Dispersal potential does not predict recent range expansions of sub-Antarctic plant species

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Abstract

Dispersal influences many key aspects of plant ecology at both fine- and broad scales. However, dispersal events are challenging to quantify as they are difficult to observe and measure accurately, despite the importance of understanding species' dispersal capacity. In this study, we quantified dispersal estimates for the dominant vascular flora of sub-Antarctic Marion Island, using a mechanistic model to estimate dispersal potential via anemochory and standardised experiments that simulate dispersal events via zoochory, human activity, and thalassochory, to test if dispersal capacity correlates to contemporary range expansion of the island's native and alien species. Our results demonstrate the broad range of dispersal potential in the island's flora and represent the first quantification of the dispersal potential (via multiple vectors) of the dominant vascular flora in the sub-Antarctic. Dispersal potential was not related to range expansion rates of native or alien species, suggesting that other mechanisms are responsible for the variation observed in species range expansion rates. Although this finding contradicts expectations and evidence from some other studies, it is consistent with research conducted in alpine regions (which may be climatically and physiognomically similar to this sub-Antarctic study site) where factors such as demography and competition are more important predictors of species range expansion than their dispersal ability, dispersal syndromes, or dispersal-related traits.

Introduction

Propagule dispersal facilitates the movement of species across both fine (i.e. colonization of new habitat patches; Grubb 1977; Bullock et al. 1995; Evangelista et al. 2016) and broad spatial scales (i.e. colonization of new regions; Nogales et al. 2012; Heleno and Vargas 2015). Indeed, limited dispersal has been linked to low species richness and, at shorter time scales, reduced plant abundance (Osem et al. 2002). For example, dispersal limitation can delay the revegetation of formerly cultivated fields adjacent to semi-natural grasslands (Öster et al. 2009). Thus, even where sites are suitable for species, sites may remain uncolonized due to the absence of adequate dispersal, emphasising the importance of understanding the dispersal process more completely, both from a theoretical and an applied perspective (Clark et al. 1998; McCormick and Jacquemyn 2014).

Dispersal is necessary to transport species' diaspores beyond their current distributions (Davies and Sheley 2007) and variation in dispersal ability within and between species may have important implications for species' geographic ranges (Thompson et al. 1999). For example, Bahn et al. (2006) found that individuals with the greatest maximum potential dispersal distances occupied the range edges of populations and were thus more likely to spread further and expand the population's range. Evidence also suggests that species with dense peripheral populations tend to have faster range expansion rates and are at lower risk of extirpation, likely as a consequence of individuals in these populations having a greater dispersal capacity (Jump and Woodward 2003; Bahn et al. 2006; Gibson et al. 2009). Additionally, Goldberg and Lande (2007) showed that dispersal potential can limit range expansion rates, especially when its effect is combined with factors like competition. Moreover, in some clades dispersal positively correlates with range size depending (Alzate and Onstein 2022). As a result, the explicit consideration of species' dispersal capacity when studying the responses of species to changing environmental conditions typically produces more accurate predictions of species distributions (Engler et al. 2009; Urban et al. 2016) and can give us a better understanding of the relative importance of the different factors that limit or increase species ranges and facilitate the colonization of newly suitable habitats.

Many recent range shifts appear to be in response to contemporary climate change altering the distribution of suitable habitats (Lenoir et al. 2008; Berg et al. 2010; McConkey et al. 2012; Brusca et al. 2013; Lenoir and Svenning 2015). In general, during recent climatic warming, an upward and/or poleward shift of species ranges along elevational and latitudinal gradients has been observed (Walther et al. 2005; Wilson et al. 2005; Parmesan 2006; Kelly and Goulden 2008; Rosenzweig et al. 2008; VanDerWal et al. 2013). Indeed, globally species have shifted upslope by an average of 92 ± 455 m/°C (mean $\pm$ SD) at their distribution's warm limits and by 131 ± 465 m/°C at cool limits since 1802 (Freeman et al. 2018).

However, species have displayed considerable variation in range expansion rates in response to climate change (Crimmins et al. 2011; Svenning et al. 2014). For example, in the European Alps, most species shifted upslope, with some species experiencing an upward shift exceeding 100 m in elevation over the 20th century, while other species' distributions contracted downslope (Rumpf et al. 2018). This suggests that a species' response to warming may vary strongly due to, for example, species-specific differences in physiological tolerances, biological requirements, and environmental requirements (e.g. how they are affected by biotic interactions and their nutrient requirements; Frei et al. 2010; Wisz et al. 2013). In addition, the variation observed in species range expansions is likely also related to factors such as the species' habitat preferences and life history strategies (with faster range shifts being observed in species with herb, moss, or graminoid growth forms that have shorter life cycles; Lenoir et al. 2008).

Dispersal capacity may also be an important driver of variation in range expansion rates, with species that are capable of dispersing further being expected to be more efficient at tracking shifts in suitable habitat (Ibrahim et al. 1996; Kirkpatrick and Barton 1997; Angert et al. 2011). However, studies have not typically examined the degree to which species' dispersal potential is related to rates of range expansion, with only a few exceptions. For example, Bahn et al. (2006) found dispersal potential to have significant effects on population growth and range expansion rates, while Shigesada and Kawasaki (2002) shows the benefit of considering the theoretical impact of dispersal on range expansion.

Sub-Antarctic Marion Island provides a useful model system for examining how inter-specific variation in dispersal capacity might be related to range expansion rates, as a rapid expansion of both alien and native plant species distributions in response to warming has been observed in recent decades. Between 1966 and 2004, the island's native flora experienced an average upslope expansion of 70 m (SE = 30, n = 22 species) in response to a temperature increase of 1.2 °C over a period of *c.* four decades (le Roux and McGeoch 2008a, b). However, a lot of variation in the range expansion rates of species on the island has also been observed, with range expansion (and contraction) rates of native species ranging from − 126 to + 388 m

elevation (le Roux and McGeoch 2008b). Several of the alien species on Marion Island have also experienced rapid range expansions since the 1990s, with pronounced variation in the non-native flora's range expansions as some species have shown minimal changes in their distribution over the same period (le Roux and McGeoch 2013). Indeed, range expansion rates of the island's alien flora that have increased their distribution ranged from 0.56 to 1.84 km^2/ yr.

The aim of this research, therefore, was to test if greater dispersal capacity (via anemochory, zoochory, anthropogenic activity, and thalassochory) is correlated with the magnitude of recent changes in the ranges of indigenous and alien vascular plant species on sub-Antarctic Marion Island. We expected dispersal capacity to be positively correlated to the rate of range expansion because dispersal affects local and regional species distribution patterns (García et al. 2017) and is hypothesized to allow more efficient climate tracking (Corlett and Westcott 2013). Although thalassochory likely does not contribute to the range expansion of species into the inland regions of the island, we expected that it could contribute to the expansion of alien species around Marion Island's coast.

We also investigated the role of two other potential drivers of inter-specific variation in species' range expansion rates: habitat specificity, and species functional traits. We expected there to be a negative correlation between habitat specificity and range expansion rates since habitat-specific species are restricted to specific (and potentially isolated and/or localized) habitats while generalists have a greater chance of finding suitable habitats (Dullinger et al. 2012; Lamsal et al. 2018; Ainsworth and Drake 2020). We also expected functional traits that contribute to increases in a plant's dispersal ability (e.g. taller species likely dispersing further via anemochory; Nathan 2006; Thomson et al. 2011) or contribute to the species' reproductive output (Leuning et al. 1995) to be positively correlated to species range expansion rate since the production of more diaspores will increase a species chance of successful dispersal beyond its current distribution.

Materials And Methods

Study site

Terrestrial habitats within the sub-Antarctic comprise several islands and small archipelagos located between *c*. 40–50° S in the Southern Ocean. These islands are generally small and very isolated (*c*. 500–1000 km from the nearest continent). Marion Island (46°54' S, 37°45' E; approximately 290 km^2) is the larger of two South African sub-Antarctic islands, which, along with Prince Edward Island (46°38'S, 37°57' E; *c*. 45 km^2), comprise the Prince Edward Islands (PEIs; Greve et al. 2017). The PEIs are relatively young (*c*. 450 000 years), are of volcanic origin, and are characterized by a maritime climate with cool temperatures, small daily and seasonal temperature ranges, and strong, almost continuous, westerly winds (Hedding et al. 2015). Marion Island is inhabited by 41 vascular plant species (22 indigenous and 18 alien species) and *c*. 200 bryophyte and lichen species (Smith et al. 2001; Greve et al. 2017).

Climate change has resulted in significant increases in mean temperatures and a decrease in mean annual precipitation across Marion Island since the 1950s (Smith 2002; le Roux and McGeoch 2008a). These climatic changes have had several ecological, physiological, and geophysical consequences (see e.g. Chown and Smith 1993; Smith 2002). Marion Island, therefore, provides a useful model system for studying the biological impacts of climate change due to having experienced rapid climate shifts over the last half-century, without the confounding effects of other anthropogenic disturbances (other than limited biological invasions, chiefly in the low altitude areas; Bergstrom and Chown 1999; Smith 2002).

Range expansion rates for native species of Marion Island are available from a study that compared species' upper altitudinal limits over a 40-year period (le Roux and McGeoch 2008b). Therefore, for native species range expansion rate is measured as the mean altitudinal range shift per year. For alien species, range expansion rates are available from a study that compiled historic alien species occurrences and compared these data to recent vegetation survey data from across the entire island (le Roux et al. 2013). In this dataset, expansion rates were estimated as the total contemporary range of each species divided by the number of years since introduction to the island.

Sampling And Laboratory Methods

Four methods were used to estimate the dispersal potential of Marion Island's angiosperm flora via anemochory, thalassochory, anthropogenic activity, and epizoochory. Endozoochory was not examined because there is little evidence to suggest that any of the island's seabirds consume plant material (Gleeson and Van Rensburg 1971). Seabirds were the only animals considered for zoochory because they are the only taxon that has the potential to act as vectors for successful plant dispersal across the island. Other animals, such as fur- and elephant seals, are less likely to disperse diaspores inland because they usually remain along the coastline for breeding, molting, and resting (Mulaudzi et al. 2008). Although evidence also suggests that the mice on sub-Antarctic islands consume a substantial amount of seeds of many species (mostly native species; Angel et al. 2009), it is unlikely that successful dispersal takes place through mice since the diaspores found on the island do not possess traits that would enable them to pass through a mouse's digestive system in a viable state (following Traveset et al. 2014).

