

# The influence of landscape, climate and history on spatial genetic patterns in keystone plants (*Azorella*) on sub-Antarctic islands

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## Abstract

The distribution of genetic variation in species is governed by factors that act differently across spatial scales. To tease apart the contribution of different processes, especially at intermediate spatial scales, it is useful to study simple ecosystems such as those on sub-Antarctic oceanic islands. In this study, we characterize spatial genetic patterns of two keystone plant species, *Azorella selago* on sub-Antarctic Marion Island and *Azorella macquariensis* on sub-Antarctic Macquarie Island. Although both islands experience a similar climate and have a similar vegetation structure, they differ significantly in topography and geological history. We genotyped six microsatellites for 1,149 individuals from 123 sites across Marion Island and 372 individuals from 42 sites across Macquarie Island. We tested for spatial patterns in genetic diversity, including correlation with elevation and vegetation type, and clines in different directional bearings. We also examined genetic differentiation within islands, isolation-by-distance with and without accounting for direction, and signals of demographic change. Marion Island was found to have a distinct northwest–southeast divide, with lower genetic diversity and more sites with a signal of population expansion in the northwest. We attribute this to asymmetric seed dispersal by the dominant northwesterly winds, and to population persistence in a southwestern refugium during the Last Glacial Maximum. No apparent spatial pattern, but greater genetic diversity and differentiation between sites, was found on Macquarie Island, which may be due to the narrow length of the island in the direction of the dominant winds

and longer population persistence permitted by the lack of extensive glaciation on the island. Together, our results clearly illustrate the implications of island shape and geography, and the importance of direction-dependent drivers, in shaping spatial genetic structure.

#### KEYWORDS

direction-dependent dispersal, genetic diversity, Macquarie Island, Marion Island, microsatellites, spatial genetic structure

## 1 | INTRODUCTION

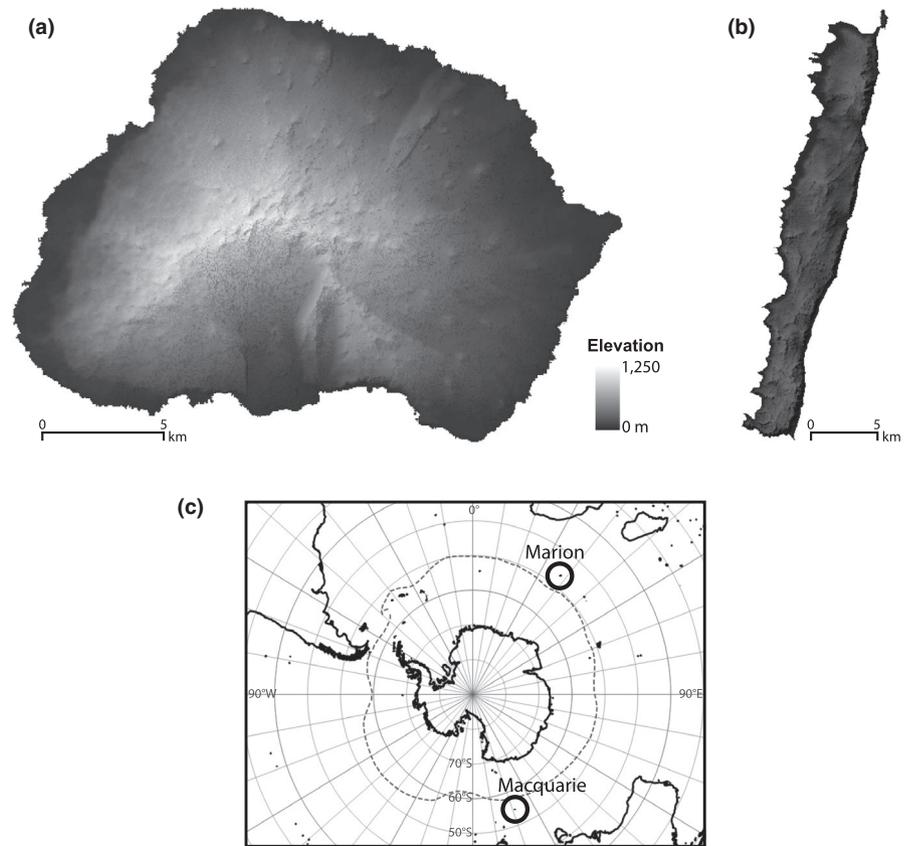
Distributions of species are shaped by various factors including environmental properties, biological interactions and species traits, which may act differently across spatial scales. At large spatial scales, long-distance dispersal, geological processes and physical barriers shape the biogeography of species (González-Wevar et al., 2018; Lee et al., 2017; Postaire, Gélín, Bruggemann, & Magalon, 2017; Sanmartín & Ronquist, 2004; Whittaker, Triantis, & Ladle, 2008). At finer spatial scales, local dispersal becomes increasingly important, driven primarily by the biology of the species and the local environment as experienced by individuals (LaRue, Holland, & Emery, 2018; Manel, Schwartz, Luikart, & Taberlet, 2003). In contrast, the relative contributions of processes shaping distributions at intermediate spatial scales (typically tens to hundreds of kilometres) are more difficult to tease apart, as dispersal is less frequent and landscapes become spatially heterogeneous (Lenoir et al., 2012; Lin et al., 2013; Mertes & Jetz, 2018). To this end, scale-dependent approaches are often needed to fully appreciate the importance of dispersal on genetic diversity patterns. While dispersal in animal species depends primarily on the movement and behaviour of individuals, for plants it can be more complex; for example, patterns of gene flow at intermediate spatial scales may reflect differences in pollen versus seed dispersal dynamics (Dick, Hardy, Jones, & Petit, 2008; Hamilton, 1999; Loveless & Hamrick, 1984).

Given the complexity of the processes that underlie species distributions at intermediate spatial scales, it is often easier to disentangle the contributions of factors influencing the spatial dynamics of species in simpler ecosystems. The ecosystems of sub-Antarctic islands provide good models for investigating evolutionary processes at intermediate scales as they typically comprise a small number of species with a simple trophic structure (Chown & Convey, 2007), and yet island landscapes are sufficiently complex to have both biotic and abiotic heterogeneity (Bergstrom & Chown, 1999). For most sub-Antarctic islands, natural colonization results from low-frequency long-distance dispersal events (Hardouin et al., 2010; Jansen van Vuuren & Chown, 2007; Kalwij, Medan, Kellermann, Greve, & Chown, 2019; Mortimer, Jansen van Vuuren, Meiklejohn, & Chown, 2012; Stevens, Greenslade, Hogg, & Sunnucks, 2006), which may act as a strong homogenizing force on intra-island genetic diversity. Long-distance dispersal also plays an important role in shaping the biogeographical patterns of the

region's indigenous flora, with more similar floras occurring on islands that are geographically closer (Greve, Gremmen, Gaston, & Chown, 2005; Shaw, Spear, Greve, & Chown, 2010; Wace, 1960). At small spatial scales (<3 km), anisotropic (i.e., directionally dependent) short-distance dispersal has been found to play a pivotal role in shaping the genetic diversity of the cushion plant *Azorella selago* on Marion Island (Born, Le Roux, Spohr, McGeoch, & Jansen van Vuuren, 2012), with the dispersal dynamics largely dependent on the direction and strength of local prevailing winds. At the intermediate, or island, scale, these patterns are more difficult to interpret. For example, studies on invertebrate species on Marion Island (Grobler, Bastos, Treasure, & Chown, 2011; McGaughan, Convey, Stevens, & Chown, 2010; Mortimer & Jansen van Vuuren, 2007; Mortimer et al., 2012; Myburgh, Chown, Daniels, & Jansen van Vuuren, 2007) have revealed complex genetic patterns, which hint at the interplay of various processes, including past glaciations, volcanic activity, persistence in refugia and barriers to dispersal by geological structures.

