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RESEARCH ARTICLE

Repeat photography reveals long-term climate change impacts on sub-Antarctic tundra vegetation

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Abstract

Questions: At high latitudes, anthropogenic climate change and invasive species threaten biodiversity, often with interacting effects. Climate change not only impacts native plant species directly by driving distribution and abundance of species, but indirectly through the influence on community dynamics and habitat suitability to invasive species. A key obstacle to quantifying vegetation change in the sub-Antarctic is the scarcity of cloud-free satellite imagery in a region with near-permanent cloud cover and lack of long-term plot data. In this paper, we aim to address the following questions: how has vegetation in the sub-Antarctic changed between 1965 and 2020? What are the roles of climate change and invasive species in driving these changes?

Location: The study was conducted on Marion Island in the sub-Antarctica.

Methods: We quantified vegetation change by analysing repeat ground photography between 1965 and 2020, accompanied by an analysis of climate trends and invasive plant species' cover changes over the same period.

Results: Total vegetation cover was significantly higher in 2020 than in 1965 in all habitats other than in the coastal saltspray habitat, indicating an increase in overall biomass on the island. The more responsive 'generalist' plant species have expanded across the island, whilst the more 'specialised' plant species have not significantly changed in cover, with the exception of the mire graminoids, which have declined. Marion Island has thus undergone significant vegetation change, showing a greening trend across most habitats in the last five decades. This has been accompanied by aridification, an increase in mean air temperature, changes in wind direction and wind speed, and an increase in invasive mouse populations. The three most widespread invasive plant species have also expanded their ranges, especially in areas influenced by animal disturbance and nutrient input.

Conclusions: In congruence with research from Northern-hemisphere tundra and other islands in the sub-Antarctic, these results provide substantive empirical evidence for the interacting effects of climate change and invasive species on sub-Antarctic tundra vegetation, as has long been predicted.

KEYWORDS
climate change, generalist species, global change, global greening, invasive species, repeat photography, sub-Antarctic tundra, tundra greening, vegetation change, vegetation greening

1 | INTRODUCTION

The composition and structure of vegetation largely governs ecosystem function. Therefore, vegetation change can significantly impact ecosystem dynamics and result in loss of biodiversity (Nolan et al., 2018; Nunez et al., 2019). Drivers of vegetation change vary greatly across regions, with climate change (Nunez et al., 2019), invasive species (Bergstrom & Chown, 1999), habitat loss (Skowno et al., 2021), land-use change (Hoffman et al., 2019) and increased CO_2 (Chen et al., 2011) being among the most significant drivers globally. At high latitudes, anthropogenic climate change and invasive species particularly threaten biodiversity, often with antagonistic effects (Frenot et al., 2005; Bergstrom et al., 2015; Piao et al., 2020; IPCC, 2022). Changes in temperature or rainfall, for example, not only impact all native plant species directly by driving distribution and abundance of species (Chen et al., 2011), but indirectly through the influence on community dynamics (Allan et al., 2013; Hoffmann et al., 2019) and habitat suitability to invasive species (Lee et al., 2017).

Most regions around the world have observed negative impacts of climate change, with high latitudes often experiencing disproportionate effects (Myers-Smith et al., 2011; Hoffmann et al., 2019). Warming is the predominant climate trend at high latitudes, with temperatures increasing faster than at mid- and low latitudes in recent decades (Hinzman et al., 2005; Myers-Smith et al., 2011; Xia et al., 2020), accompanied by drying in most of the southern high latitudes (Bergstrom & Chown, 1999; le Roux & McGeoch, 2008a). The implications for the native biota that is adapted to the cold, humid conditions, may be severe. For instance, climate change has shifted species distributions (le Roux & McGeoch, 2008b), altered species interactions (Allan et al., 2013; Hoffmann et al., 2019), and to a more severe extent, caused ecosystem collapse (Bergstrom et al., 2015) in southern high latitudes. Warming may also increase above-ground biomass, as has been shown in vascular plant-dominated Antarctic tundra (Day et al., 2008). The islands in the sub-Antarctic have been described as 'sentinels of change' (Ansorge et al., 2017), because they are expected to be highly sensitive to changes in temperature and rainfall, and in some cases have been shown to be so (le Roux & McGeoch, 2008b; Bergstrom et al., 2015). The full impacts of climate change on vegetation in the sub-Antarctic (Hoffmann et al., 2019), and the southern hemisphere in general (Hoffman et al., 2019), are, however, poorly understood.