The dispersal units of 18 vascular plant species (five of which are alien to Marion Island) were collected from multiple locations across Marion Island to account for possible intra-specific variations in size, mass, or morphology. The release height (i.e., the vertical distance between the dispersal unit when attached to the plant and the ground surface) of each dispersal unit collected was measured in the field.

Quantifying wind dispersal potential (PD$_{ane}$)

Horizontal wind speeds were recorded at a height of 0.5 and 1 m above the ground using Gill ultra-sonic wind sensors (Gill Instruments, England) at 17 weather stations installed around Marion Island since 2018 (see Goddard et al. 2022 for details). Wind speeds were summarized from all stations, and subsequent analyses were limited to data from two weather stations with the highest and lowest mean wind speeds.

A seed drop test was conducted under controlled laboratory conditions (following the methods of Jongejans and Telenius 2001). A minimum of ten trials were conducted per species. For each seed drop test, a video recording was taken (using a Nikon d5600 camera; Nikon, Tokyo) and the footage was analyzed using video analysis software Tracker (https://physlets.org/tracker/) to estimate the terminal velocity of each dispersal unit (i.e. the constant speed that a freely falling object reaches before the resistance of the medium through which it is falling prevents further acceleration):

$$v_t = \frac{d}{t} \text{ (Eq. 1)}$$

where d is the distance travelled by the diaspore (the height from which the seed drops; a height of 1 m was used for all species since the vascular plants on the island are all low-growing and 1 m is enough for each species to reach v_t; Thompson 2011) and t is the time taken for the diaspore to cover that distance (following the methods of Nathan et al. 2008). For species with small diaspores that were not reliably visible via Tracker (*Montia fontana*, *Sagina procumbens*, *Colobanthus kerguelensis*, and *Cerastium fontanum)*, a stopwatch was used to estimate t. A total of 30 seed drop trials were conducted for this subset of species to account for the lower accuracy of this method. The terminal velocity (v_t), together with the release height (h) and horizontal wind speeds (u) at each species' mean release height (estimated by applying the power-law equation to wind speed data) were used to calculate the potential dispersal distance of each dispersal unit (x_d):

$$x_d = h\frac{u}{v_t} \text{ (Eq. 2)}$$

where x_d and h are in meters (m) and u and v_t are in meters per second (m/s).

In addition to this wind dispersal potential experiment, we examined and identified diaspores from samples collected by Hedding et al. (2015) when investigating aeolian transport (and possible plant dispersal) around two landforms on Marion Island. Diaspores were identified against the samples collected for this study.

Quantifying dispersal potential via zoochory (PD$_{zoo}$)

We estimated the epizoochoric dispersal potential of Marion Island's plant species by quantifying the attachment potential (PD$_{zoo}$ for attachment to feathers) of their diaspores, following methods based on Will et al. (2007). The dispersal potential of the diaspores was quantitatively estimated using the attachment of seeds to turkey contour feathers as a proxy for dispersal via zoochory. Only feathers of similar width, length, and texture were used. Feathers were replaced if seed removal resulted in damage to the feather or a change in the feather's texture. The experiment took place under controlled laboratory conditions to avoid the influence of wind and was conducted with diaspores that were stored at 4−6°C to retain the original seed shape and to prevent excessive desiccation. A feather was swept manually over the diaspores of a given species, with removal and counting of diaspores from the feather after every trial (a total of 32 trials per species). PD$_{zoo}$ is calculated as the percentage of diaspores that adhere to the feathers.

$$\%PD_{zoo} = \frac{D_a}{D_{all}}\% \text{ (Eq. 3)}$$

where D_a is the number of attached diaspores and D_{all} is the number of dispersal units used for a given species.

The surface texture and structure of diaspores are important traits for regulating attachment potential and, therefore, images of the diaspores were taken through a scanning electron and/or a light microscope. The size, surface texture, shape, and specialized structure on the surface of each species' diaspores were recorded (following guidelines from Hoque 2016; see Table 1). Diaspores < *c.* 3 mm diameter were categorized as "small" (i.e. < 3 mm), with the remainder categorized as "large".

Table 1
The morphological traits and the levels assigned to the diaspores
of different species

Morphological traits	Levels
Size	small (< 3 mm), large (> 3 mm)
Shape	spherical, ovate, cyathiform, fusiform
Texture	smooth, textured
Specialized structure	none, hairs, hooks

Quantifying dispersal potential via anthropogenic activity (PD$_{anthro}$)

To determine the dispersal potential of Marion Island's angiosperm flora through anthropogenic activity, a second experiment was run to determine the attachment potential (PD_{anthro}) of diaspores to coated nylon material commonly worn as an outer layer during fieldwork on Marion Island. The material was cut into 16 x 16 cm squares (one square per species). A square was lightly pressed against ten diaspores of a single species for a total of 32 trials per species, replacing diaspores after each trial. The attached diaspores were removed from the material and counted after each trial, with PD_{anthro} calculated as:

$$\%PD_{anthro} = \frac{D_a}{D_{all}}\% \text{ (Eq. 4)}$$

Quantifying dispersal potential by thalassochory (PD$_{thala}$)

Seed buoyancy and viability after immersion in artificial seawater were used as proxies of each species' ability to be successfully dispersed by water around and within Marion Island (and potentially to the nearby Prince Edward Island). Artificial seawater was formulated following the methods of Kaladharan (2000): 1.75 kg of sea salt crystals were dissolved in 50 ℓ of freshwater along with 50 g of calcium chloride and 5 g of sodium bicarbonate. The following day, the solution was filtered and 0.1N NaOH was used to adjust the pH of the solution to that of natural seawater (c. 8.1).

The buoyancy test was conducted following the methods of Danvind and Nilsson (1997). Ten diaspores were placed in a beaker filled with artificial seawater refrigerated at 6°C (to mimic the mean sea surface temperature around Marion Island; Mélice et al. 2003). There were two replicates and one control (diaspores that were put in distilled water) for each species. The number of sunken diaspores was counted after 1, 5, 15, and 30 minutes, 1 hour, and then 1, 2, and 3 days thereafter (the testing period lasted a total of 6 days). The beakers were stirred after counting sunken diaspores to reduce the effects of surface tension. Buoyant diaspores were assumed to be more capable of dispersal through sea and/or inland water bodies than their sunken counterparts.

The diaspores that remained afloat in the artificial seawater were blotted dry, placed in Petri dishes with damp filter paper, and incubated in a phytotron (25 °C) for 24 hours to increase permeability before being tested for diaspore viability using the tetrazolium test. A 1% concentration of tetrazolium solution was prepared (2.5 g added to 250 mℓ of distilled water). The diaspores were put into different test tubes (with each species assigned a test tube) and submerged in tetrazolium solution. The seeds were then incubated in a water bath at 40°C for 1−3 hours depending on the diaspores' permeability, according to the guidelines of Patil and Dadlani (2009). For species with diaspores that floated, a control (i.e. separate sets of each species' seeds) was placed in distilled water, incubated, and stained to determine viability in the absence of exposure to artificial seawater. The diaspores were then rinsed with distilled water. The inner structures of diaspores were inspected with the naked eye or under a microscope, with live structures showing a bright or pale red lustrous appearance. As an estimate of dispersal potential via thalassochory, the values for buoyancy (%) and viability (%) were averaged for an integrated proxy for thalassochory.

Species were subsequently ranked (rank 1−18, in ascending order) by their estimated dispersal potential for each of the four dispersal modes considered. Then, to estimate a combined relative dispersal potential for each species (i.e., to estimate the total dispersal potential for each species relative to the other species), the rank of each species for the four dispersal mechanisms was summed to serve as an estimate for each species' total dispersal potential.

Alternative potential drivers of species range expansion on Marion Island

In addition to investigating the relationship between dispersal and species range expansion, we investigated whether species with high habitat specificity had slower range expansion rates. We estimated the habitat specificity of Marion Island's plant species as the proportion of Gremmen's (1981) 41 vegetation units from which each species had been recorded (with species that occur in more units being assumed to be less habitat-specific). These data were collected c. 30 years prior to the data used for the calculation of alien species expansion rates (i.e. when some alien species had considerably smaller ranges), and therefore may overestimate the habitat specificity of some alien species that have since colonized additional vegetation units. However, for the native species, we consider these data an accurate estimate of their habitat specificity.

We also investigated the relationship between species' range expansion rates and functional traits because functional traits can, directly and indirectly, contribute to dispersal capacity (e.g. a species growth rate affects the timing of its reproductive stage, and the production of larger seed crops also increases chances of successful dispersal; Honnay et al., 2005). Data for ten functional traits was extracted from Mathakutha et al. (2019) for all species for which range expansion rate data were available

Statistical analyses

We assessed the relationship between the dispersal estimates for the four dispersal syndromes and overall dispersal potential using Spearman correlation tests. To analyse the relationship between range expansion and the estimates for all four dispersal syndromes, bootstrap regression models (run via the "car" package) were used (due to the relatively low number of species examined). We also ran a multivariate robust linear model for native species to test the effects of all four dispersal syndromes on the range expansion of native species using the rlm function (in the "MASS" package). This analysis was not repeated for the alien plant species due to the number of alien species being too small. Univariate linear models were also used to examine the relationship between the four dispersal syndromes, diaspore morphological traits, and species' range expansion rates for both the island's native and alien species, and multivariate linear models were used to test for a relationship between habitat specificity, species functional traits, and species' range expansion.

All analyses were run using R statistical software (R Core Team 2021), with additional functions from the boot (Canty 2002) and corrplot (Wei et al. 2017) packages. Although a considerable amount of information could be drawn from this study's statistical outcomes, it is important to note the unique challenges of analysing data from a small number of species from this relatively species-poor island and the resultant limitations in statistical power.

Results

The average masses of the diaspores of alien species ranged from 7–90 mg and that of native species ranged from 1–630 mg. The seed release heights of species ranged from 18–360 mm and 82–205 mm for indigenous and alien species, respectively (Table 6). Species showed a wide variety of diaspore shapes, sizes, and textures (Fig. 1). A small proportion of species, such as *Uncinia compacta* (Fig. 1F) and *Acaena magellanica* (Fig. 1I), have diaspores with hooks or other similar structures that facilitate attachment to dispersal vectors.