In this study, we focus on two congeneric keystone plant species in the sub-Antarctic, *A. selago* Hook.f. (Apiaceae) on Marion Island and *Azorella macquariensis* Orchard on Macquarie Island. Both species are low-growing, compact plants with a cushion growth form. They play an important role as pioneer species, colonizing unstable scoriaceous, gravel and peat slopes, recent lava flows, and the forelands of retreating glaciers. They are considered keystone species because they host diverse epiphyte and invertebrate communities and facilitate the occurrence of many of these species at higher elevations (Bergstrom et al., 2015; Hugo, McGeoch, Marshall, & Chown, 2004; McGeoch, Le Roux, Hugo, & Nyakaty, 2008; Le Roux & McGeoch, 2010). The structure of the small, flat, lightweight fruits suggests that they are wind-dispersed (Hausmann, McGeoch, & Boelhouwers, 2010; Orchard, 1989). Their pollination biology is unknown, but the depauperate insect community on these islands suggests that wind-pollination or selfing is likely (Chown & Marshall, 2008; Convey, 2007; Lord, 2015). *Azorella selago* is widely distributed on sub-Antarctic islands and in southern South America. On Marion Island, it is found in most vegetation types and is common from sea level to ~650 m a.s.l. (Phiri, McGeoch, & Chown, 2009). Palynological studies confirm the presence of *A. selago* at various localities across Marion Island very soon after the last glacial retreat (Schalke & Van Zinderen Bakker, 1971; Scott, 1985; Scott & Hall, 1983). Whether the species survived in one or more refugia during the Last Glacial Maximum (LGM) or whether it recolonized the island

**FIGURE 1** Geographical orientation of Marion and Macquarie islands. Topography of (a) Marion Island and (b) Macquarie Island, and (c) their locations in the Southern Ocean. The position of the Antarctic Polar Frontal Zone is indicated by the dashed line. Elevation data provided by David Hedding (University of South Africa) for Marion Island and the Australian Antarctic Division for Macquarie Island, and world coastline data provided by Natural Earth



from a source population on another sub-Antarctic island, or even from South America, remains unknown. A previous study based on a limited number of samples collected mostly from coastal sites on Marion Island revealed no genetic variation for the plastid *trnH-psbA* region, while significant structure was detected with amplified fragment length polymorphisms (Mortimer, McGeoch, Daniels, & Jansen van Vuuren, 2008). Given these contrasting results and the limited sample sizes included in their analysis, these authors stressed the need for increased sampling effort before developing conclusions about the processes that structure genetic diversity in these populations. *A. macquariensis* is endemic to Macquarie Island, where it dominates fellfield vegetation on the upland plateau but occasionally occurs at lower elevations (Bergstrom & Selkirk, 1999; Copson, 1984; Selkirk, Seppelt, & Selkirk, 1990; Taylor, 1955). It was recognized as a distinct species from *A. selago* due to differences in leaf and floral morphology (Orchard, 1989). However, this distinctiveness has been questioned (Martinez, 1993), and a recent molecular phylogeny infers a close sister relationship between *A. selago* and *A. macquariensis* (Plunkett & Nicolas, 2017).

Here we quantify and compare the spatial genetic structure of these two keystone plants across Marion and Macquarie islands. Both islands are strongly influenced by the Antarctic Circumpolar Current and its associated West-Wind Drift, but have very different geological histories and physical dimensions (Bergstrom & Chown, 1999). Marion Island is a volcanic island located in the Indian Ocean sector of the Southern Ocean and is more than 1,500 km distant from the nearest continental landmass (Figure 1a,c). Macquarie Island is located midway between Australia and Antarctica and is an

emerged oceanic crust complex (Figure 1b,c). There are major differences in the landscapes of the islands: Marion Island is roughly circular in shape, with a strong elevational gradient from its coastline to a central plateau with its highest peak reaching 1,230 m; Macquarie Island is a low-lying ribbon of land with its major axis running roughly north-south and with steep coastal slopes rising to a central undulating plateau with a maximum height of only 433 m (Figure 1). Although both islands are thought to be less than 500,000 years old (Adamson, Selkirk, Price, Ward, & Selkirk, 1996; McDougall, Verwoerd, & Chevallier, 2001; Quilty, 2007), there are notable differences in glacial histories that may translate into contrasting biogeographical histories for species found on these islands. Macquarie Island was never glaciated to any significant extent (Adamson, Selkirk, & Colhoun, 1988; Ledingham, & Pedersen, 1984). Marion Island, on the other hand, experienced intense glacial periods and was largely covered by ice during the LGM (Boelhouwers, Meiklejohn, Holness, & Hedding, 2008; Hall, 2004; Hall, Meiklejohn, & Bumby, 2011). However, ice-free areas did exist during the LGM (Hall et al., 2011) and may have acted as refugia for species.

Our aim here is to document spatial genetic patterns in *Azorella* species across two sub-Antarctic oceanic islands, and to place our results within the abiotic setting of these islands. We extensively sampled *Azorella* across Marion and Macquarie Islands, and present the first molecular ecology results for any organism on Macquarie Island. Using genotypic data from highly informative microsatellite markers, our aims were to: (a) assess spatial patterns in genetic diversity, genetic differentiation, spatial genetic structure and

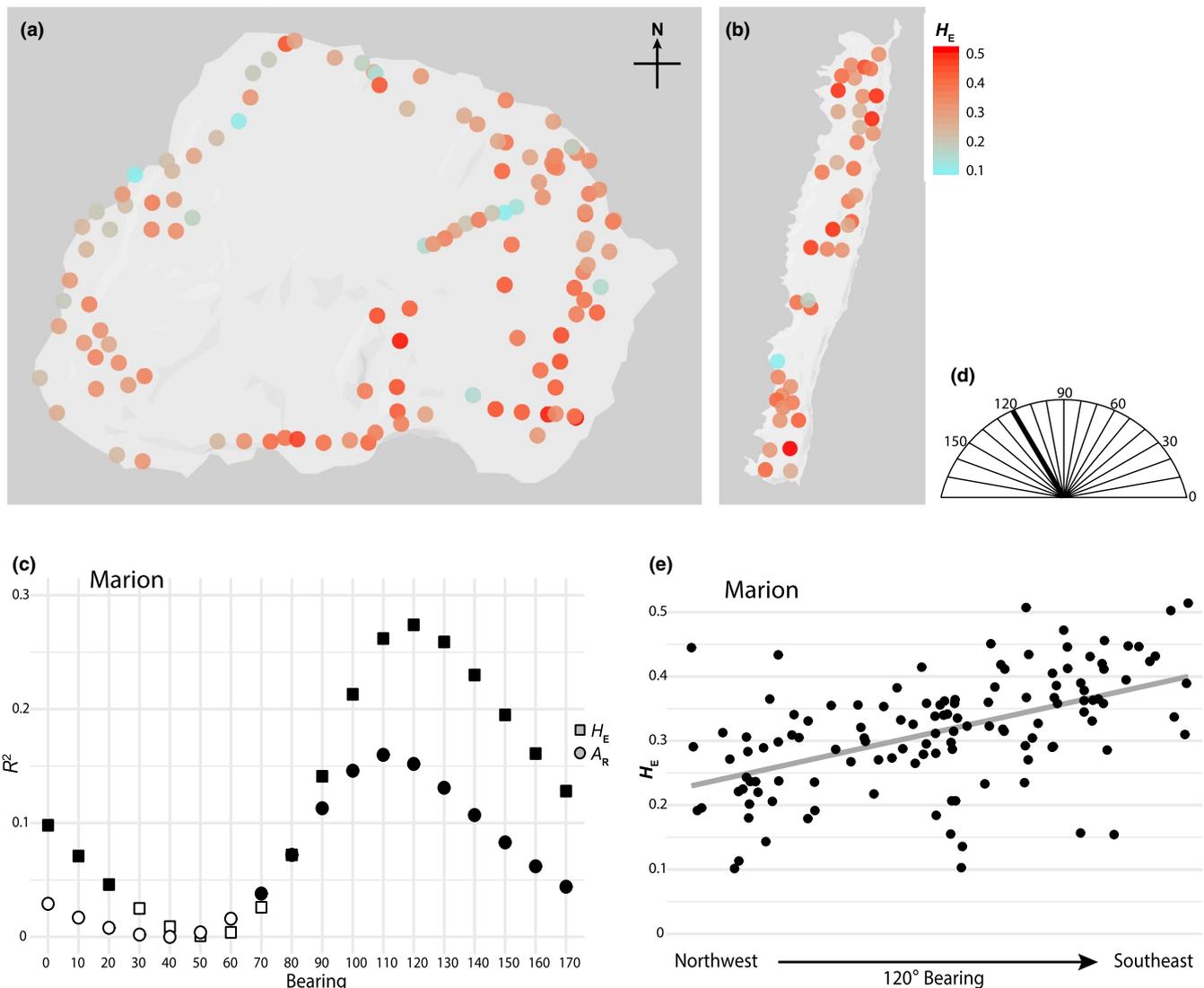
demographic change in *Azorella* on the two islands; and (b) evaluate interactions of these genetic patterns with current and historical factors, including wind patterns, topography, glaciation history, elevation and vegetation type.