These impacts are also expected to interact with the risks posed to these environments by invasive alien species (Convey & Lebouvier, 2009; IPBES, 2023). The increased establishment and spread of invasive species in the sub-Antarctic is thought to have been exacerbated by a warming and drying climate (McGeoch et al., 2015; McClelland et al. 2018a; Hoffmann et al., 2019), notably by increasing habitat suitability for invasive species due to the amelioration of the harsh climatic conditions in the sub-Antarctica On the islands in the sub-Antarctic, invasive species are often associated with disturbed environments, with fauna being the key direct non-anthropogenic disturbance (Smith et al., 2001). Indeed, on many sub-Antarctic islands, invasive species mostly occur in close proximity to fauna (Haussmann et al., 2013; Hoffmann et al., 2019), such as around seal and penguin colonies (le Roux et al., 2013). Some invasive plant species, such as *Poa annua* and *Agrostis stolonifera*, have also reached dominance in such disturbed environments (Haussmann et al., 2013), outcompeting native plant species (Gremmen et al., 1998; Mathakutha et al., 2019; Ripley et al., 2020), which may cause disruption to biological processes. While the impacts of invasive species in the sub-Antarctic are not well understood, they are projected to grow with warming and drying of the region, resulting in wholesale changes to species and communities (Chown et al., 2008; Convey & Lebouvier, 2009). This includes projections of widespread change to vegetation (Smith & Steenkamp, 1990).

Despite the expectations of vegetation change on sub-Antarctic islands, owing to the interactive effects of warming, drying and invasive species, little evidence exists to demonstrate this is happening. Some evidence exists for Macquarie Island in the sub-Antarctic (Bergstrom et al., 2015), but the extent of change across the islands of the region, which vary considerably in their topography and climate history (Hodgson et al., 2014) is unknown. The key obstacles to quantifying vegetation change at the landscape level in the sub-Antarctic are the scarcity of cloud-free satellite imagery in a region with near-permanent cloud cover (Fitzgerald et al., 2021), lack of historical survey data and limited access to the region. Since many modern techniques used for studying vegetation change rely on satellite imagery (Xie et al., 2008) or long-term plot data (De Cáceres et al., 2015), most change detection techniques cannot effectively be implemented in the sub-Antarctic (Bricher, 2015; Fitzgerald et al., 2021). Moreover, while the analysis of vegetation change with satellite imagery has been successful in analysing overall vegetation cover in high latitudes such as the Arctic (Stow et al., 2004), it cannot be used to identify change in smaller vegetation units, patches and species composition (Bricher, 2015; Fitzgerald et al., 2021). Differentiating vegetation from satellite imagery for change detection is not possible in vegetation that has similar spectral signatures between supposedly distinct vegetation units (Xie et al., 2008). Indeed, this was the case on Macquarie Island, where the digital signatures were not distinct between the vegetation units studied, and the analysis could thus not effectively detect change from satellite imagery (Fitzgerald et al., 2021). Therefore, a more ground-based technique to quantify vegetation change at a high resolution is necessary in cloudy environments and in vegetation with indistinct vegetation units.

Repeat photography is one of the most informative and well-established methods available to quantify vegetation change trends (Webb et al., 2010; Hoffman & Rohde, 2011; Knight & Fitchett, 2020;

Bayr, 2021). Often, historical photographs are the only available record of past vegetation characteristics if historical plot data do not exist. Repeat photography can be used to contextualise projected vegetation change by studying past vegetation change trajectories and comparing them to projected future scenarios (Hoffmann et al., 2019). In this way, repeat photography may be particularly suitable for cloudy environments (Bricher, 2015; Fitzgerald et al., 2021), where cloud-free satellite imagery is limited. Furthermore, Landsat satellite imagery has only been available since the 1970s and initially at 30 m resolution, making high-resolution comparisons challenging. Repeat photography has been used in the sub-Arctic to investigate shrub expansion (Sturm et al., 2001; Myers-Smith et al., 2011) and on Macquarie Island to assess vegetation change caused by invasive European rabbits (*Oryctolagus cuniculus;* Fitzgerald et al., 2021). Seasonal changes in both climate and vegetation cover in the sub-Antarctic are not as pronounced as in more temperate biomes, due to the thermal stability, hyperoceanic climate (Convey, 2020) and minimal dieback of perennial species in winter (Smith et al., 2001). Therefore, this resampling technique may likely capture major directional shifts in tundra, such as change in plant cover, dominance or structure, which are relatively independent of short-term seasonal effects (Hoffman et al., 2020). The approach therefore has much potential for deployment elsewhere in the sub-Antarctica.