The highest and lowest average wind speeds (u) at the 17 (st) stations were recorded at stations 1 and 15 ($u_{st1,0.5m}$ = 0.428; $u_{st1,1m}$ = 2.572 m/s; $u_{st15,0.5}$ = 6.942 m/s; $u_{st15,1m}$ = 7.87 m/s). Relatively short potential dispersal distances (PD$_{ane}$) were estimated for anemochory, with *Poa cookii* having the longest estimated potential dispersal distance (100 mm), followed by *Poa pratensis* and *Agrostis stolonifera* (50 mm), while for all other species it was < 30 mm (Table 2).

Table 2
The dispersal potential of plant species on Marion Island via four dispersal syndromes, their ranking (R) for each of the dispersal modes, and their overall dispersal potential ranking. Species marked with an asterisk (*) are alien species. PD$_{ane}$ = potential dispersal via anemochory, PD$_{zoo}$ = dispersal potential via zoochory, PD$_{anthro}$ = dispersal potential through anthropogenic activity, PD$_{thala}$ = dispersal potential via thalassochory, and PD$_{overall}$ = overall dispersal potential

All species	PD$_{ane}$ (m)	R$_{ane}$	PD$_{thala}$ (%)	R$_{thala}$	PD$_{anthro}$ (%)	R$_{anthro}$	PD$_{zoo}$ (%)	R$_{zoo}$	PD$_{overall}$
Acaena magellanica	0.021	13	0.025	5.5	9.7	17.0	53.1	18.0	53.5
Agrostis stolonifera*	0.056	17	0.450	14.0	6.9	16.0	20.0	16.0	63.0
Azorella selago	0.021	12	0.263	10.0	0.3	4.5	7.8	9.0	35.5
Callitriche antarctica	0.011	8	0.025	5.5	0.3	4.5	5.9	6.5	24.5
Cerastium fontanum*	0.011	7	0.0	2.5	0.0	1.5	8.1	10.0	21.0
Colobanthus kerguelensis	< 0.001	1	0.0	2.5	0.3	4.5	5.0	3.0	11.0
Cotula plumosa	0.012	9	0.615	16.0	32.8	18.0	6.6	8.0	51.0
Crassula moschata	0.003	3	0.175	7.0	0.6	7.0	8.8	11.0	28.0
Juncus scheuchzerioides	0.005	6	0.300	11.0	2.5	9.0	5.6	4.5	30.5
Montia fontana	0.003	4	0.575	15.0	3.8	11.5	5.6	4.5	35.0
Poa annua*	0.016	10	0.390	12.0	3.1	10.0	5.9	6.5	38.5
Poa cookii	0.105	18	0.250	9.0	6.6	14.5	14.1	15.0	56.5
Poa pratensis*	0.053	16	0.0	2.5	1.6	8.0	9.7	12.0	38.5
Polypogon magellanicus	0.033	15	0.225	8.0	4.4	13.0	32.2	17.0	53.0
Pringlea antiscorbutica	0.019	11	0.710	17.0	0.0	1.5	1.6	1.0	30.5
Ranunculus biternatus	0.002	2	0.815	18.0	0.3	4.5	4.4	2.0	26.5
Sagina procumbens*	0.004	5	0.0	2.5	6.6	14.5	10.6	13.0	35.0
Uncinia compacta	0.021	14	0.425	13.0	3.8	11.5	13.8	14.0	52.5

Table 3
Bootstrapped univariate regression models examining the relationship between species range expansion rates of native species and the spread rates of alien species *vs* dispersal potential via anemochory (PD$_{ane}$), zoochory (PD$_{zoo}$), anthropogenic activity (PD$_{anthro}$), and thalassochory (PD$_{thala}$)

Dispersal syndrome	Coefficient	F	p-value	Bootstrap conf. int. (2.5−97.5%)
Indigenous species				
PD$_{ane}$	13.204	0.001	0.9896	-5267.8−4202.3
PD$_{zoo}$	-0.838	0.201	0.6629	-12.4−4.6
PD$_{anthro}$	-3.482	1.453	0.2534	-17.9−5.6
PD$_{thala}$	-0.252	0.062	0.8073	-2.7−2.0
Alien species				
PD$_{ane}$	-20.81	4.725	0.1180	0.4−2.0
PD$_{zoo}$	-0.042	0.401	0.5716	-0.3−0.5
PD$_{anthro}$	0.093	0.670	0.4729	-0.2−0.3
PD$_{thala}$	0.001	0.002	0.9678	-0.1 − 0.1

Table 4
Linear models examining the relationship between species range expansion rates and species functional traits. Results for native species are shown in the top part of the table, and for alien species in the lower part. The asterisk (*) marks significant relationships

Native species	Coefficient	DF	F	p-value	R^2
Height (mm)	-110.896	1 and 11	0.028	0.871	< 0.001
Leaf area (mm^2)	-109.510	1 and 11	0.404	0.538	< 0.001
Specific leaf area (mm^2.mg^{-1})	-86.579	1 and 11	4.084	0.068	0.205
Leaf chlorophyll content per unit area (mg.m^{-2})	-0.124	1 and 11	0.103	0.755	< 0.001
Leaf chlorophyll content per unit mass (mg)	-216.730	1 and 11	4.578	0.056	0.230
Specific root length (mg^{-1})	-56.130	1 and 10	0.962	0.350	< 0.001
Root diameter (mm)	-13.400	1 and 10	0.012	0.915	< 0.001
Leaf nitrogen concentration [N]	-217.	1 and 9	0.829	0.390	< 0.001
Leaf phosphorus concentration [P]	-75.740	1 and 9	2.708	0.134	0.146
Leaf toughness (N)	109.580	1 and 9	2.639	0.139	0.141
Alien Species					
Height (mm)	-0.008	1 and 3	16.21	0.028*	0.792
Leaf area (mm^2)	-0.001	1 and 3	2.782	0.194	0.308
Specific leaf area (mm^2.mg^{-1})	0.033	1 and 3	0.355	0.593	< 0.001
Leaf chlorophyll content per unit area (mg.m^{-2})	-0.007	1 and 3	3.484	0.159	0.383
Leaf chlorophyll content per unit mass (mg)	-2.056	1 and 3	4.731	0.118	0.483
Specific root length (mg^{-1})	0.012	1 and 3	8.921	0.058	0.665
Root diameter (mm)	-2.401	1 and 3	0.937	0.405	< 0.001
Leaf nitrogen concentration [N]	0.348	1 and 1	2.500	0.359	0.429
Leaf phosphorus concentration [P]	-0.204	1 and 1	0.005	0.957	< 0.001
Leaf toughness (N)	-1.673	1 and 3	4.558	0.122	0.471

Diaspores of the indigenous species *Acaena magellanica*, *Azorella selago*, *Polypogon magellanicus*, *Agrostis stolonifera*, *Poa annua*, and *Poa cookii* were identified from the samples collected by Hedding et al. (2015) in sediment traps installed at Mesrug (205 m a.s.l.), the Third Sister (244 m a.s.l.), and Katedraalkrans (750 m a.s.l.) at a height of 0.5 m above the ground surface.

When quantifying thalassochory, species displayed a variety of responses to being exposed to seawater for prolonged periods (Table 2). The diaspores of *Cerastium fontanum*, *Colobanthus kerguelensis*, and *Sagina procumbens* showed poor buoyancy, with all their diaspores sinking in < 1 hour. In contrast, the diaspores of *Ranunculus biternatus*, *Uncinia compacta*, and *Cotula plumosa* had the highest buoyancy (up to 82% of diaspores remaining afloat over 6 days; Table 7). Diaspore viability after the buoyancy test varied markedly, with *Pringlea antiscorbutica* having the highest proportion of viable diaspores (0.77) followed by *Montia fontana* (0.75; Table 7). When combining buoyancy with viability, *Ranunculus biternatus* had the highest estimate of potential dispersal via thalassochory (PD_{thala} = 0.82). Buoyancy and seed viability after exposure to seawater were not statistically related (p = 0.093, R^2 = 0.12).

Many of Marion Island's plant species had a low attachment potential to the coated nylon material used in this study as a representation of field clothing (PD_{anthro}). The PD_{anthro} of most species only ranged from 0–4.3% (Table 2). However, *Acaena magellanica* and *Cotula plumosa* had PD_{anthro} values of 9.7% and 32.8% respectively. Diaspores tended to attach better to bird feathers than they did to clothing material, with PD_{zoo} ranging from 5% (*Colobanthus kerguelensis*) to 53% (*Acaena magellanica*).

Overall, the study showed a broad range of dispersal potential amongst the species, with the alien species *Agrostis stolonifera* having the highest overall dispersal potential ranking (Table 2). Additionally, there was no correlation between species ranks for the dispersal syndromes (although there were weak positive correlations between PD_{ane}, PD_{anthro}, and PD_{zoo} with $PD_{overall}$; see Fig. 2).

There was no significant relationship between any of the four dispersal modes and the rate of range expansion of native species, or the spread rate of alien species (Table 2). However, there was a significant negative relationship between the spread rates of alien species and their average heights (r = −0.919, p = 0.028, R^2 = 0.79). The relationships between alien plant species spread rates and other functional traits were not significant. No functional traits were significant predictors of the range expansion rates of native species. The multivariate linear model for native species also showed no significant relationship between the range expansion of native species, habitat specificity, plant height (included because it is a significant predictor for the expansion rates of alien species), and all of the dispersal modes (all p > 0.4, see Table 5).

All but two of the relationships between dispersal capacity and morphological traits were not statistically significant (Table 1). There was a significant difference between the PD_{ane} of native species with different specialised structures (p = 0.004) and PD_{thala} was significantly greater for smooth diaspores (p = 0.03). There was also no significant relationship between morphological traits and the range expansion rates of both the native and alien species (Table 1).

There was no significant relationship between habitat specificity and the range expansion of both native (p = 0.61) and alien species (p = 0.31). Native species occurred in most vegetation units, with *Ranunculus biternatus* recorded in all 41 of the island's vegetation units. *Ranunculus biternatus* was followed by *Polypogon magellanicus* and *Montia fontana*, occupying 38 and 37 vegetation units respectively (Table 8).