## 2 | MATERIALS AND METHODS

### 2.1 | Study system

Marion Island (46.9°S, 37.8°E) is part of the Prince Edward Island archipelago along with the smaller Prince Edward Island, and is situated within the Polar Frontal Zone of the Antarctic Circumpolar

Current (Figure 1). Roughly elliptical in shape, with the longer axis oriented east-west, Marion Island is 290 km<sup>2</sup> in area, with coastal plains, ridges and valleys surrounding central highlands (Chown, Gremmen, & Gaston, 1998; Hänel & Chown, 1998). The climate on Marion Island is hyperoceanic, characterized by low but stable temperatures (mean temperature ~6°C, mean daily temperature range <3°C, mean seasonal temperature range ~4°C), high precipitation (2,000–3,000 mm annually) and humidity (~80%), and near complete cloud cover on most days (Rouault, Mélice, Reason, & Lutjeharms, 2005; Le Roux, 2008). The dominant wind direction is from the west, as expected from the island's location in a belt of strong large-scale westerly atmospheric circulation. Northwesterly winds are, on



**FIGURE 2** Sampling sites and genetic diversity of *Azorella selago* on Marion Island and *Azorella macquariensis* on Macquarie Island. Location and expected heterozygosity ( $H_E$ ) of sampling sites on (a) Marion Island and (b) Macquarie Island. (c) For Marion Island, values of  $R^2$  from linear regressions between  $H_E$  or  $A_R$  (number of alleles adjusted by rarefaction to 10 samples per site) and measures of site position transformed by directional bearings. Filled symbols indicate bearings with a significant correlation ( $p < .05$ ). Site positions were transformed using the equation:  $L = x(\cos \theta) - y(\sin \theta)$ , where  $x$  and  $y$  correspond to the longitude and latitude of each site, respectively, and  $\theta$  corresponds to (d) 18 fixed bearings from 0° to 170° at 10° intervals, with 0° corresponding to the east-west direction. The 120° bearing is highlighted. (e) For Marion Island, for the 120° bearing, which had the highest  $R^2$  value, scatterplot showing the correlation between  $H_E$  and transformed measures of site position, and regression line [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

average, the strongest (>10 m/s) followed by south-westerly winds (7 m/s) (Rouault et al., 2005; Le Roux, 2008). The island frequently experiences gale force winds (>15 m/s). Marion Island's terrestrial vegetation has been classified into various types including coastal vegetation, biotic herbfield, mire, drainage line and fernbrake vegetation in lowlands, and fellfield and polar desert at higher elevations (Gremmen & Smith, 2008; Huntley, 1971; Smith & Mucina, 2006). *Azorella selago* occurs in most vegetation types and is common from sea level to ~670 m a.s.l. (Phiri et al., 2009).

Macquarie Island (54.6°S, 158.9°E) is about 1,000 km southwest of New Zealand and is situated to the north of the Polar Frontal Zone (Figure 1). It forms a narrow rectangle, +34 km long and 5 km wide, with the long axis oriented nearly north-south. The island is 128 km<sup>2</sup> in area and consists mostly of a plateau which rises from 150 to 433 m a.s.l. (Chown et al., 1998; Selkirk et al., 1990). Like Marion Island, the climate is hyperoceanic, characterized by low but stable temperatures (mean ~ 6°C, mean daily range ~3.5°C, mean seasonal range ~3.2°C), moderate precipitation (958 mm annually), high humidity (~80%) and near complete cloud cover on most days. Over two-thirds of winds are from a direction between west (~10 m/s) and northwest (~9 m/s), and gale force winds occur often (Adams, 2009; McGlone, 2002). The vegetation has been classified into grassland, herbfield, mire, fernbrake and feldmark (fellfield), with grassland and feldmark dominating the plateau uplands (Selkirk et al., 1990; Taylor, 1955). *Azorella macquariensis* is mostly found on the plateau at 200–400 m a.s.l. altitude (Bricher, Lucieer, Shaw, Terauds, & Bergstrom, 2013; Selkirk et al., 1990), but occasionally occurs at lower elevations, usually as isolated cushions. The species is the dominant vascular species in feldmark habitats on Macquarie Island (Bergstrom & Selkirk, 1999; Copson, 1984; Taylor, 1955).

## 2.2 | Sampling

Leaf samples of *A. selago* were taken from multiple individuals at sites across Marion Island (1,149 individuals from 123 sites) (Figure 2a), and leaf samples of *A. macquariensis* were taken from multiple individuals at sites across Macquarie Island (372 individuals from 42 sites) (Figure 2b). Sites were sampled opportunistically to cover the species' distributions across each island and span their elevational ranges. Geographical position and elevation of each collection site were recorded with a Garmin eTrex Vista or Trimble Differential GPS unit. Leaf samples were dried and conserved on silica gel.

## 2.3 | DNA extraction, genotyping and data quality control

Total genomic DNA was extracted using a NucleoSpin Plant II DNA extraction kit (Macherey-Nagel). Samples were genotyped using six species-specific microsatellite markers: azo5, azo6, azo11, azo13, azo17 and azo23 (Molecular Ecology Resources Primer Development, 2010). Of the eight polymorphic markers originally described, two (azo14 and azo21) were excluded from analyses after a preliminary

study showed they may present null alleles. Markers were amplified following the protocol of Cerfonteyn, Le Roux, Jansen van Vuuren, and Born (2011). Genotyping was performed on an ABI 3730 automated sequencer (Applied Biosystems) using the GS500LIZ size standard (Applied Biosystems).