Here we use repeat photography to assess vegetation change on sub-Antarctic Marion Island. The island has shown rapid climate change since the first record in 1949 (mean temperature increase of 1°C between the 1950s and 1990s; le Roux & McGeoch, 2008a) and has a significant complement of invasive alien plant, invertebrate and vertebrate species (originally cats [*Felis catus*] and mice [*Mus musculus*], now only mice; Greve et al., 2017). Given vegetation changes recorded in Arctic tundra (Myers-Smith et al., 2011; Hoffmann et al., 2019) and sub-Antarctic tundra (Convey & Lebouvier, 2009; Bergstrom et al., 2015), as well as changes in individual alien and indigenous species' distributions on Marion Island (le Roux & McGeoch, 2008b; le Roux et al., 2013), more specifically, the documented impacts of both vertebrate (McClelland et al., 2018) and invertebrate (McGeoch et al., 2015) invasive alien species on the island, and changing climates, we expected substantial change in vegetation generally. Specifically we expect that: (1) vegetation change has occurred across the island; (2) habitat generalists (see Section 2 for definitions) have increased in cover in all habitats; (3) habitat specialists have not increased in cover due to their reliance on more explicit environmental conditions; and (4) alien plant species have spread on Marion Island with consequent impacts on the distribution and cover of native species.

2 | METHODS

2.1 | Study site

Marion Island (46°54’ S, 37°45′ E; hereafter MI) is a ca 290 km^2 remote South African sub-Antarctic island (Figure 1). The island has a chronically cool, thermally stable, oceanic climate with mean annual precipitation of ca 2000 mm (le Roux & McGeoch, 2008a). The mean temperatures of the coldest and warmest months differ by ca 3.6°C, and diurnal temperatures vary by ca 1.9°C (le Roux & McGeoch, 2008a). Seasonal variation in both climate and biomass is thus not pronounced in sub-Antarctic tundra vegetation (Convey, 2020), especially in comparison to more temperate sites (Huntley, 1971). The island has a relatively recent origin, ca 450,000 years B.P., with the last glacial maximum occurring around 34,500 years ago (Rudolph et al., 2020). The geology consists of pre-glacial grey lava and post-glacial black lava with ca 130 more recent red scoriaceous cones scattered around the island (Rudolph et al., 2020).

The flora comprises 21 native species (Chau et al., 2020) and 17 non-native vascular plant species (Greve et al., 2017), along with 134 bryophyte species and 100 lichen species (Øvstedal & Gremmen, 2001). To differentiate between specialists and generalists, plant species with limited habitat preferences and thus narrow niches which are restricted to specific habitats (Brouat et al., 2004; Ainsworth & Drake, 2020), such as species limited to high-salinity soils, are considered specialist species on MI. On the other hand, habitat generalists may occupy multiple habitat types, because of their broader niche preferences (Denelle et al., 2020). Habitat specialists can thus be divided into halophilous species (*Crassula moschata* and *Leptinella plumosa*), hygrophilous species (*Carex dikei*, *Juncus scheuchzerioides*, *Limosella australis*) and coprophilous species (*Callitriche antarctica*, *Poa cookii*, *Montia fontana*). All other species ($n = 13$) are considered habitat generalists (see Huntley, 1971; le Roux & McGeoch, 2008b). Due to the harsh climate on MI, vegetation distribution is closely coupled with abiotic conditions, such as exposure to wind and temperature (Smith & Steenkamp, 2001; Cramer et al., 2022). On the coast, in and around seal colonies and seabird breeding sites, such as penguin rookeries, the distribution of plant species is more biotically driven, by manuring and trampling by animals, where coprophilous species thrive. Wherever salt spray occurs in areas highly exposed to waves, halophytes thrive (Smith et al., 2001). If drainage is impeded, only hygrophilous species are generally able to grow (Huntley, 1971).

Feral domestic cats were introduced to the island in 1949 to control the increasing invasive mouse population (Bester et al., 2002). Shortly after the cats arrived, they rapidly increased in numbers and started predating on seabirds and soon caused severe declines in seabird populations, especially in burrowing petrels, although they were extirpated by 1991 (Bester et al., 2002). Since the extirpation, the population of mice increased, with peak densities increasing by 430% between 1980 and 2011 (McClelland et al., 2018). Mice have a negative impact on the physical environment and on all aspects of biodiversity on MI (Greve et al., 2020). They have a severe impact on macro-invertebrates (Chown et al., 2002), decreasing their abundance, biomass and body size, leading to changes in nutrient cycling and decomposition in which invertebrates are integral (Smith et al., 2002). Although the impact of mice on vegetation is not well known, mice eat the seeds of some plant species (Smith et al., 2002) and tunnel and burrow through vegetation (Phiri et al., 2009).