Table 5 Results from simple linear models examining the relationship between diaspore morphological traits and the range expansion rates of native species and the spread rates of alien species. All native species had the same texture (specialised str = specialised structure)

Native Species	Morphological trait	F value	p-value
PD_{ane}	Size	1.332	0.273
	Shape	3.006	0.087
	Texture	0.710	0.393
	Specialised str.	9.518	0.005
PD_{zoo}	Size	1.346	0.271
	Shape	1.973	0.189
	Texture	1.213	0.294
	Specialised str.	2.242	0.157
PD_{anthro}	Size	1.391	0.263
	Shape	43.973	< 0.001
	Texture	1391	0.263
	Specialised str.	0.072	0.931
PD_{thala}	Size	0.090	0.770
	Shape	0.875	0.490
	Texture	5.809	0.035
	Specialised str.	0.167	0.849
Range expansion	Size	0.045	0.837
	Shape	0.356	0.786
	Texture	2.121	0.173
	Specialised str.	0.344	0.717
Alien Sp.			
PD_{ane}	Size	4.242	0.132
	Shape	4.242	0.132
	Specialised str.	4.242	0.132
PD_{zoo}	Size	0.206	0.687
	Shape	0.206	0.687
	Specialised str.	0.206	0.687
PD_{anthro}	Size	0.032	0.869
	Shape	0.032	0.869
	Specialised str.	0.032	0.869
PD_{thala}	Size	2.364	0.222
	Shape	2.364	0.222
	Specialised str.	2.364	0.222
Spread rate	Size	0.579	0.502
	Shape	0.579	0.502
	Specialised str.	0.579	0.502

Table 6 The mean height and seed weight of plant species included in this study (from Mathakutha et al. 2019)

Species name	Mean height (mm)	Mean weight (mg)	Mean height (m)
Acaena magellanica	136.1	196.4	0.12
Agrostis stolonifera	188.1	77.4	0.19
Azorella selago	157.8	1.2	0.16
Callitriche antarctica	76.3	1.4	0.08
Cerastium fontanum	100.8	0.2	0.10
Colobanthus kerguelensis	7.7	0.1	0.01
Cotula plumosa	60.9	0.4	0.06
Crassula moschata	19.3	0.5	0.02
Juncus scheuchzerioides	52.8	5.3	0.05
Montia fontana	31.3	0.5	0.03
Poa annua	82.3	42.9	0.08
Poa cookii	362.0	629.7	0.36
Poa pratensis	205.5	45.1	0.21
Polypogon magellanicus	143.4	88.7	0.14
Pringlea antiscorbutica	151.7	3.8	0.15
Ranunculus biternatus	18.1	2.2	0.02
Uncinia compacta	109.0	58.7	0.11
Sagina procumbens	25.7	0.02	0.03

Table 7 Results from the buoyancy and viability tests (PD_{thala} = dispersal potential via thalassochory). The cumulative number of sunken diaspores was recorded at eight different time intervals (1 min. = number of sunken diaspores after 1 minute; 5 min = number of sunken diaspores 5 minutes after the previous observation; etc.). Viability was also recorded for control samples that were not exposed to artificial seawater (PD_{thala} for control sample %).

Species	1 min	5 min	15 min	30 min	1 hr	1 day	2 days	3 days	# of buoyant diaspores after 6 days	Buoyancy after 6 days %	# of viable diaspore after buoyancy test	Viability %	PD_{thala} %	PD_{thala} for control sample %
Acaena magellanica	0	0	0	0	0	0	7	19	1	5	0	0	2.5	30
Agrostis stolonifera	0	0	0	0	0	0	0	2	18	90	0	0	45.0	70
Azorella selago	2	2	3	4	4	4	9	12	8	40	1	12.5	26.3	0
Callitriche antarctica	3	4	4	4	4	6	19	19	1	5	0	0	2.5	60
Cerastium fontanum	20	20	20	20	20	20	20	20	0	0	0	0	0.0	0
Colobanthus kerguelensis	9	18	20	20	20	20	20	20	0	0	0	0	0.0	0
Cotula plumosa	0	0	0	0	0	0	2	2	18	90	6	33	61.5	90
Crassula moschata	0	0	0	0	0	0	2	13	7	35	0	0	17.5	30
Juncus scheuchzerioides	0	0	0	0	0	3	8	8	12	60	0	0	30.0	50
Montia fontana	0	1	1	1	3	4	12	12	8	40	6	75	57.5	90
Poa annua	0	1	0	0	0	4	11	13	7	35	3	43	39.0	10
Poa cookii	1	1	1	1	1	2	5	10	10	50	0	0	25.0	40
Poa pratensis	0	0	0	0	0	0	5	20	0	0	0	0	0.0	0
Polypogon magellanicus	0	0	0	0	0	0	1	15	5	25	1	20	22.5	80
Pringlea antiscorbutica	0	0	0	0	0	0	1	7	13	65	10	77	71.0	100
Ranunculus biternatus	0	0	0	0	0	0	0	1	19	95	13	68	81.5	80
Uncinia compacta	0	0	0	0	0	0	1	3	17	85	0	0	42.5	50
Sagina procumbens	4	20	20	20	20	20	20	20	0	0	0	0	0.0	0

Table 8 The number of plant habitats in which each of Marion Island's species are recorded (extracted from Gremmen, 1981) and the upslope range shifts of native plant species (extracted from le Roux & McGeoch 2008) and range expansion rates of alien plant species (extracted from le Roux et al. 2013)

Native species	Number of habitats recorded from	Upslope shift over 40 years (m)
Acaena magellanica	28	22
Azorella selago	20	75
Callitriche antarctica	12	0
Colobanthus kerguelensis	5	275
Cotula plumosa	9	-16
Crassula moschata	5	-25
Juncus scheuchzerioides	23	116
Montia fontana	37	27
Poa cookii	23	69
Polypogon magellanicus	38	158
Pringlea antiscorbutica	2	234
Ranunculus biternatus	41	24
Uncinia compacta	13	89
Alien species	Number of habitats recorded from	Rate of spread since discovery (km².yr^{-1})
Agrostis stolonifera	5	0.56
Cerastium fontanum	3	0.68
Poa annua	11	1.48
Poa pratensis	1	0.29
Sagina procumbens	1	1.84

Discussion

This study shows that the magnitude of recent changes in the ranges of native and alien plant species on Marion Island are not related to their dispersal potential. This is consistent with studies conducted in alpine regions of Europe where factors such as demography, competition, and the thermal requirements and nutrient demands of species were more important predictors of species range expansion than their dispersal ability, dispersal syndromes, or dispersal-related traits (Rumpf et al. 2018; Scherrer et al. 2020). Variation in habitat specificity and species life-history strategies (as estimated from functional traits) provide potential alternative mechanisms that could drive interspecific variation in expansion rates, but these variables were also not related to the rate of range shifts in native species, with only plant height being related to the range expansion of alien species.

Based on the mean dispersal distances estimated by the mechanistic model (PD_{ane}), anemochory has limited potential to expand species' ranges, despite the windy conditions experienced on Marion Island (see also Born et al. 2012). Seed drop height is likely the most important of the variables contributing to each species' PD_{ane} since the tallest species had the highest PD_{ane} (*Poa cookii*, 0.36 m and *Poa pratensis*, 0.21 m). Additionally, all the species in the study had similar terminal velocities (likely because none of the species' diaspores have structures that slow seed drop speeds; Andersen 1993). Despite the short mean PD_{ane} values estimated from the mechanistic model, samples from Hedding et al. (2015) show that diaspores of varying PD_{ane} can, indeed, be transported by the wind across the island. The traps used by Hedding et al. (2015) were located several meters from the nearest vegetation, but trapped seeds from six different species. This outcome highlights the limitations that come with only using mean dispersal distances and the constraint of not being able to consider rarer, more extreme dispersal events even within common seed dispersal modes (Nathan et al., 2012).

The components that were combined to quantify PD_{thala} (*viz.* buoyancy and viability) varied independently of each other, with species like *Ranunculus biternatus* and *C. plumosa* demonstrating both good buoyancy and high viability even after being in seawater for prolonged periods. Although results showed no significant differences between the PD_{thala} estimates of species in all size and shape categories, it is worth noting that all the species with the poorest buoyancy during the experiment (*viz. Cerastium fontanum, Colobanthus kerguelensis*, and *Sagina procumbens*) have small ($\leq$ 1 mm) and spherical seeds, traits that are often associated with poor buoyancy (Carthey et al. 2016). *Poa pratensis* was the only species with a low PD_{thala} estimate whose diaspores did not sink within the first day of the buoyancy trials. Its diaspores' ovate shape may be related to the reason they remained afloat for longer periods compared to that of other "poor dispersers" species. It is of interest that three of the four species that have the lowest dispersal potential via thalassochory are aliens, suggesting that it is less likely that these non-natives will spread via thalassochory to nearby Prince Edward Island than the exchange of indigenous species between the two neighbouring islands.

There is a lot of variation in the dispersal potential of plant species through zoochory and anthropogenic activity. *Acaena magellanica* and *Polypogon magellanicus* had the highest attachment potential to feathers, and both of these species' diaspores have traits that a known to facilitate adhesion: *A. magellanica* diaspores have hooks and a rough texture that can facilitate attachment to animals (Sorensen 1986; Hovstad et al. 2009), while *P. magellanicus* has long awns, small hair-like structures on their pedicel and rachis, and seeds that are small enough to get tucked between animal fur or feathers (Stiles 2000b). Additionally, *A. magellanica* had one of the highest attachment potentials to clothing material, exceeded only by *Cotula plumosa*. Although *C. plumosa* does not have traits that are typically associated with adhesion, its attachment to materials is likely due to its seeds being small and having a slim, elongated shape that increases its surface area for attachment (Sorensen 1986).

Dispersal capacity was not important in explaining the differences between species range expansion rates on Marion Island, but evidence suggests that differences in dispersal between species may play a bigger role in determining interspecific variation in the range expansion rates in other systems. For example, Hampe (2011) found support for the largely accepted idea that the frequency of a species' diaspores being dispersed beyond their current range limits is a major constraint for the rapid range expansion of many plant species. Indeed, diaspores of the highly invasive plant species *Mikania micrantha* tended to be more morphologically suited for long-distance dispersal the further they were from their source populations (i.e. diaspores far from source populations were lighter in mass, had greater plume loading, and smaller pappus radii). This pattern suggests that genetically-controlled dispersal-related traits were selected for during the species' range expansion across southern China (Huang et al. 2015). Similarly, LaRue et al. (2019) found that intra-specific variation in dispersal will likely increase the potential for local populations of *Cakile edentula* to keep pace with the changing climatic conditions across the beaches of the Laurentian Great Lakes. All these studies were based in systems with less harsh climatic conditions, on species with growth forms that are not commonly found on Marion island (i.e. tall, woody trees that have greater dispersal advantage because of their height; see Hampe 2011; Thomson et al. 2011), and possess structures that are usually associated with specific dispersal syndromes (Huang et al. 2015; LaRue et al. 2019), whereas most of Marion Island's species possessed no specialised structures.

