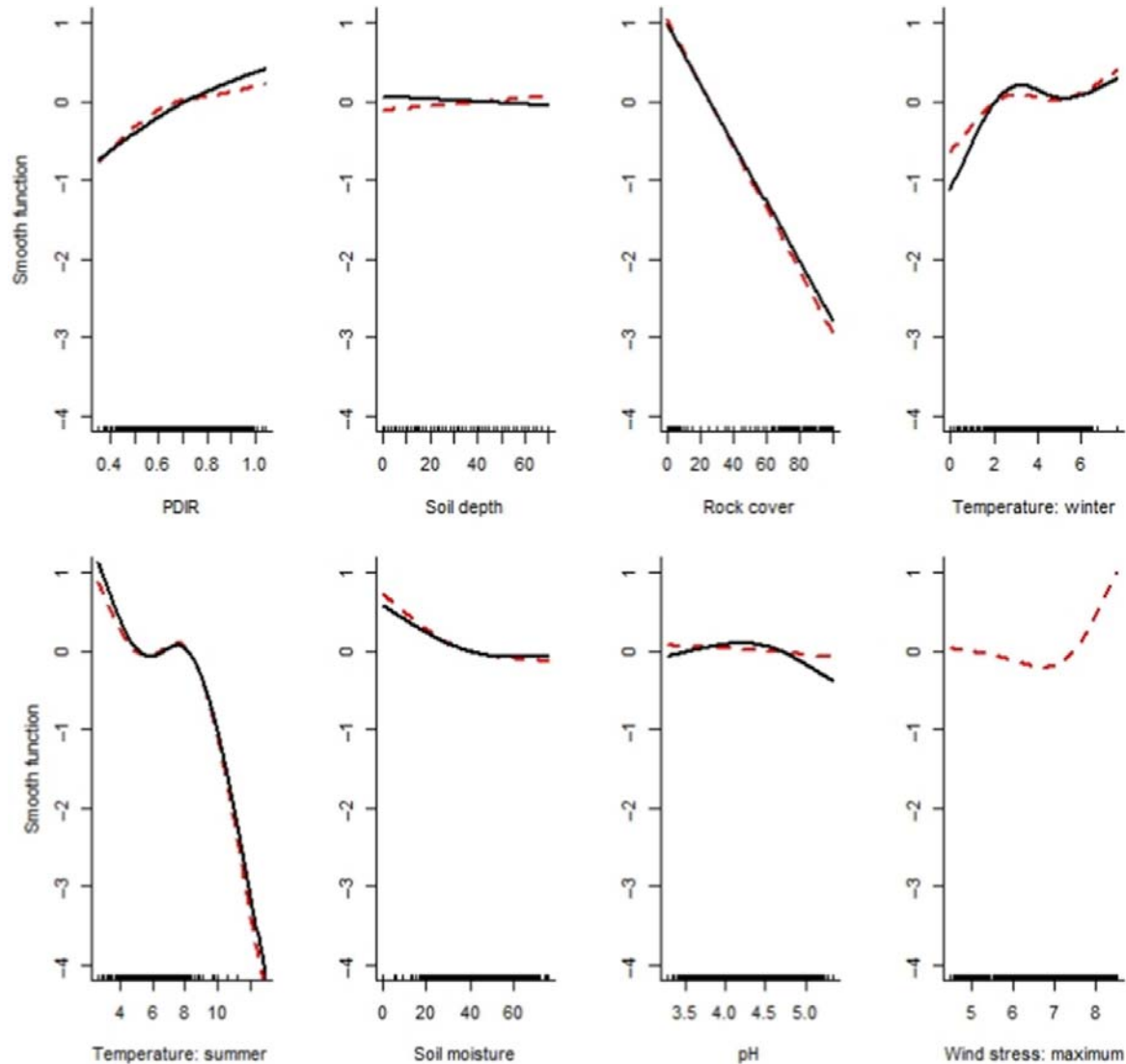


FIGURE 5. Individual predictor variables' response curves for vegetation cover in GAMs. Tick marks on the x-axis indicate observed values. Solid black lines represent the response curves in the simple model (excluding wind stress predictor variables), while dashed red lines represent the response curves in the full model. PDIR = potential direct incident radiation

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 (Figure 6). 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).