During the same time period, many alien plant species established on MI, with eight now being invasive (Greve et al., 2017). Four invasive plant species are widespread on MI, particularly concentrated in the coastal areas (*Poa annua*, *Agrostis stolonifera*, *Sagina procumbens*, *Cerastium fontanum*; le Roux et al., 2013).

2.2 | Repeat photography

The advantages of repeat photography analyses in sub-Antarctic tundra vegetation, which generally has low vascular species richness, is that firstly, plant guilds can easily be identified from photographs. Secondly, seasonal variation in biomass is not as pronounced as in more temperate biomes, due to the perennial species having minimal dieback in winter (Smith & Steenkamp, 2001). This makes identification of plant guilds possible from photographs taken throughout the year. Only one deciduous species, *Acaena magellanica*, occurs on MI (Smith & Steenkamp, 2001). To avoid misinterpretation of plant cover changes due to seasonal differences in matched photographs, our interpretations focussed on the perennial component of the vegetation.

Historical photographs that encompass all habitats of MI were sourced from researchers that visited the island in 1965 ($n=59$; Brian Huntley) and 1980 ($n=10$; Marthan Bester). These were the earliest available historical photographs on MI of which the year was documented. Mean annual temperatures on MI increased rapidly from the 1960s and rainfall decreased concurrently (Bergstrom & Chown, 1999; le Roux & McGeoch, 2008a). Therefore, historical photographs from the 1960s are an ideal baseline for assessing the impact of changes in temperature and rainfall on the vegetation of the island. The photographs were originally captured as 35-mm colour slides. The sites of the historical photographs (hereafter referred to as 'historical') were relocated in the field in 2019/2020 (hereafter 'repeat'). The repeat photography approach described by Rohde and Hoffman (2012) was followed. For each historical photograph, the camera position was located as close as possible to the original site to capture the repeat photograph. The GPS location, elevation and photographic information were recorded, and a detailed ecological survey was conducted at each site. This was done by dividing the field of view into general habitats, recording an in-field description of the vegetation, and then identifying all vascular plant species together with an estimate of the aerial percentage cover of each species in each habitat estimated by trained observers following Daubenmire (1959). The repeat photograph was overlaid on the original photograph to obtain an exact match to the original using Adobe Photoshop CS5 (Adobe, San Jose, CA, USA).

2.3 | Cover estimates of vegetation change derived from an analysis of photographs

Within each photograph, polygons were drawn around habitats that could be identified from the historical photographs (as was also done in the field). To address the close association of certain range-restricted species (specialists) with specific environmental or biotic factors, which confines them to a given habitat, plant cover within each habitat was estimated (rather than only at the island scale) following Daubenmire (1959). Five habitat complexes were informed by Smith and Steenkamp's (2001) key to identifying habitats on MI (see Appendix S1 for a description of these habitats). Cover was estimated based on 'plant guild' (see also Smith & Steenkamp, 2001), rather than species, because the inconspicuous species, such as the mat- forming herbs that occur around fauna, were difficult to differentiate in the photographs. Therefore, while photographs were divided into habitats to account for specialist species, plant cover changes were still estimated per guild. A plant guild consists of a group of species that utilise resources in a similar manner and since they have similar resource requirements usually occur together in similar habitats (Simberloff & Dayan, 1991). It thus includes taxonomic and ecological characteristics. However, most plant guilds are only represented by a single species (see Appendix S2 for a description of plant guilds), due to the low species richness on the island; thus, the analysis was mostly done at the species-level as suggested by van der Merwe et al. (2023) for monitoring of vegetation in species-poor environments. To reduce the observer effect on cover estimates, within each habitat the cover of each visible plant guild in the historical and repeat photograph was estimated by two researchers with detailed knowledge of the habitats and flora of MI, and the average value was used for each observation. Twelve plant guilds were identified as follows: bryophyte, pteridophyte, mire graminoid, tussock graminoid, epiphytic graminoid, alien grass, alien herb, mat dicotyledon ('dicot' hereafter), cushion dicot, rosette dicot, erect dicot, and suffrutescent herb (Appendix S2). The cover of bare soil and/or rock and water evident in the photographs was also estimated. In total, 100 paired polygons were recorded in the historical and repeat photographs. In 21 polygons, however, only the total vegetation cover could be estimated, as the field of view was too distant to estimate the cover of different plant guilds in different habitats. Polar desert was the only habitat excluded from the analysis because historical photographs in polar desert are scarce, partially because of extreme weather conditions through most of the year, and no vascular plants occur here.