Scoring was done using GENEMAPPER 3.7 (Applied Biosystems), and the full data set was double-scored by two people. Genotyping errors, including null alleles, stuttering and large allele dropout, were estimated with MICRO-CHECKER version 2.2.3 (Van Oosterhout, Hutchinson, Wills, & Shipley, 2004). We tested for departure from Hardy-Weinberg equilibrium and for linkage disequilibrium between all pairs of loci using exact tests in GENEPOP 4.7 (Rousset, 2008). In addition, we assessed the informativeness of our microsatellite data set by calculating probabilities of identity, a measure of a marker's ability to distinguish individuals, in GENALEX 6.5 (Peakall & Smouse, 2012).

## 2.4 | Genetic diversity

We calculated the number of alleles per locus ( $A$ ), observed heterozygosity ( $H_O$ ), expected heterozygosity ( $H_E$ ) and inbreeding index ( $F_{IS}$ ) for each site using GENALEX 6.5 (Peakall & Smouse, 2012). We also calculated the number of alleles per locus accounting for sample size variation among sites using rarefaction ( $A_R$ ) in HP-RARE 1.1 (Kalinowski, 2005). To determine if these measures were significantly different between islands, Welch t-tests were performed in R version 3.5.1 (R Core Team, 2018).

We assessed whether genetic diversity ( $H_E$ ) was correlated with elevation and/or vegetation type as these have been shown to affect the population density of *Azorella* on sub-Antarctic islands (Phiri et al., 2009). We superimposed our sampled sites on the vegetation map of Smith and Mucina (2006) to determine the vegetation type (coastal, mire-slope, fellfield or polar desert) of each site on Marion Island. We did not test for effects of vegetation type on Macquarie Island as *Azorella* is typically associated only with fellfield vegetation there. We used TOROCOR 1.0 (Hardy, 2009) to determine if variables displayed spatial autocorrelation and quantified it using Moran's  $I$  statistic for quantitative variables (elevation and  $H_E$ ) or its equivalent for categorical variables (vegetation type) (Hardy, 2009). Each variable was tested using complete randomizations (9,999 permutations among samples). The association between elevation and  $H_E$  was quantified by Pearson's correlation coefficient, and the association between vegetation type and  $H_E$  by an intraclass correlation coefficient. To account for spatial autocorrelation, associations between  $H_E$  and environmental variables were tested using torus-translation randomizations (9,999 permutations) on Marion Island, and associations between  $H_E$  and elevation using complete randomization (9,999 permutations) on Macquarie Island (Harms, Condit, Hubbell, & Foster, 2001). To perform torus-translation randomizations, sites were positioned onto eight equal spatial grids, and within each grid sites were located within one to nine transects depending on the number of sites per grid.

We also assessed whether genetic diversity showed spatial clines with directional bearings on each island. Site positions were transformed using the equation:  $L = x(\cos \theta) - y(\sin \theta)$ , where  $x$  and  $y$  correspond to the longitude and latitude of the site in UTM, respectively, and  $\theta$  corresponds to 18 fixed bearings from  $0^\circ$  to  $170^\circ$  at  $10^\circ$  intervals, with  $0^\circ$  corresponding to the east–west orientation (Figure 2d). Correlations between transformed measures of site position for each bearing and  $H_E$  or  $A_R$  were calculated using linear regression in MICROSOFT EXCEL 2013. To determine the direction of the cline, we assessed which bearings were associated with a significant correlation ( $p < .05$ ) and which had the highest determination coefficient ( $R^2$ ).

## 2.5 | Genetic differentiation

We examined the partitioning of genetic variation among and within sites and individuals for each island separately by performing analyses of molecular variance (AMOVAs) with 1,000 permutations in ARLEQUIN version 3.5.2.2 (Excoffier & Lischer, 2010). For each island, we also calculated pairwise  $F_{ST}$  between sites, with 999 permutations to assess significance, using GENALEX 6.5 (Peakall & Smouse, 2012).

## 2.6 | Spatial genetic structure

We assessed spatial genetic structure (SGS) on each island following the procedure of Vekemans and Hardy (2004) as implemented in the software SPAGED1 1.3 (Hardy & Vekemans, 2002). Given limited dispersal, genetic differentiation between sites is expected to increase with the spatial distance between them (Hardy & Vekemans, 1999; Rousset, 1997; Vekemans & Hardy, 2004). To assess the spatial genetic structure, values of  $F_{ST}/(1 - F_{ST})$  between sites, a measure of genetic differentiation, were regressed on the natural logarithm of the spatial distance between sites ( $\ln(d_{ij})$ ) to get the regression slope ( $b_{Ld}$ ). To test the significance of the observed spatial genetic structure values, spatial positions of individuals were permuted 9,999 times to obtain the frequency distribution of  $b_{Ld}$  under the null hypothesis that pairwise  $F_{ST}/(1 - F_{ST})$  and  $\ln(d)$  are uncorrelated. To visualize the spatial structure, pairwise  $F_{ST}/(1 - F_{ST})$  values were averaged over a set of distance intervals ( $d$ : 0–1, 1–2, 2–3, 3–4, 4–5, 5–6, 6–7, 7–8, 8–9, 9–10, 10–12.5, 12.5–15, 15–17.5, 17.5–20, 20–25, 25–35 km) and plotted against mean spatial distance in each distance interval.

Bearing analyses were also performed to test for the presence of directional patterns in the spatial genetic structure relationship (Falsetti & Sokal, 1993). A positive correlation coefficient ( $r$ ) between  $F_{ST}/(1 - F_{ST})$  and spatial distance was shown for those bearings ( $\theta$ ) where gene flow in the direction of the bearing is weak (Born et al., 2012). For this analysis, the matrix ( $D$ ) of the natural logarithms of spatial distances between each pair of sites ( $\ln(d_{ij})$ ) was transformed into 18 new matrices ( $D_0$  to  $D_{170}$ ) by weighting each distance by the squared cosine of the angle  $\alpha_{ij}$  (the arc between the vector connecting sites  $i$  and  $j$  and a reference vector [ $\theta = 0^\circ$  to  $170^\circ$ ,

at  $10^\circ$  intervals rotated anticlockwise, with  $0^\circ$  indicating the east–west direction]). This transformation weights each spatial distance by its alignment with a test direction. Regressions between a data matrix of values of  $F_{ST}/(1 - F_{ST})$  between sites and  $D_0$  to  $D_{170}$  matrices were evaluated via Mantel tests with significance determined by permutation tests using PASSAGE 2 (Rosenberg, 2000; Rosenberg & Anderson, 2011).

## 2.7 | Demographic change

We tested for evidence of recent population expansion and reduction at each site using the Wilcoxon signed rank test for heterozygosity deficiency and heterozygosity excess, respectively (Cornuet & Luikart, 1996; Girod, Vitalis, Leblois, & Fréville, 2011). We performed tests in the program BOTTLENECK 1.2.02 (Piry, Luikart, & Cornuet, 1999) under the one-step stepwise mutation model (SMM) and infinite allele model (IAM) and with 1,000 replicates.