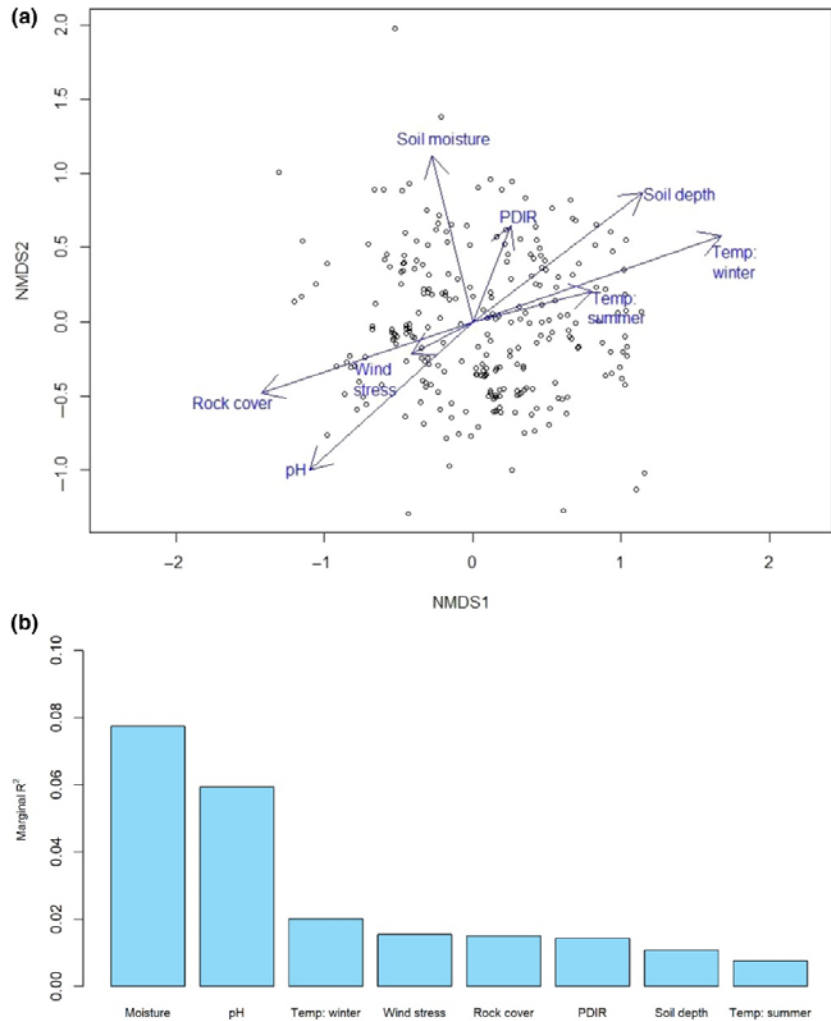


FIGURE 6. (a) Non-metric multidimensional scaling (nMDS) ordination plot showing variables impact on species composition (Stress = 0.18), symbols indicate sampled quadrats; (b) Variable importance, as assessed by marginal R^2 values, from the PERMANOVA. Temp = soil temperature

4 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 nonlinearly 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-occurs 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 nonlinear 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 & 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 stream banks, *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 (le Roux & Luoto, 2014; Vonlanthen, Bühler, et al., 2006). 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. Filibeck et al., 2019; Vonlanthen, Kammer, et al., 2006). 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, Aalto, et al., 2013). 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.

4.1 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 (a) areas with strong winds (chronic and/or extreme winds) as it is a mechanical stress, (b) 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 & Luoto, 2015), (c) dry areas where wind enhances evaporation and the potential for plants to experience greater moisture stress (Zhang et al., 2007), (d) areas with thin soils which are more susceptible to desiccation (Bertiller et al., 1996) and (e) Arctic and alpine areas where it affects snow drift (Dadic et al., 2010; Sturm et al., 2001). Wind may also have an indirect effect by interacting with other climatic factors (see e.g. Ashcroft et al., 2009; Kullman & Loyer, 2005). As a result, the large recent changes in global wind patterns may have direct consequences for species distributions and interactions between species (Young & Ribal, 2019; Young et al., 2011), as well as indirect impacts (e.g. by affecting seed dispersal; Kling & 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 understorey 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* Dahinden et al., 2017; Williams & Jackson, 2007). 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. Gómez-Ruiz & Lacher Jr, 2019; Parmesan & Hanley, 2015; Radchuk et al., 2019). 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. SLA) 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 & Ribal, 2019; Young et al., 2011; 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 (a) examined in the context of landscape-level biological patterns (i.e. related to topography), and (b) 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 the 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.

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AUTHORS' 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.

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