Dispersal may also not be an important contributor to the range dynamics of species on Marion Island because this sub-Antarctic island is mountainous and particularly rugged. Indeed, dispersal was typically found to play an important role in determining the rate of species' range expansion when species were expanding their ranges across broader scales and/or in flatter topographies, rather than moving upslope. The steep elevational gradient that occurs on Marion Island likely presents a unique set of complexities that may not be relevant in flatter or more undulating systems (see Wang et al. 2021) and the role of dispersal, much like that of biotic interactions, may change along elevational gradients (Von der Lippe et al. 2013; Barber et al. 2016). For example, Zelikova et al. (2008) found that the occurrence of zoochoric dispersal events tends to decrease with increasing elevation. Additionally, Tonkin et al. (2017) suggest that dispersal limitations play a significant role in the metacommunity structuring near streams along elevational gradients, with lower elevations presenting less resistance to dispersal.

There may be differences in the factors that influence the expansion patterns of native and alien species. On Marion Island, alien species are strongly limited to lower altitudes and mostly occupy coastal areas that are frequently characterized by higher biotic disturbance and nutrient content (e.g. coastal areas where trampling and manuring by seals and seabirds occurs and where there tends to be higher human traffic; Smith et al. 2001; see also le Roux et al. 2013), while native species occur across most of the island's elevational gradient. This is probably because the distribution of most alien species is not yet in equilibrium with the environment (Veran et al. 2016). Therefore, it is likely that at least some alien species on the island are yet to occupy all environmentally suitable areas simply due to dispersal limitations (Chytrý et al. 2008; Sax and Gaines 2008; Ripley et al. 2020). This was clearly demonstrated by Williamson et al. (2009) who found a significant positive relationship between the residence time of alien species and their range sizes in Europe. Similar patterns were observed for aliens found on Marion Island (le Roux et al. 2013) and on neighbouring Prince Edward Island (Ryan et al. 2003). However, both the indigenous and alien species lacked clear dispersal potential-range expansion relationships, despite the two groups having different functional traits, different distributions and aliens likely still not being at equilibrium. Indeed, Mathakutha et al. (2019) found that Marion Island's invasive species had lower plant height, smaller leaf area, lower frost tolerance, and higher specific leaf area than their native counterparts. It is, therefore, likely that the aliens' plant heights contribute to their continual spread in lower regions since they experience more traffic and lower plant heights allow diaspores to attach to human and animal vectors with ease. Furthermore, their lower frost tolerance will likely not inhibit their spread because of the continual increase in the island's temperatures. It is also likely that the aliens on Marion Island will withstand other changes in environmental conditions caused by climate change better than their native counterparts due to their phenotypic plasticity (Yu-Peng et al. 2004; Matesanz et al. 2015; Irl et al. 2021).

The results of this study additionally show that there is no relationship between species' habitat specificity and how fast they are spreading across Marion Island. These findings contrast with some studies that have suggested that generalist species tend to expand their ranges more rapidly than specialists (Oliver et al. 2009; Harrison et al. 2018). Observations from Marion Island may differ from other studies because of the relatively high compositional and abiotic similarities between some of Gremmen's (1981) vegetation types (see e.g. the smaller number of vegetation units proposed by Smith and Steenkamp 2001). It is, therefore, possible for a species to occupy multiple similar vegetation types (and, therefore, technically be classified as a generalist with low habitat specificity) but only cover a small portion of Marion Island since the vegetation types are small and located in similar portions of the island. Vegetation types might, therefore, not be a good proxy for habitat specificity in this system and perhaps in the future using species distribution models may have better potential to judge habitat specificity (McCune 2016).

The morphological and functional traits of the diaspores were also not strongly related to species' range expansion rates in either native or alien species. This is in contrast to, e.g., Cochrane et al. (2015) who showed that variation in seed traits can affect range dynamics. Although morphological traits were not correlated with species range expansion rates in this study, some morphological traits were associated with differences in dispersal

potential. For example, species with hairy diaspores had higher PD_{ane} estimates than species with hooks or no specialised structures. Furthermore, species that have diaspores with smooth surfaces had higher thalassochory potential estimates than the textured ones. Therefore, the practice of considering the morphological traits of species found on Marion Island and other regions where similar observations have been made may still have some utility for approximating the relative spread potential of newly introduced species (see e.g. Saastamoinen et al. 2018). This is especially likely if the species possess morphological traits that are associated with specific dispersal syndromes (e.g. plumes and wings for anemochory) that would give them dispersal-related advantages over the species that currently inhabit the island (with no specialised morphological traits; Thuiller et al. 2006; Molina-Montenegro et al. 2018; Chen and Giladi 2020).

Plant height was the only functional trait that was a significant predictor of the range expansion rates of alien species. Interestingly, though, the negative correlation between height and range expansion indicates that taller species have lower spread rates and suggests that height does not give the dispersal advantage to these alien species that has been observed in other studies (Gómez 2007; Thomson et al. 2011; Dangremond et al. 2020). However, examining a much larger dataset, Thomson et al. (2018) found that the strong positive association between plant height, dispersal, and range expansion rates is due to tall plant species typically investing heavily in larger or more dispersal structures. Indeed, the tallest alien species on Marion Island included in this study, *Poa pratensis*, may not be spreading as rapidly as would be expected because the diaspores for this species do not possess structures that increase the probability of successful dispersal via anemochory or biotic vectors. Because the aliens currently occupy regions of high disturbance and human traffic (Smith and Gremmen 2001), shorter-statured species (i.e. *Poa annua* and *Sagina procumbens*) may be spreading more rapidly because they can tolerate trampling disturbances and their diaspores are small enough to attach to biotic vectors and be dispersed to new sites. Indeed, *Sagina procumbens*, which has the smallest diaspores amongst all the species in the study (< 1 mm) and which only grows to be 25 mm tall, has the highest range expansion rate (1.8 km^2/ yr) of the alien flora on Marion Island. Although height was the only significant predictor of alien species' range expansion among the functional traits considered, other traits may also be important to consider in future studies. For example, the contribution of clonal reproduction to species spread could be prioritized (Ryan et.al.,2003). Furthermore, the size of seed crops could be hypothesized to be positively related to range expansion rates since, all else being equal, greater seed production would increase the chance of seeds dispersing further and improve the probability of at least some of the dispersed seeds establishing in suitable habitats (in line with the propagule pressure concept in invasion biology; Lockwood et al., 2009).

Conclusion

This study represents the first quantification of the dispersal potential of the dominant vascular plant species of a sub-Antarctic island. Although dispersal potential was not related to species spread rates, the dispersal estimates show that alien species may spread across and around the island through at least four different dispersal modes. The study, therefore, confirms the importance of management recommendations that limit the spread of alien species by, for example, eradicating newly invading plants through physical or chemical means or adopting a containment strategy should eradication attempts be unsuccessful (Auld and Johnson 2014). Additionally, the clothing and equipment worn and used while walking on the islands should always be cleaned to reduce the potential for anthropogenic dispersal of the alien plant species (as stated by the island's management plan; Prince Edward Islands Management Plan Working Group 2010). Plant species that are found in parts of the island frequented by seabirds and other animals should potentially be monitored more closely and managed accordingly since they are more likely to spread via zoochory. More generally, the data generated (dispersal potential estimates, diaspore morphological traits) and compiled (habitat specificity data) in this study can serve as unique contributions to understanding the biology of these plant species and the ecology of the sub-Antarctic islands.

Declarations

Data availability

The data used for this study are provided in the link below:

https://figshare.com/s/d48df2f893dbaac75339

References

1. Ainsworth A, Drake DR (2020) Classifying Hawaiian plant species along a habitat generalist-specialist continuum: Implications for species conservation under climate change. PLoS One 15: e0228573. https://doi.org/10.1371/journal.pone.0228573

2. Andersen MC (1993) Diaspore morphology and seed dispersal in several wind-dispersed Asteraceae. Am J Bot 80: 487–492. https://doi.org/10.1002/j.1537-2197.1993.tb13830.x

3. Angel A, Wanless RM, Cooper J (2009) Review of impacts of the introduced house mouse on islands in the Southern Ocean: are mice equivalent to rats? Biol Invasions 11: 1743–1754. https://doi.org/10.1007/s10530-008-9401-4

4. Angert AL, Crozier LG, Rissler LJ, Gilman SE, Tewksbury JJ, Chunco A J (2011) Do species' traits predict recent shifts at expanding range edges? Ecol Lett 14: 677–689. https://doi.org/10.1111/j.1461-0248.2011.01620.x

5. Auld BA, Johnson SB (2014) Invasive alien plant management. CABI Reviews 9: 1–12.

6. Alzate A, Onstein R E (2022) Understanding the relationship between dispersal and range size. Ecol Lett 25(10): 2303–2323. https://doi.org/10.1111/ele.14089

7. Bahn V, O'Connor RB, Krohn W (2006) Effect of dispersal at range edges on the structure of species ranges. Oikos 115: 89–96. https://onlinelibrary.wiley.com/doi/abs/10.1111/j.2006.0030-1299.14825.x

8. Barber Q E, Nielsen SE, Hamann A (2016) Assessing the vulnerability of rare plants using climate change velocity, habitat connectivity, and dispersal ability: a case study in Alberta. Canada. Reg Environ Change 16: 1433–1441. https://doi.org/10.1007/s10113-015-0870-6

9. Berg MP, Kiers ET, Driessen G, Van Der Heijden M, Kooi BW, Kuenen F, Liefting M, Verhoef HA, Ellers J (2010) Adapt or disperse: understanding species persistence in a changing world. Glob Chang Biol 16: 587–598. https://doi.org/10.1111/j.1365-2486.2009.02014.x

10. Bergstrom DM, Chown SL (1999) Life at the front: history, ecology and change on southern ocean islands. Trends Ecol Evol 14: 472–477. https://doi.org/10.1016/S0169-5347(99)01688-2

11. Born C, le Roux PC, Spohr C, McGeoch MA, Van Vuuren BJ (2012) Plant dispersal in the sub-Antarctic inferred from anisotropic genetic structure. Mol Ecol 21: 184–194. https://doi.org/10.1111/j.1365-294X.2011.05372.x