## 3 | RESULTS

### 3.1 | Data

For Marion Island, the final data set comprised 1,149 individuals from 123 sites (7–10 individuals per site; mean: 9.34) genotyped for six microsatellite (simple sequence repeat [SSR]) markers. For Macquarie Island, the final data set comprised 372 individuals from 42 sites (6–15 individuals per site; mean: 8.86) genotyped for five microsatellite (SSR) markers (Figure 2a,b; Tables S1 and S2). Marker *azo13* was excluded from the data set for Macquarie Island because it displayed a high proportion of null alleles. The genomes of members of the genus *Azorella* are highly conserved, and relatively few polymorphic markers were found for *Azorella* (Molecular Ecology Resources Primer Development, 2010). However, the microsatellites used here were all highly informative and reliable for distinguishing individuals as estimated by probabilities of identity ( $p < .05$ ). Allele frequencies at most sites on Marion and Macquarie islands conform to those expected under Hardy–Weinberg equilibrium, with only six sites on Marion and nine sites on Macquarie showing significant departures from Hardy–Weinberg equilibrium across loci. No significant linkage disequilibrium between loci across populations was detected for either species.

### 3.2 | Genetic diversity and its spatial attributes

The number of alleles per locus ranged from two to 13 for *Azorella se-lago* on Marion Island, and from 5 to 11 for *Azorella macquariensis* on Macquarie Island (Table 1). Mean values of genetic diversity measures ( $A$ ,  $A_R$ ,  $H_O$  and  $H_E$ ) for each island are presented in Table 2 and for each site in Table S1. Expected heterozygosity ranged from .102 to .514 on Marion Island (mean  $\pm$  SD = .315  $\pm$  .089) and from .167 to .511 on Macquarie Island (mean  $\pm$  SD = .377  $\pm$  .073). Mean values of  $A$ ,  $A_R$ ,  $H_O$  and  $H_E$  were slightly but significantly higher ( $p < .05$ ) for sites

**TABLE 1** Genotypic characteristics of microsatellite loci for *Azorella selago* on Marion Island and *Azorella macquariensis* on Macquarie Island

Locus	Marion				Macquarie			
	Total A	Mean A per site (range)	Mean $H_O$	Mean $H_E$	Total A	Mean A per site (range)	Mean $H_O$	Mean $H_E$
azo5	13	2.98 (1-6)	.38	.37	6	3.05 (1-5)	.45	.44
azo6	10	3.31 (1-7)	.39	.40	11	4.57 (2-8)	.70	.64
azo11	10	2.54 (1-5)	.58	.46	5	1.55 (1-3)	.05	.10
azo17	5	1.79 (1-3)	.15	.15	5	2.24 (1-3)	.32	.31
azo23	6	1.72 (1-3)	.14	.13	8	3.00 (1-5)	.39	.40
azo13	2	1.97 (1-2)	.39	.38	—	—	—	—

Abbreviations: A, number of alleles;  $H_O$ , observed heterozygosity;  $H_E$ , expected heterozygosity.

on Macquarie Island than Marion Island. Very few sites on either of these islands displayed inbreeding, with the inbreeding index ranging from  $-0.556$  to  $0.362$  on Marion Island (mean  $\pm$  SD =  $-0.071 \pm 0.155$ ) and from  $-0.358$  to  $0.522$  on Macquarie Island (mean  $\pm$  SD =  $-0.003 \pm 0.214$ ) (Table 2; Table S1).

To assess the level of correlation between genetic diversity and the environmental variables, elevation and vegetation type, we performed correlation tests after correcting for spatial autocorrelation within variables. On Marion Island,  $H_E$ , elevation and vegetation type were significantly spatially autocorrelated, with the regression slopes for  $H_E$  =  $-0.024$  ( $p < .01$ ), elevation =  $-0.010$  ( $p < .01$ ) and vegetation type =  $-0.007$  ( $p < .01$ ). No significant associations were found between  $H_E$  and elevation or vegetation type. Pearson's correlation coefficient between  $H_E$  and elevation was  $0.122$  ( $p > .05$ ), and intraclass correlation coefficient between  $H_E$  and vegetation type was  $0.047$  ( $p > .05$ ). On Macquarie Island, only elevation was found to be significantly spatially autocorrelated, with the regression slope =  $-0.009$  ( $p < .01$ ). No significant correlation was found between  $H_E$  and elevation ( $r = 0.099$ ,  $p > .05$ ).

We assessed whether variation in genetic diversity has a directional orientation. For *A. selago* on Marion Island,  $H_E$  values correlated significantly with transformed site position values for bearings  $0^\circ$ – $20^\circ$  and  $80^\circ$ – $170^\circ$  ( $p < .05$ ), for which  $R^2$  values ranged from  $0.05$  to  $0.27$ .  $A_R$  values correlated significantly with transformed site position values for bearings  $70^\circ$ – $170^\circ$  ( $p < .05$ ), for which  $R^2$  values ranged from  $0.04$  to  $0.16$ . For both  $H_E$  and  $A_R$ , the strength of the regressions followed a periodic function against compass direction, with the highest  $R^2$  value associated with the bearing  $120^\circ$  for  $H_E$  and  $110^\circ$  for  $A_R$  (Figure 2a,c; Table S3). These bearings indicate a cline in genetic diversity along the northwest–southeast direction, with  $H_E$  and  $A_R$  increasing towards the southeast (Figure 2e). For *A. macquariensis* on Macquarie Island, no bearing presented a significant correlation between  $H_E$  or  $A_R$  and transformed site position values ( $p > .05$ ), indicating the absence of a cline along any directional bearing (Figure 2b; Table S3).

### 3.3 | Genetic differentiation

Analyses of molecular variance indicated that the vast majority of genetic variation was within individuals (Marion: 93.5%, Macquarie: 86.0%), with a much smaller yet significant portion found between sites (Marion: 7.6%, Macquarie: 10.6%;  $p = .001$ ) (Table 3). On Marion Island, pairwise  $F_{ST}$  values ranged from 0 to  $0.399$  (mean  $\pm$  SD =  $0.073 \pm 0.067$ ). For individual sites, the proportion of pairwise  $F_{ST}$  values that were significant ( $p < .05$ ) varied from  $0.139$  to  $0.984$  (mean  $\pm$  SD =  $0.493 \pm 0.202$ ) (Table S1), but there was no apparent spatial pattern in the location of sites with particularly high or low proportions of significant pairwise  $F_{ST}$  values (Figure S1a). On Macquarie Island, pairwise  $F_{ST}$  values ranged from 0 to  $0.471$  (mean  $\pm$  SD =  $0.104 \pm 0.085$ ). For an individual site, the proportion of pairwise  $F_{ST}$  values that were significant varied from  $0.317$  to 1 (mean  $\pm$  SD =  $0.653 \pm 0.189$ ) (Table S1), but again we did not detect any apparent spatial pattern in the variation (Figure S1b).

### 3.4 | Spatial genetic structure

For *A. selago* on Marion Island, a significant positive relationship was found between  $F_{ST}/(1 - F_{ST})$  and the distance between sites (i.e., isolation-by-distance [IBD]), with the regression slope  $b_{Ld} = 0.021$  ( $p < .001$ ). In contrast, for *A. macquariensis* on Macquarie Island, no significant IBD was found, with  $b_{Ld} = -0.004$  ( $p = .81$ ) (Figure 3).

