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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 standardized 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, emphasizing 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

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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 $°C^{-1}$ (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 twentieth 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 over 40 years (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 et al. 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^{-1}.

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. Both alien and indigenous species were expected to show a positive relationship between dispersal capacity and rates of range expansion, with alien species additionally expected to show greater dispersal potential than indigenous species (based on, e.g., Zhang et al. 2023).

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 and, therefore, expanding their geographic range limits (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 and 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 examples in 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. 2013).

At least 20 dispersal units of 18 vascular plant species (five of which are alien to Marion Island) were collected from 42 locations across Marion Island (chiefly within 6 km from the island's research station) to account for possible intra-specific variations in size, mass, or morphology. Vascular plant species for which too few propagules could be found were excluded from experiments and analyses; many of these are localized alien species that are being actively controlled (Greve et al. 2017). 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 averaged across from all stations for subsequent analyses.

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):

$$v_t = \frac{d}{t} \qquad (1)$$

where d is the distance traveled 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; Thomson et al. 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):

$$x_d = h\frac{u}{v_t} \qquad (2)$$

where x_d and h are in meters (m) and u and v_t are in meters per second (m s^{-1}).

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.

$$\%\text{PD}_{zoo} = \frac{D_a}{D_{all}}\% \qquad (3)$$

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."

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 16×16 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:

$$\%\text{PD}_{anthro} = \frac{D_a}{D_{all}}\% \qquad (4)$$

While transport via clothing items is thought to be a major driver of propagule dispersal on Marion Island, this method did not account for other dispersal routes (e.g., boots). Other intra-island dispersal routes (e.g., transport by helicopters or by containers that are slung to huts) that were more common in the past (though only restricted to a few weeks a year) are now considered to be rare due to strict biosecurity measures, and unlikely to have a major impact on propagule dispersal (Winzer et al. 2023).

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 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 min, 1 h, 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 h 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℃ for 1–3 h 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 provide a quantitative measure of habitat specificity by scoring the suitability of each vegetation unit based on the presence or absence of a species from surveyed plots in each vegetation unit. 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: whole plant height, leaf area, specific leaf area, leaf chlorophyll content (per unit area and per unit mass), specific root length, root diameter, leaf nitrogen concentration, leaf phosphorus concentration, and leaf toughness. These traits were selected as they represent different axes of trait space occupied by the plants of Marion Island (Mathakutha et al. 2019). Data were not available for all species for all traits (missing for 8% of trait-species combinations for alien species and 5% for native species); species with missing trait data were excluded from analyses for those traits.

Statistical analyses

We assessed the relationship between the dispersal estimates for the four dispersal syndromes and overall dispersal potential using Spearman correlation tests. To analyze the relationship between range expansion and the estimates for all four dispersal syndromes, bootstrap regression models (run via the "car" package; Fox and Weisberg 2019) were

used (due to the relatively low number of species examined). 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. 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; Venables and Ripley 2002). This analysis was not repeated for the alien plant species due to the number of alien species being too small.

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 analyzing 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 to 90 mg and that of native species ranged from 1 to 630 mg. The seed release heights of species ranged from 18 to 360 mm and 82 to 205 mm for indigenous and alien species, respectively (see Online resource 1). Species showed a wide variety of diaspore shapes, sizes, and textures (Fig. 1,

see also Online resource 2). 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 m.s^{-1}; $u_{st1,1m}$ = 2.572 m.s^{-1}; $u_{st15,0.5}$ = 6.942 m. s^{-1}; $u_{st15,1m}$ = 7.87 m.s^{-1}). 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).

Wind-transported diaspores of the indigenous species *A. magellanica*, *Azorella selago*, *Polypogon magellanicus*, *A. stolonifera*, *Poa annua,* and *P. 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 *C. fontanum, C. kerguelensis*, and *S. procumbens* showed poor buoyancy, with all their diaspores sinking in < 1 h. 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; see Online resource 3). Diaspore viability after the buoyancy test varied markedly, with *Pringlea antiscorbutica* having the highest proportion of viable diaspores (0.77) followed by *M. fontana* (0.75; Online resource 3. When combining
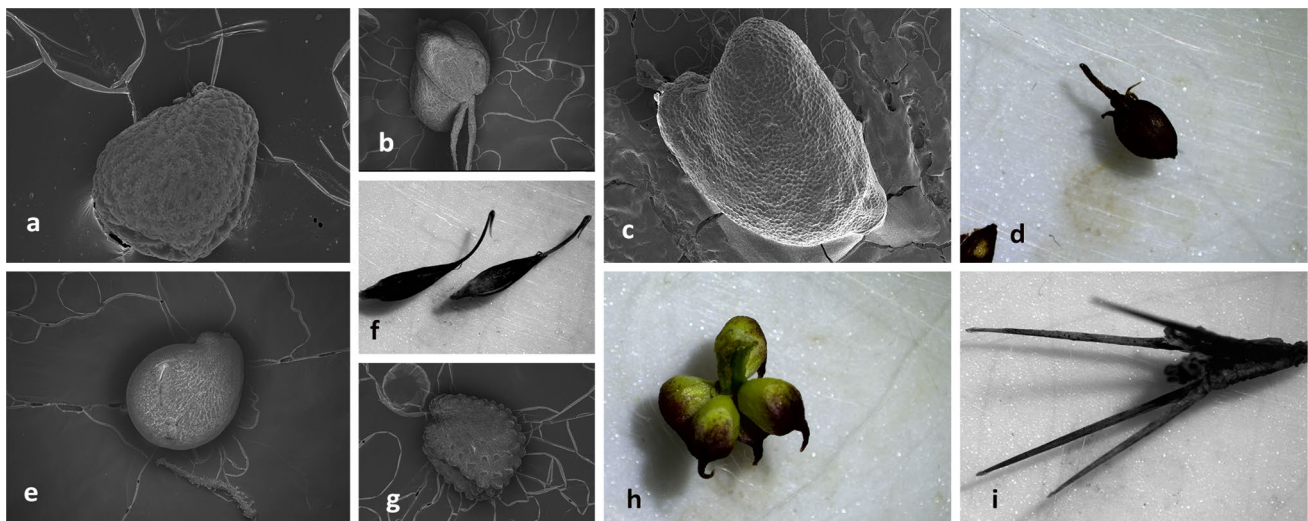