12. Brusca RC, Wiens JF, Meyer WM, Eble J, Franklin K, Overpeck JT, Moore W (2013) Dramatic response to climate change in the Southwest: Robert Whittaker's 1963 Arizona Mountain plant transect revisited. Ecol Evol 3: 3307–3319. https://doi.org/10.1002/ece3.720

13. Bullock SH, Mooney HA, Medina E (1995). Seasonally dry tropical forests. UK: Cambridge University Press.

14. Carthey AJ et al. (2016) How seed traits predict floating times: a biophysical process model for hydrochorous seed transport behaviour in fluvial systems. Freshw Biol 61: 19–31. https://doi.org/10.1111/fwb.12672

15. Canty AJ (2002). Resampling methods in R: the boot package. The Newsletter of the R Project Volume, 2(3), 2–7.

16. Chen SC, Giladi I (2020) Variation in morphological traits affects dispersal and seedling emergence in dispersive diaspores of *Geropogon hybridus*. Am J Bot 107: 436–444. https://doi.org/10.1002/ajb2.1430

17. Chown S, Smith V (1993) Climate change and the short-term impact of feral house mice at the subAntarctic Prince Edward Islands. Oecologia 96: 508–516. https://doi.org/10.1007/BF00320508

18. Chytrý M, Maskell LC, Pino J, Pyšek P, Vilà M, Font X, Smart SM (2008) Habitat invasions by alien plants: a quantitative comparison among Mediterranean, subcontinental and oceanic regions of Europe. Journal of Applied Ecology J Appl Ecol 45: 448–458. https://doi.org/10.1111/j.1365-2664.2007.01398.x

19. Clark JS, Macklin E, Wood L (1998) Stages and spatial scales of recruitment limitation in southern Appalachian forests. Ecol Monogr 68: 213–235.

20. Cochrane A, Yates CJ, Hoyle GL, Nicotra AB (2015) Will among-population variation in seed traits improve the chance of species persistence under climate change? Glob Ecol Biogeogr 24: 12–24. https://doi.org/10.1111/geb.12234

21. Corlett RT, Westcott DA (2013) Will plant movements keep up with climate change? Trends Ecol Evol 28: 482–488. https://doi.org/10.1016/j.tree.2013.04.003

22. Crimmins SM, Dobrowski SZ, Greenberg JA, Abatzoglou JT, Mynsberge AR (2011) Changes in climatic water balance drive downhill shifts in plant species' optimum elevations. Science 331: 324–327. https://doi.org/10.1126/science.1199040

23. Dangremond EM, Simpson LT, Osborne TZ, Feller I C (2020) Nitrogen enrichment accelerates mangrove range expansion in the temperate-tropical ecotone. Ecosystems 23: 703–714. https://doi.org/10.1007/s10021-019-00441-2

24. Danvind M, Nilsson C (1997) Seed floating ability and distribution of alpine plants along a northern Swedish river. J Veg Sci 8: 271–276. https://doi.org/10.2307/3237356

25. Davies KW, Sheley RL (2007) A conceptual framework for preventing the spatial dispersal of invasive plants. Weed Sci 55: 178–184. https://doi.org/10.1614/WS-06-161

26. Dullinger S, Gattringer A, Thuiller W, Moser D, Zimmermann NE, Guisan A, Willner W, Plutzar C, Leitner M, Mang T (2012) Extinction debt of high-mountain plants under twenty-first-century climate change. Nat Clim Chang 2: 619–622. https://doi.org/10.1038/nclimate1514

27. Engler R, Randin CF, Vittoz P, Czáka T, Beniston M, Zimmermann NE, Guisan A (2009) Predicting future distributions of mountain plants under climate change: does dispersal capacity matter? Ecography 32: 34–45. https://doi/epdf/10.1111/j.1600-0587.2009.05789.x

28. Evangelista A, Frate L, Carranza ML, Attorre F, Pelino G, Stanisci A, (2016) Changes in composition, ecology and structure of high-mountain vegetation: a re-visitation study over 42 years. AoB Plants 8: 4–4. https://doi.org/10.1093/aobpla/plw004

29. Freeman BG, Lee-Yaw JA, Sunday JM, Hargreaves AL, (2018) Expanding, shifting and shrinking: The impact of global warming on species' elevational distributions. Glob Ecol Biogeogr 27: 1268–1276. https://doi.org/10.1111/geb.12774

30. Frei E, Bodin J, Walther GR (2010) Plant species' range shifts in mountainous areas - all uphill from here? Bot Helv 120: 117–128. https://doi.org/10.1007/s00035-010-0076-y

31. García C, Klein EK, Jordano P (2017) Dispersal processes driving plant movement: challenges for understanding and predicting range shifts in a changing world. J Ecol 105: 15–15. https://doi.org/10.1111/1365-2745.12705

32. Gibson SY, Van Der Marel RC, Starzomski BM (2009) Climate change and conservation of leading-edge peripheral populations. Conserv Biol 23: 1369–1373.

33. Gleeson J, Van Rensburg P (1971) Feeding ecology of the house mouse. *Mus musculus* on Marion Island S. Afr. J. Antarct. Res 12: 34–39

34. Goddard, K. A., Craig, K. J., Schoombie, J., & le Roux, P. C. (2022). Investigation of ecologically relevant wind patterns on Marion Island using Computational Fluid Dynamics and measured data. Ecol Modell 464, 109827. https://doi.org/10.1016/j.ecolmodel.2021.109827

35. Goldberg EE, Lande R (2007) Species' borders and dispersal barriers. Am Nat 170: 297–304. https://doi.org/10.1086/518946

36. Gómez J (2007) Dispersal-mediated selection on plant height in an autochorously dispersed herb. Plant Syst Evol 268: 119–130. https://doi.org/10.1007/s00606-007-0568-4

37. Gremmen NJM (1981) The vegetation of the subantarctic islands, Marion and Prince Edward. PhD thesis. Radboud University Nijmegen, The Netherlands.

38. Greve M, Steyn C, Mathakutha R, Chown SL (2017) Terrestrial invasions on sub-Antarctic Marion and Prince Edward Islands. Bothalia - Afr Biodivers Conserv 47: 1–21. https://doi/abs/10.4102/abc.v47i2.2143

39. Grubb PJ (1977) The maintenance of species-richness in plant communities: the importance of the regeneration niche. Biol Rev 52: 107–145.

40. Hampe A (2011) Plants on the move: The role of seed dispersal and initial population establishment for climate-driven range expansions. Acta Oecol 37: 666–673. https://doi.org/10.1016/j.actao.2011.05.001

41. Harrison TL, Simonsen A K, Stinchcombe J R, Frederickson M E (2018) More partners, more ranges: generalist legumes spread more easily around the globe. Biol Lett 14: 20180616. https://doi/epdf/10.1098/rsbl.2018.0616

42. Hedding DW, Nel W, Anderson RL (2015) Aeolian processes and landforms in the subAntarctic: preliminary observations from Marion Island. Polar Res 34: 26365. https://doi.org/10.3402/polar.v34.26365

43. Heleno R, Vargas P (2015) How do islands become green? Glob Ecol Biogeogr 24: 518–526. https://doi/abs/10.1111/geb.12273

44. Honnay O, Jacquemyn H, Bossuyt B, Hermy M (2005) Forest fragmentation effects on patch occupancy and population viability of herbaceous plant species. New Phytol 166(3): 723–736. https://doi.org/10.1111/j.1469-8137.2005.01352.x

45. Hoque MA (2016) Pummelo: Characterization, floral biology, fruit growth, propagation, storage behaviour and processing. Lambert Academic Publishing, Germany.

46. Hovstad KA, Borvik S, Ohlson M (2009) Epizoochorous seed dispersal in relation to seed availability-an experiment with a red fox dummy. J Veg Sci 20: 455–464. https://doi.org/10.1111/j.1654-1103.2009.01049.x

47. Huang F, Peng S, Chen B, Liao H, Huang Q, Lin Z, Liu G (2015) Rapid evolution of dispersal-related traits during range expansion of an invasive vine *Mikania micrantha*. Oikos 124: 1023–1030. https://doi.org/10.1111/oik.01820

48. Ibrahim KM, Nichols RA, Hewitt GM (1996) Spatial patterns of genetic variation generated by different forms of dispersal during range expansion. Heredity 77: 282–291. https://doi.org/10.1038/hdy.1996.142

49. Irl SD, Schweiger AH, Steinbauer MJ, Ah-Peng C, Arévalo JR, Beierkuhnlein C, Chiarucci A, Daehler C C, Fernández-Palacios JM, Flores O (2021) Human impact, climate and dispersal strategies determine plant invasion on islands. J Biogeogr 48(8): 1889–1903. https://doi.org/10.1111/jbi.14119

50. Jongejans E, Telenius A (2001) Field experiments on seed dispersal by wind in ten umbelliferous species (Apiaceae). Plant Ecol 152: 67–78. https://doi.org/10.1023/A:1011467604469

51. Jump AS, Woodward FI (2003) Seed production and population density decline approaching the range-edge of *Cirsium* species. New Phytol 160: 349–358. https://doi.org/10.1046/j.1469-8137.2003.00873.x

52. Kaladharan P (2000) Artificial seawater for seaweed culture. Indian JFish 47: 257–260.

53. Kelly AE, Goulden ML (2008) Rapid shifts in plant distribution with recent climate change. Proc Natl Acad Sci USA 105: 11823–11826. https://doi.org/10.1073/pnas.0802891105

54. Kirkpatrick M, Barton NH (1997) Evolution of a species' range. Am Nat 150: 123–123.

55. Lamsal P, Kumar L, Aryal A, Atreya K, (2018) Invasive alien plant species dynamics in the Himalayan region under climate change. Ambio 47: 697–710.

56. La Rue EA, Emery NC, Briley L, Christie MR (2019) Geographic variation in dispersal distance facilitates range expansion of a lake shore plant in response to climate change. Divers Distrib 25: 1429–1440. https://doi.org/10.1111/ddi.12951

57. le Roux PC, McGeoch MA (2008a) Changes in climate extremes, variability and signature on sub-Antarctic Marion Island. Clim Change 86: 309–329. https://doi.org/10.1007/s10584-007-9259-y

58. — (2008b) Rapid range expansion and community reorganization in response to warming. Glob Chang Biol 14: 2950–2962. https://doi.org/10.1111/j.1365-2486.2008.01687.x

59. le Roux PC, Ramaswiela T, Kalwij JM, Shaw JD, Ryan PG, Treasure AM, McClelland GT, McGeoch MA, Chown SL (2013) Human activities, propagule pressure and alien plants in the sub-Antarctic: Tests of generalities and evidence in support of management. Biol Conserv 161: 18–27. https://doi.org/10.1016/j.biocon.2013.02.005

60. Lenoir J, Gégout JC, Marquet P, De Ruffray P, Brisse H (2008) A significant upward shift in plant species optimum elevation during the 20th century. Science 320: 1768–1771. https://doi.org/10.1126/science.1156831

61. Lenoir J, Svenning J C (2015) Climate-related range shifts-a global multidimensional synthesis and new research directions. Ecography 38: 15–28.