To determine whether the spatial genetic structure has a directional component, we performed SGS analyses after transforming distance matrices for different bearings. On Marion Island, SGS analyses with bearing transformations revealed positive and significant relationships between the matrix of  $F_{ST}/(1 - F_{ST})$  values and  $D_{0^\circ}$ ,  $D_{10^\circ}$  and  $D_{100^\circ}$ – $D_{170^\circ}$  spatial distance matrices ( $p < .01$ ) (Figure 4a). On Macquarie Island, bearing analyses detected positive and significant relationships between the genetic distance matrix and  $D_{100^\circ}$ – $D_{120^\circ}$  matrices ( $p < .05$ ) (Figure 4b). This indicates that there is a positive relationship between genetic differentiation between sites and

**TABLE 2** Sampling and genotypic characteristics for *Azorella selago* on Marion Island using six microsatellite loci and *Azorella macquariensis* on Macquarie Island using five microsatellite loci

Island	S	Total N	N	A	A <sub>R</sub>	H <sub>O</sub>	H <sub>E</sub>	F <sub>IS</sub>	Global F <sub>ST</sub>	Pairwise F <sub>ST</sub>
Marion	123	1,149	9,341 (7–10)	2,382 (1.33–3.33)	2,078 (1.27–2.72)	.338 (.08–.58)	.315 (.10–.51)	–.071 (–.56–.36)	.076	.073 (0–.399)
Macquarie	42	372	8,857 (6–15)	2,881 (1.60–3.40)	2,502 (1.53–3.11)	.384 (.18–.63)	.377 (.17–.51)	–.003 (–.36–.52)	.106	.104 (0–.471)

Notes: Mean values and ranges across loci per site are shown for N, A, A<sub>R</sub>, H<sub>O</sub>, H<sub>E</sub>, F<sub>IS</sub>, and pairwise F<sub>ST</sub>.

Abbreviations: A, number of alleles; A<sub>R</sub>, number of alleles, adjusted by rarefaction to 10 samples per site; F<sub>IS</sub>, fixation index/inbreeding coefficient; H<sub>E</sub>, expected heterozygosity; H<sub>O</sub>, observed heterozygosity; N, number of individuals sampled per site; S, number of sites; total N, total number of individuals sampled.

distance between sites generally in the northwest–southeast direction on both islands.

### 3.5 | Demographic change

Multiple sites on both Marion and Macquarie islands showed a signal of population expansion, as characterized by a significant deficiency in heterozygosity ( $p < .05$ ). On Marion Island, these sites were concentrated in the west and north of the island, with 24 sites showing significant heterozygosity deficiency under the SMM model and six sites under the IAM model (Figure 5a; Figure S2a). On Macquarie Island, eight sites under the SMM model and six sites under the IAM model showed significant heterozygosity deficiency, mostly in two groups in the north and central part of the island (Figure 5b; Figure S2b). A few sites on Marion Island, mostly in the southeast, showed a signal of population bottleneck, as characterized by a significant excess in heterozygosity ( $p < .05$ ) (Figure 5a; Figure S2a). No sites on Macquarie Island displayed a signal of population bottleneck under the SMM model, but there were four sites in the northern half of the island under the IAM model (Figure S2b).

## 4 | DISCUSSION

The different spatial genetic patterns recovered for *Azorella selago* on Marion Island (distinct northwest–southeast gradient in both genetic diversity, genetic structure and signatures of demographic change) and *Azorella macquariensis* on Macquarie Island (no spatial gradient in genetic diversity or demographic change but spatial genetic structure in a narrow northwest–southeast direction) may be attributed to several mechanisms: asymmetric dispersal caused by dominant northwesterly winds across the specific landscapes of the islands, history of glaciation or lack thereof, and environmental differences between the western and eastern sides of the islands (perhaps more pronounced for Marion compared to Macquarie). Also, for Marion Island specifically, the arrival of long-distance migrants in the southeast leeward side of the island may have contributed to the spatial patterns. These factors are not mutually exclusive, and are discussed in more detail below.

### 4.1 | Spatial genetic patterns

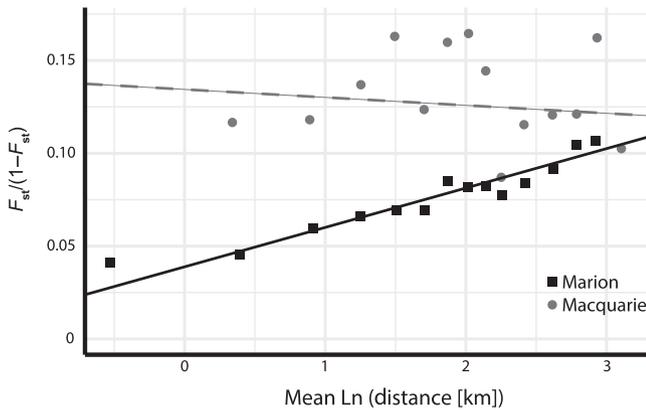
A strong spatial signal was detected in the patterns of genetic variation of *Azorella* on Marion Island, with the southeast portion of the island being generally distinct from the rest of the island. These southeastern sites had higher genetic diversity and were more likely to show evidence of population bottlenecks, whereas sites across the rest of the island had lower genetic diversity and were more likely to show signals of population expansion. SGS analyses detected significant IBD on Marion Island, suggesting that dispersal across the island may be limited and that the highest gene flow predominantly occurs between neighbouring sites.

To date, island-wide genetic studies on Marion Island have mostly focused on terrestrial microarthropods, with complex patterns and

**TABLE 3** Partition of genetic variation by analysis of molecular variance (AMOVA) for *Azorella selago* on Marion Island and *Azorella macquariensis* on Macquarie Island ( $p = .001$ )

Marion			Macquarie		
Source of variation	df	vc (%)	Source of variation	df	vc (%)
Between sites	122	7.59	Between sites	41	10.56
Between individuals within sites	1,026	-1.04	Between individuals within sites	330	3.34
Within individuals	1,149	93.45	Within individuals	372	86.09
Total	2,297	100	Total	743	100

Abbreviations: df, degrees of freedom; vc, variance component.

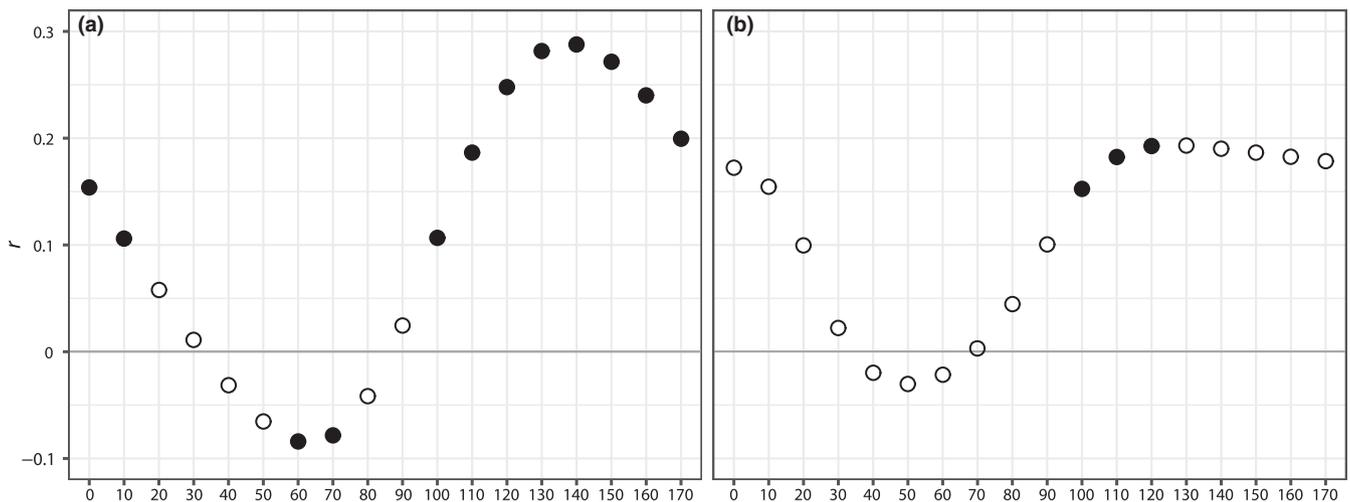


**FIGURE 3** Spatial genetic structure, or isolation-by-distance, in *Azorella selago* on Marion Island and *Azorella macquariensis* on Macquarie Island. Mean values of  $F_{ST}/(1 - F_{ST})$  in different distance classes between sites (mean distances plotted) for Marion Island and Macquarie Island, and regression lines. Only distance classes with greater than 50% of sites represented are shown (all except 20–25 and 25–35 km for Marion Island and 0–1 and 25–35 km for Macquarie Island)