Fig. 1 Variety in the shape and texture of diaspores from the island's species. **a** *Sagina procumbens* (*c*. 1 mm maximum length), **b** *Callitriche antarctica* (*c*. 2 mm), **c** *Pringlea antiscorbutica* (*c*. 4 mm), **d** *Azorella selago* (*c*. 4 mm)*,* **e** *Montia fontana* (*c*. 1.1 mm)*,*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

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

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	2.5	5.5	9.7	17.0	53.1	18.0	53.5
*Agrostis stolonifera**	0.056	17	45.0	14.0	6.9	16.0	20.0	16.0	63.0
Azorella selago	0.021	12	26.3	10.0	0.3	4.5	7.8	9.0	35.5
Callitriche antarctica	0.011	8	2.5	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	61.5	16.0	32.8	18.0	6.6	8.0	51.0
Crassula moschata	0.003	3	17.5	7.0	0.6	7.0	8.8	11.0	28.0
Juncus scheuchzerioides	0.005	6	30.0	11.0	2.5	9.0	5.6	4.5	30.5
Montia fontana	0.003	4	57.5	15.0	3.8	11.5	5.6	4.5	35.0
*Poa annua**	0.016	10	39.0	12.0	3.1	10.0	5.9	6.5	38.5
Poa cookii	0.105	18	25.0	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	22.5	8.0	4.4	13.0	32.2	17.0	53.0
Pringlea antiscorbutica	0.019	11	71.0	17.0	0.0	1.5	1.6	1.0	30.5
Ranunculus biternatus	0.002	2	81.5	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	42.5	13.0	3.8	11.5	13.8	14.0	52.5

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

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 (Spearman rank correlation: r_s = 0.12, n = 18, p = 0.093).

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 to 4.3% (Table 2). However, *A. magellanica* and *C. 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% (*C. kerguelensis*) to 53% (*A. magellanica*).

Overall, the study showed a broad range of dispersal potential among the species, with the alien species *A. stolonifera* having the highest overall dispersal potential ranking (Table 2). However, across all dispersal modes, there was no significant difference in dispersal potential between the alien and indigenous species (Wilcox test: all p > 0.18). 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

Fig. 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 color) of the pairwise correlations. Correlations marked with crosses were not significant

native species, or the spread rate of alien species (Table 3). However, there was a significant negative relationship between the spread rates of alien species and their average heights (Spearman rank correlation: $r_s = -0.919$, $n = 5$, $p = 0.028$). 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 (Spearman rank correlation: all $p > 0.4$).

All but two of the relationships between dispersal capacity and morphological traits were not statistically

significant (Online resource 4). There was a significant difference between the PD_{ane} of native species with different specialized structures (ANOVA: $F_{2,10} = 9.518$, $p = 0.005$) and PD_{thala} was significantly greater for smooth diaspores (ANOVA: $F_{2,10} = 5.809$, $p = 0.03$; see Fig. 3). There was also no significant relationship between morphological traits and the range expansion rates of both the native and alien species (Table 4).