62. Leuning R, Kelliher FM, De Pury D, Schulze ED (1995) Leaf nitrogen, photosynthesis, conductance and transpiration: scaling from leaves to canopies. Plant Cell Environ 18: 1183–1200. https://doi.org/10.1111/j.1365-3040.1995.tb00628.x

63. Lockwood J L, Cassey P, Blackburn T M (2009) The more you introduce the more you get: the role of colonization pressure and propagule pressure in invasion ecology. Divers Distrib 15: 904–910. https://doi.org/10.1111/j.1472-4642.2009.00594.x

64. Matesanz S, Horgan-Kobelski T, Sultan SE (2015) Evidence for rapid ecological range expansion in a newly invasive plant. AoB Plants 7: 38–38. https://doi.org/10.1093/aobpla/plv038

65. Mathakutha R, Steyn C, le Roux PC, Blom IJ, Chown SL, Daru BH, Ripley BS, Louw A, Greve M (2019) Invasive species differ in key functional traits from native and non-invasive alien plant species. J Veg Sci 30: 994–1006. https://doi.org/10.1111/jvs.12772

66. McConkey KR, Prasad S, Corlett RT, Campos-Arceiz A, Brodie JF, Rogers H, Santamaria L (2012) Seed dispersal in changing landscapes. Biol Conserv 146: 113–113. https://doi.org/10.1016/j.biocon.2011.09.018

67. McCormick MK, Jacquemyn H (2014) What constrains the distribution of orchid populations? New Phytol 202: 392–400. https://doi.org/10.1111/nph.12639

68. McCune J (2016) Species distribution models predict rare species occurrences despite significant effects of landscape context. J Appl Ecol 53: 1871–1879. https://doi.org/10.1111/1365-2664.12702

69. Mélice J, Lutjeharms J, Rouault M, Ansorge I (2003) Sea-surface temperatures at the subAntarctic islands Marion and Gough during the past 50 years. S Afr J Sci 99: 363–366.

70. Molina-Montenegro MA, Acuña-Rodríguez IS, Flores TS, Hereme R, Lafon A, Atala C, Torres-Díaz C (2018) Is the success of plant invasions the result of rapid adaptive evolution in seed traits? Evidence from a latitudinal rainfall gradient. Front Plant Sci 9: 208–208. https://doi.org/10.3389/fpls.2018.00208

71. Mulaudzi TW, Hofmeyr G, Bester MN, Kirkman SP, Pistorius PA, Jonker F, Makhado AB, Owen J, Grimbeek RJ, (2008) Haulout site selection by southern elephant seals at Marion Island. African Zoology 43: 25–33.

72. Nathan R (2006) Long-distance dispersal of plants. Science 313: 786–788. https://doi.org/10.1126/science.1124975

73. Nathan R, Schurr FM, Spiegel O, Steinitz O, Trakhtenbrot A, Tsoar A (2008) Mechanisms of long-distance seed dispersal. Trends Ecol Evol 23: 638. https://doi.org/10.1016/j.tree.2008.08.003

74. Nathan R, Klein E, Robledo-Arnuncio J J, Revilla E, (2012) Dispersal kernels. Oxford University Press, Oxford, UK.

75. Oliver T, Hill JK, Thomas CD, Brereton T, Roy DB (2009) Changes in habitat specificity of species at their climatic range boundaries. Ecol Lett 12: 1091–1102. https://doi.org/10.1111/j.1461-0248.2009.01367.x

76. Osem Y, Perevolotsky A, Kigel J (2002) Grazing effect on diversity of annual plant communities in a semi-arid rangeland: interactions with small-scale spatial and temporal variation in primary productivity. J Ecol 90: 936–946. https://doi.org/10.1046/j.1365-2745.2002.00730.x

77. Öster M, Ask K, Cousins SA, Eriksson O (2009) Dispersal and establishment limitation reduces the potential for successful restoration of semi-natural grassland communities on former arable fields. J Appl Ecol 46: 1266–1274. https://doi.org/10.1111/j.1365-2664.2009.01721.x

78. Parmesan C (2006) Ecological and evolutionary responses to recent climate change. Annu Rev Ecol Evol Syst 37: 637–669.

79. Patil V, Dadlani M (2009) Tetrazolium test for seed viability and vigour. Handbook of seed testing, 209–241.

80. Prince Edward Islands Management Plan Working Group (2010) Prince Edward Islands Management Plan. 0.2. DST-NRF Centre of Excellence for Invasion Biology. Stellenbosch University, South Africa.

81. R Core Team (2021). R: A language and environment for statistical computing. R Foundation of Statistical Computing. Vienna, Austria.

82. Ripley BS, Edwardes A, Rossouw MW, Smith VR, Midgley GF (2020) Invasive grasses of sub-Antarctic Marion Island respond to increasing temperatures at the expense of chilling tolerance. Ann Bot 125: 765–773. https://doi.org/10.1093/aob/mcz156

83. Rosenzweig C, Karoly D, Vicarelli M, Neofotis P, Wu Q, Casassa G, Menzel A, Root TL, Estrella N, Seguin B (2008) Attributing physical and biological impacts to anthropogenic climate change. Nature 453: 353–357. https://doi.org/10.1038/nature06937

84. Rumpf SB, Hülber K, Klonner G, Moser D, Schütz M, Wessely J, Willner W, Zimmermann NE, Dullinger S (2018) Range dynamics of mountain plants decrease with elevation. Proc Natl Acad Sci USA 115: 1848–1853. https://doi.org/10.1073/pnas.1713936115

85. Ryan P, Smith V, Gremmen N (2003) The distribution and spread of alien vascular plants on Prince Edward Island. Afr J Mar Sci 25: 555–562. https://doi.org/10.2989/18142320309504045

86. Saastamoinen M, Bocedi G, Cote J, Legrand D, Guillaume F, Wheat C W, Fronhofer E A, Garcia C, Henry R, Husby A, (2018) Genetics of dispersal. Biol Rev 93, 574–599. https://doi.org/10.1111/brv.12356

87. Sax DF, Gaines SD (2008) Species invasions and extinction: the future of native biodiversity on islands. Proc Natl Acad Sci USA105: 11490–11497. https://doi.org/10.1073/pnas.0802290105

88. Scherrer D, Vitasse Y, Guisan A, Wohlgemuth T, Lischke H (2020) Competition and demography rather than dispersal limitation slow down upward shifts of trees' upper elevation limits in the Alps. J Ecol 108: 2416–2430. https://doi.org/10.1111/1365-2745.13451

89. Shigesada N, Kawasaki K (2002) Invasion and the range expansion of species: effects of long-distance dispersal. In: Dispersal Ecology: 42nd Symposium of the British Ecological Society. Ed. by Bullock JM et al. Cambridge University Press: 350–373.

90. Smith V (2002) Climate change in the sub-Antarctic: an illustration from Marion Island. Clim Change 52: 345–357. https://doi.org/10.1023/A:1013718617277

91. Smith V, Gremmen N (2001) *Turgidosculum complicatulum* on sub-Antarctic Marion Island: carbon acquisition response to climate change. Polar Biol 24: 455–459. https://doi.org/10.1007/s003000100248

92. Smith V, Steenkamp M (2001) Classification of the terrestrial habitats on Marion Island based on vegetation and soil chemistry. J Veg Sci 12: 181–198. https://doi.org/10.2307/3236603

93. Sorensen AE (1986) Seed dispersal by adhesion. Annu Rev Ecol Syst17: 443–463.

94. Stiles EW (2000) Animals as seed dispersers. In: Seeds: The Ecology of Regeneration in Plant Communities. Ed. by Fenner M. CABI Publishing: 111–124. https://doi.org/10.1079/9780851994321.0111

95. Thompson K, Gaston KJ, Band SR (1999) Range size, dispersal and niche breadth in the herbaceous flora of central England. J Ecol 87: 150–155. https://doi.org/10.1046/j.1365-2745.1999.00334.x

96. Thomson FJ, Letten AD, Tamme R, Edwards W, Moles AT (2018) Can dispersal investment explain why tall plant species achieve longer dispersal distances than short plant species. New Phytol 217: 407–415. https://doi.org/10.1111/nph.14735

97. Thomson FJ, Moles AT, Auld TD, Kingsford RT (2011) Seed dispersal distance is more strongly correlated with plant height than with seed mass. J Ecol 99: 1299–1307. https://doi.org/10.1111/j.1365-2745.2011.01867.x

98. Thuiller W, Richardson DM, Rouget M, Proches Ş, Wilson JR (2006) Interactions between environment, species traits, and human uses describe patterns of plant invasions. Ecology 87: 1755–1769. https://doi.org/10.1890/0012-9658(2006)87[1755:IBESTA]2.0.CO;2

99. Tonkin JD, Tachamo Shah RD, Shah DN, Hoppeler F, Jähnig SC, Pauls SU (2017) Metacommunity structuring in Himalayan streams over large elevational gradients: The role of dispersal routes and niche characteristics. J Biogeogr 44: 62–74. https://doi.org/10.1111/jbi.12895

100. Traveset A, Heleno R, Nogales M (2013) The ecology of seed dispersal. In: Seeds: The Ecology of Regeneration in Plant Communities. Ed. by Fenner and M. CABI Publishing: 85–110. https://www.uv.mx/personal/tcarmona/files/2010/08/Willson-y-Traveset-2000.pdf

101. Urban MC, Bocedi G, Hendry AP, Mihoub JB, Pe'er G, Singer A, Bridle J, Crozier L, De Meester L, Godsoe W (2016) Improving the forecast for biodiversity under climate change. Science 353: 8466–8466. https://doi.org/10.1126/science.aad8466

102. Van Der Wal J, Murphy HT, Kutt AS, Perkins GC, Bateman BL, Perry JJ, Reside AE (2013) Focus on poleward shifts in species' distribution underestimates the fingerprint of climate change. Nat Clim Chang 3: 239–243. https://doi.org/10.1038/nclimate1688