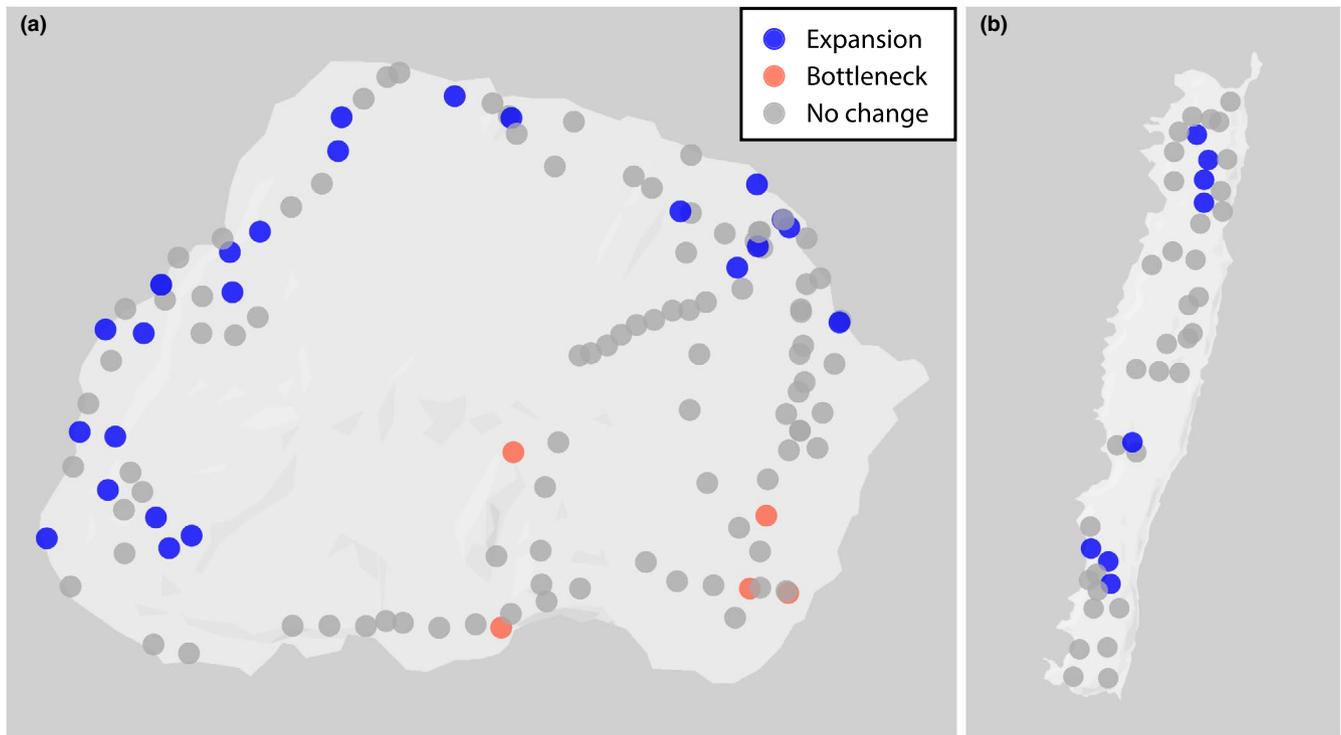
significant spatial structure linked to high genetic diversity being reported for weevils, springtails and mites (see Grobler, Janse van Rensburg, Bastos, Chimimba, & Chown, 2006; McGaughan et al.,

2010; Mortimer et al., 2012; Myburgh et al., 2007). Although we do not detect such complex patterns for *A. selago*, one striking similarity with previous work is the noticeable difference between the western and eastern parts of Marion Island, in part driven by climatic differences. However, the exact mechanisms behind the contrasting levels of spatial complexity and genetic diversity between *Azorella* and arthropods remain unclear and speculative. Possible contributors include faster rates of molecular evolution in arthropods compared to *Azorella*, differences in mode of dispersal including active movement in arthropods compared to passive movement in *Azorella*, differences in range size and habitat specificity, and possible occurrence of self-pollination in *Azorella* versus the dominance of outcrossing in arthropods.

In the first molecular ecology study of any organism on Macquarie Island, we found no strong spatial genetic pattern for *A. macquariensis*, with an absence of clinal patterns in genetic diversity. When we included spatial orientation in our SGS analyses, only a small number of bearings in a northwest-southeast direction showed signal of IBD, indicating the influence of the strong westerly winds. Although some sites displayed signals of population expansion, these sites were scattered in several groups around the island, and probably reflect local catastrophic events and organismal responses rather than general trends across the island.



**FIGURE 4** Direction-dependent spatial genetic structure in *Azorella selago* on Marion Island and *Azorella macquariensis* on Macquarie Island. Values of the correlation coefficient  $r$  from linear regressions between  $F_{ST}/(1 - F_{ST})$  and transformed distance matrices that account for directional bearings for (a) Marion Island and (b) Macquarie Island. Distance matrices were transformed for bearings from 0° to 170° at 10° intervals, with 0° corresponding to the east-west direction. Filled symbols indicate bearings with a significant correlation ( $p < .05$ )



**FIGURE 5** Demographic change in sites of *Azorella selago* on Marion Island and *Azorella macquariensis* on Macquarie Island. Sites with significant heterozygosity deficiency or heterozygosity excess, evidence for recent population expansion or bottleneck, respectively, inferred under the stepwise mutation model (SMM) for (a) Marion Island and (b) Macquarie Island [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

#### 4.2 | Contemporary influences on spatial genetic patterns: Shape of the island and wind

While Marion and Macquarie islands experience similar climates, including strong winds experienced for the majority of the time from northwesterly (Adams, 2009; Le Roux, 2008; Schulze, 1971; Selkirk et al., 1990), the islands differ markedly in shape and topography. Wind and wind direction, in conjunction with island shape, probably play a major role in driving spatial genetic patterns in *Azorella*. For *A. selago* on the circular-shaped Marion Island, there is a strong clinal component to the distribution of genetic diversity, with increasing heterozygosity and allelic richness following a northwest–southeast gradient, which corresponds to the prevailing wind direction. Dispersal is clearly one of the most important factors driving spatial structure in this species, with IBD also detected in a northwest–southeast direction. Dominant wind in one direction can cause asymmetric gene flow so that sites located downwind accumulate alleles dispersed from elsewhere, and thus harbour higher levels of genetic diversity compared with sites upwind. Consistent with this expectation, *A. selago* populations in the southeast of Marion Island have the highest levels of genetic diversity. Similar patterns of genetic accumulation have been reported for plants and invertebrates that are unidirectionally dispersed via waterways, with downstream populations typically containing higher genetic diversity than their upstream counterparts (Alp, Keller, Westram, & Robinson, 2012; Kikuchi, Suzuki, & Sashimura, 2011). To the best of our knowledge, this has not yet been demonstrated for wind-dispersed species.