There was no significant relationship between habitat specificity and the range expansion of both native (Spearman rank correlation: $r_s = -0.52$, $n = 18$, $p = 0.61$) and alien species (Spearman rank correlation: $r_s = 0.41$, $n = 8$, $p = 0.31$). 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 *P. magellanicus* and *M. fontana*, occupying 38 and 37 vegetation units, respectively (Online resource 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	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	− 51.3–9.7
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

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

Fig. 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}; ANOVA: $F_{2,10} = 9.518$, $p = 0.005$). **b** Diaspore texture affects thalassochory dispersal potential (PD_{thala}; %) of diaspores (ANOVA: $F_{2,10} = 5.809$, $p = 0.035$). Whiskers indicate the range of values, boxes the interquartile range, and the horizontal line median values. Groups not sharing a common letter differ significantly
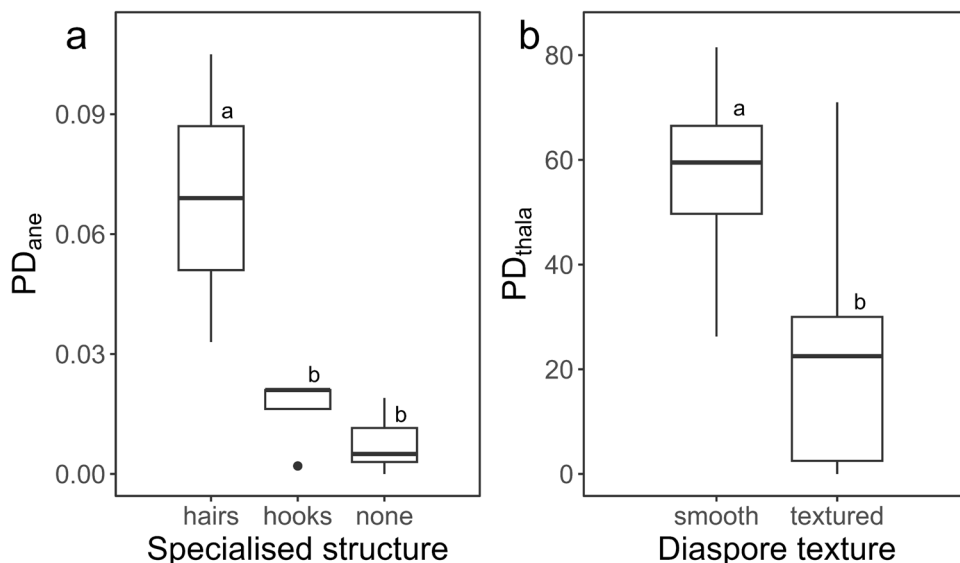
Table 4 Linear models examining the relationship between species range expansion rates and species functional traits

	Coefficient	df	F	p	R^2
Native species					
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

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

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} (*P. cookii*, 0.36 m and *P. 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 *R. 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. *C. fontanum, C. kerguelensis,* and *S. procumbens*) have small (≤ 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 neighboring islands.

There is a lot of variation in the dispersal potential of plant species through zoochory and anthropogenic activity. *Acaena magellanica* and *P. magellanicus* had the highest attachment potential to feathers, and both of these species' diaspores have traits that are 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 2000). Additionally, *A. magellanica* had one of the highest attachment potentials to clothing material, exceeded only by *C. 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 specialized structures.

Dispersal may also not be an important contributor to the range dynamics of species on Marion Island. Indeed, while Alzate and Onstein (2022) demonstrates that dispersal typically positively affects range size; they also document how this relationship may also be contingent on other factors. Furthermore, the limited contribution of dispersal to the observed range shifts on the island may be attributed to the steep elevational gradient, which likely presents a unique set of complexities that may not be relevant in flatter or more undulating systems (see Wang et al. 2000): 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.

Despite there being no significant difference between the dispersal potential of alien and native species, other factors may potentially differentially influence the current distributions and range expansion patterns for these two groups of plant species on the island. At present, 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 neighboring 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 (Mathakutha et al. 2019), different distributions (le Roux et al. 2013) and aliens likely still not being at equilibrium.

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 specialized 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 specialized 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 Steenkamp 2001), shorter-statured species (i.e., *P. annua* and *S. 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, *S. procumbens*, which has the smallest diaspores among 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^{-1}) 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).

Climate change is altering the distribution of suitable habitat across Marion Island, with warmer temperatures correlated with the majority of the island's vascular plant species expanding their distributions (le Roux and McGeoch 2008b). Shifting climatic conditions may also affect species dispersal rates, thereby influencing species probability of successfully colonizing newly suitable habitat. For example, if wind speeds continue to increase on Marion Island (as observed from the 1960s until the early 2000s; le Roux and McGeoch 2008a), a proportional increase in anemochory can be expected (see also Bullock et al. 2012). In contrast, if rainfall at the island decreases further (Hedding and Greve 2018) it is likely that the potential for hydrochory (e.g., via streams and overland flow during heavy rainfall events) will be lower. Dispersal potential via zoochory on Marion Island may also be impacted by climate change (e.g., through changes in the abundance or distribution of seabirds; see e.g., Cooper and Lutjeharms 1992; Momberg et al. 2023), but the positive impact of alien cat eradication on seabird abundances on this island (Dilley et al. 2017) will possibly have a greater effect, particularly through the potential for a greater abundance of seabirds nesting at higher altitudes again which could accelerate the spread of plant species upslope (see le Roux and McGeoch 2008b). As a result, forecasting the future distribution of species in response to climatic shifts should consider how climate change might affect the distribution of newly suitable habitat and species ability to disperse to those habitats.

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 potentially spread across and around Marion Island through at least four different dispersal modes (although the relative contribution of each dispersal mode to alien species spread is unknown). 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

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