103. Veran S, Piry S, Ternois V, Meynard CN, Facon B, Estoup A (2016) Modeling spatial expansion of invasive alien species: relative contributions of environmental and anthropogenic factors to the spreading of the harlequin ladybird in France. Ecography 39: 665–675. https://doi.org/10.1111/ecog.01389

104. Von Der Lippe M, Bullock JM, Kowarik I, Knopp T, Wichmann M (2013) Human-mediated dispersal of seeds by the airflow of vehicles. PLoS One 8: e52733. https://doi.org/10.1371/journal.pone.0052733

105. Walther GR, Beißner S, Burga CA (2005) Trends in the upward shift of alpine plants. J Veg Sci 16: 541–548. https://doi.org/10.1111/j.1654-1103.2005.tb02394.x

106. Wang H, Liu L, Yin L, Shen J, Li S (2000) Exploring the complex relationships and drivers of ecosystem services across different geomorphological types in the Beijing-Tianjin-Hebei region. Ecol Indic 121: 107116. https://doi.org/10.1016/j.ecolind.2020.107116

107. Wei T, Simko V, Levy M, Xie Y, Jin Y, Zemla J (2017). Package 'corrplot'. Statistician 56: e24.

108. Williamson M, Dehnen-Schmutz K, Kühn I, Hill M, Klotz S, Milbau A, Stout J, Pyšek P (2009) The distribution of range sizes of native and alien plants in four European countries and the effects of residence time. Divers Distrib 15: 158–166. https://doi.org/10.1111/j.1472-4642.2008.00528.x

109. Wilson R J, Gutiérrez D, Gutiérrez J, Martínez D, Agudo R, Monserrat VJ (2005) Changes to the elevational limits and extent of species ranges associated with climate change. Ecol Lett 8: 1138–1146. https://doi.org/10.1111/j.1461-0248.2005.00824.x

110. Wisz MS, Pottier J, Kissling WD, Pellissier L, Lenoir J, Damgaard CF, Dormann CF, Forchhammer MC, Grytnes JA, Guisan A (2013) The role of biotic interactions in shaping distributions and realised assemblages of species: implications for species distribution modelling. Biol Rev 88: 15–30. https://doi.org/10.1111/j.1469-185X.2012.00235.x

111. Yu-Peng G, Wen-Ju Z, Bo L, Jia-Kuan C (2004) Phenotypic plasticity and invasiveness of alien plants. Biodiversity Science 12: 447–447. https://doi.org/10.17520/biods.2004055

112. Zelikova, T J, Dunn RR, Sanders NJ (2008) Variation in seed dispersal along an elevational gradient in Great Smoky Mountains National Park. Acta Oecol 34: 155–162. https://doi.org/10.1016/j.actao.2008.05.002
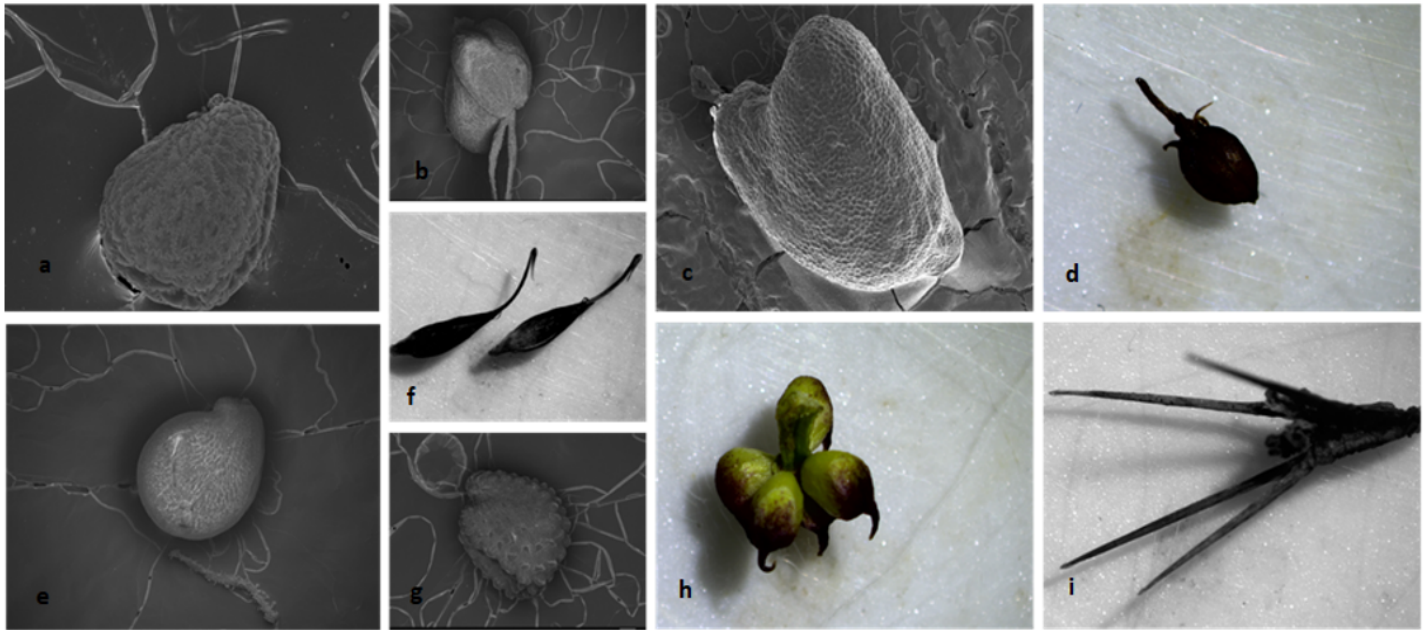
Figures

Figure 1

Variety in the shape and texture of diaspores from the island's species. (a) *Sagina procumbens* (*c.* 1 mm maximum length), (b) *Callitriche antarctica* (*c.* 2 mm), (c) *Pringlea antiscorbutica* (*c.* 4 mm), (d) *Azorella selago* (*c.* 4 mm), (e) *Montia fontana* (*c.* 1.1 mm), (f) *Uncinia compacta* (*c.* 10 mm), (g) *Cerastium fontanum* (*c.* 1 mm), (h) *Ranunculus biternatus* (*c.* 3 mm), (i) *Acaena magellanica* (*c.* 13 mm)

Figure 2

The correlation between the estimates of each species' dispersal capacity for each dispersal syndromes and the overall dispersal potential rankings (PD$_{overall}$). Values below the diagonal are the Spearman correlation coefficients, with the symbols above the diagonal representing the strength (by size) and nature (by colour) of the pairwise correlations. Correlations marked with crosses were not significant
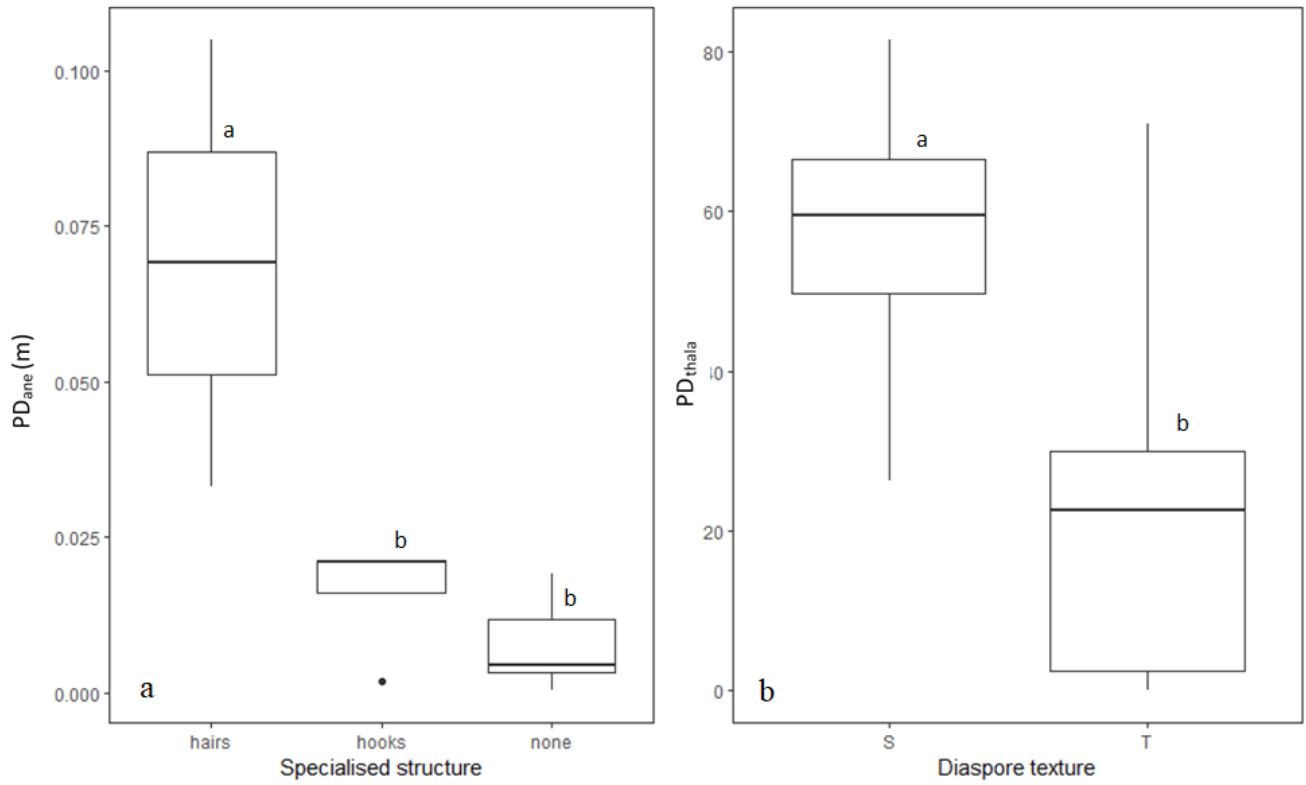
Figure 3

The morphology of diaspores affects the dispersal potential of native plant species on Marion Island: (a) Diaspore surface structures affect dispersal potential via anemochory (PD$_{ane}$; n = 13, F = 9.518, p = 0.005). (b) Diaspore texture affects thalassochory dispersal potential (PD$_{thala}$; %) of diaspores (n = 13, F = 5.809, p = 0.035). Whiskers indicate the range of values, boxes the interquartile range, and the horizontal line median values. Groups not sharing a common letter differ significantly