Our finding at the island scale closely corroborate those reported by Born et al. (2012) for *Azorella* at small spatial scales (tens to hundreds of metres), who found that directional dispersal associated with wind patterns is a principal factor in determining fine-scale population genetic structure. They found IBD to be weaker between sites experiencing stronger winds, often weakest in the direction of the prevailing winds, presumably because of greater wind dispersal; and the bearing with the weakest signal of IBD varied between sites, possibly due to differences in the dominant wind direction caused by local turbulence and topography. The impact of such local, fine-scale processes on island-scale patterns remains unclear and deserves further study.

In contrast to Marion Island, we did not find a strong directional cline in genetic diversity for *A. macquariensis* on Macquarie Island. This finding may also be the consequence of the prevailing wind interacting with the elongate shape of the island. Macquarie Island is a narrow rectangle (~34 × 5 km), with the short axis oriented WNW–ESE, in line with the direction of the prevailing winds (Selkirk et al., 1990). The short distance between the western and eastern edges of the island may not be sufficient for the development of an obvious cline.

#### 4.3 | Historical influences on spatial genetic patterns: Glaciation history and refugia

Although the shape of the islands linked to prevailing winds probably plays a major role in shaping spatial genetic diversity of *Azorella* species on Marion and Macquarie islands, we cannot rule out possible

contributions from the geological history of the islands. Marion Island has experienced at least five episodes of glaciation during the Late Quaternary (McDougall et al., 2001). The extent of glaciation during the LGM (~35–11,000 years before present) is uncertain, but it is believed to have been widespread and covered almost the entire island (Boelhouwers et al., 2008; Hall, 2004; Hall et al., 2011). Several prominent areas on the island, however, lack evidence of glaciation and may have served as ice-free refugia; these sites are largely coastal (Boelhouwers et al., 2008). Palynological studies indicate that the same plants found on Marion Island today, including *Azorella*, were present during interglacial periods (Schalke & Van Zinderen Bakker, 1971; Scott, 1985; Scott & Hall, 1983). It is therefore conceivable that refugia played an important role in the survival and persistence of the island's flora during glaciations, although repeated recolonization via long-distance dispersal from other source areas after deglaciation is also possible (Van der Putten, Verbruggen, Ochyra, Verleyen, & Frenot, 2010).

Spatial genetic patterns in *A. selago* on Marion Island are consistent with a history of survival in a southeast refugium during glacial periods (see Mortimer et al., 2012 for similar suggestions for the mite *Halozetes fulvus*). Genetic diversity, measured as expected heterozygosity and allelic richness, is highest in the southeast, where the Feldmark Plateau, a refugial area during the LGM, is located (Boelhouwers et al., 2008). From the southeast, colonization of the rest of the island could have occurred after glacial retreat via consecutive founder events, which would result in lower genetic diversity along the direction of population expansion. Similar patterns of higher genetic diversity in glacial refugia are frequently observed on the Eurasian and North American continents (Conroy & Cook, 2000; Widmer & Lexer, 2001). We also found evidence for population expansion in sites outside the southeast, which is consistent with recent colonization of those areas, although the exact timing of these demographic changes is uncertain.

On Macquarie Island, recent interpretation of geomorphological evidence suggests that glaciation was very limited (Hodgson et al., 2014; McGlone, 2002; Selkirk et al., 1990). Detailed palynological studies, which include records of *Azorella*, extend back only 7,000–9,000 years (Bergstrom, Stewart, Selkirk, & Schmidt, 2002; McGlone, 2002; Selkirk, Selkirk, Bergstrom, & Adamson, 1988), so the composition of the flora during Pleistocene glacial periods is unknown. The lack of spatial genetic structure in *A. macquariensis* on Macquarie Island is consistent with its persistence across the island throughout the Late Quaternary. The higher genetic diversity in *A. macquariensis* on Macquarie Island compared to *A. selago* on Marion Island may also be due to the persistence of a larger population on Macquarie Island throughout this period.

#### 4.4 | Other contemporary influences on spatial genetic patterns: Long-distance dispersal and ecological drivers

Another important consideration is that the area of arrival and initial colonization of long-distance migrants carried by wind to sub-Antarctic islands may not be random. Chown and Avenant (1992)

theorized that for small organisms and in areas with high winds, settling out of the air column is most likely to occur on the leeward side of the island due to turbulence created by higher topography in the island's centre. On sub-Antarctic islands, the leeward side is typically in the southeast. In support of this hypothesis, several recent natural introductions to sub-Antarctic islands were initially discovered in the leeward side of islands, including the moth *Plutella xylostella* on Marion Island and several insects on Île aux Cochons in the Crozet archipelago (Chown & Avenant, 1992). In several arthropod species on Marion Island, sites in the southeast were genetically significantly different from others, which might be due to the arrival of wind-borne individuals from outside the island to that area (Myburgh et al., 2007). On Macquarie Island, several long-distance insect migrants were detected on the eastern side of the island, although this pattern could also have resulted from nonrandom sampling by researchers (Greenslade, Farrow, & Smith, 1999). The spatial genetic pattern of *A. selago* on Marion Island, with higher genetic diversity in the southeast, is consistent with the arrival of long-distance immigrants in the southeast of the island.

Environmental heterogeneity greatly influences dispersal patterns, as dispersal alone is not a reliable indicator of potential range expansion or occupancy given that propagules need to encounter favourable habitats to settle in. Both Marion and Macquarie islands have local climate variability. For Marion Island, climatic differences are found along an east-west gradient as well as an altitudinal gradient (Le Roux, 2008), while for Macquarie Island, these are present but perhaps not as pronounced (Davies & Melbourne, 1999; Selkirk et al., 1990). On Marion Island, it has been reported that many ecological traits, including plant size, leaf size, trichome density and stomatal density, are more strongly associated with island side (i.e., leeward vs. windward) than elevation (McGeoch et al., 2008; Nyakatya, 2006). Differences in climate with island side, for example in precipitation, solar radiation and wind intensity (Nyakatya & McGeoch, 2008; Rouault et al., 2005; Le Roux, 2008; Schulze, 1971), rather than with elevation, may result in stronger effects on these species' traits (Nyakatya, 2006). In line with this, we did not find any significant correlations between genetic diversity and elevation, or with vegetation type. We did not expect to detect any signatures of adaptation given the neutral markers that we used here. However, it is imperative that future studies should focus on identifying areas of ecological importance. This is especially important in the face of a rapidly changing climate (Rouault et al., 2005) and the possibility of species only surviving change in local microrefugia into the future.

## 5 | CONCLUSIONS

Species ranges are dynamic, altered by environmental and evolutionary change and dispersal dynamics. On islands, ranges are constrained by the scale of the island and the availability of suitable habitat, and the spatial distribution of genetic variation becomes

especially important for evolutionary and ecological processes. In our study of keystone *Azorella* species on sub-Antarctic islands, we found that local climate, specifically wind patterns, in interaction with island shape, as well as historical patterns of population persistence, probably control dispersal and thus spatial patterns in genetic diversity and structure. These findings can help inform the management and conservation of biological diversity on these unique polar ecosystems, especially in the face of rapidly changing environments.

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## AUTHOR CONTRIBUTIONS

C.B., M.A.M. and B.J.V.V. designed the study. C.B., M.A.M., D.B., J.S., A.T. and B.J.V.V. collected samples. C.B., J.H.C. and B.J.V.V. generated and analysed the data. All authors contributed to the writing.

## DATA ACCESSIBILITY

GPS coordinates, elevation and vegetation type of each site and microsatellite genotypes of each sample are available in Tables S1 and S2 on Dryad: <https://doi.org/10.5061/dryad.cr12t51>.

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