While exact dates for the historical photographs are not known, the season could be identified from *Acaena magellanica* flowerheads, and grass inflorescences, such as those of *Polypogon magellanicus*. However, because environmental seasonal variation is low in sub-Antarctic tundra (Bergstrom & Chown, 1999; Convey, 2020), there are not substantial seasonal changes in plant cover. If epiphytic graminoids growing in cushion plants in fellfield increased and cover a larger area in a repeat photograph, the cushion plant cover in the photograph becomes less visible. Consequently, to avoid overestimating total vegetation cover, the cushion plant cover is simultaneously subtracted from the assessment. This does not indicate replacement of cushion plants by epiphytes, but rather overgrowing or shading of cushion plants.

2.4 | Climate data

Past climate trends for MI have only been analysed up to 2003 in detail (le Roux & McGeoch, 2008a; although see also McClelland et al., 2018) and are now outdated. To investigate general climate trends that the vegetation experienced over the study period, temperature, precipitation and wind data were analysed, available from 1949 to 2020, sourced from the National Oceanic and Atmospheric Administration's Integrated Surface Dataset using R package *worldmet* (Carslaw, 2023). The data were derived from the MI weather station located on the east coast of the island (Figure 1). Six-hourly temperature (°C) data, taken at 08:00, 14:00, 20:00 and 02:00, were averaged to daily mean, maximum and minimum temperatures. From these data, annual mean, minimum and maximum temperatures were calculated to analyse the trend over the available data period. Daily precipitation, falling mainly as rainfall (mm), was summed to a total rainfall per year. The total number of rain-free days and maximum number of consecutive rain-free days were also calculated to explore dry spells. Rainfall data were missing between 1949 and 1960 and thus only data from 1960 onwards were analysed for rainfall. Six-hourly wind measurements were averaged to mean annual wind speed ($\mathrm{m\,s^{-1}}$), and wind direction (°) per day was calculated using circular statistics in the *circular* R package (Agostinelli & Lund, 2022) and averaged to mean annual wind direction. Temperature and wind data were analysed from 1949 to 2020 to include the climate trend preceding 1965 as well.

2.5 | Statistical analysis

Paired sample Wilcoxon signed-rank tests (a non-parametric alternative to the *t*-test) were run for each polygon pair to determine whether there was a significant difference in cover of each plant guild, as well as total vegetation cover across MI ('combined data'), between 1965 and 2020. Some range-restricted plant species (i.e., specialist species in the tussock graminoid, mat dicot, rosette dicot and erect dicot guilds) do not occur across the entire island, thus a second set of tests were run for each plant guild–habitat combination to determine whether there was a difference in cover of each plant guild within each habitat between 1965 and 2020, using the R packages *car* (Fox et al., 2013) and *PairedData* (Champely, 2018).

To analyse the change in climate variables during the study period, the mean, minimum and maximum air temperature, total precipitation falling as rainfall, total number of rain-free days, maximum number of consecutive rain-free days, wind speed and wind direction were explored. General additive models (GAMs) were used to explore nonlinear trends of mean, minimum and maximum air temperature, total number of rain-free days, wind speed and wind direction and whether these variables changed significantly over the study period, using the 'gam()' function in the *mgcv*package (Wood, 2011). 'Year' was thus the explanatory variable. Parameters for GAMs were set as follows: climate variables were assumed to follow a Gaussian distribution with an identity link function. Thin plate regression splines, the default smoothing method for all smooth terms, were used (Wood, 2011). The basis dimension for each smooth term was set to the default of $k=10$, allowing for a maximum of 10 basis functions per term. Smoothing parameters were estimated using restricted maximum likelihood, the default method in *mgcv*, to avoid overfitting and to ensure robust estimates of the smooth terms (Wood, 2011). The model convergence criteria were also based on the default settings in *mgcv*, with outer iterations limited to a maximum of 200. A general linear model was run for total rainfall per year and maximum number of consecutive rain-free days, which had a linear trend over time. We also compared the 1964/1965 and 1979/1980 climate record to 2019/2020, to establish whether either of the years experienced an unusual climate and because of this may influence our interpretation of the changes in vegetation observed in the photo comparisons.

All statistical analyses were conducted with R statistical software (R Core Team, 2024), while the map was created in ArcGIS Desktop 10.4 (Environmental Systems Research Institute, Redlands, CA, USA).

3 | RESULTS

3.1 | Repeat photography

In the combined data ($n=100$ polygons), total vegetation cover was significantly higher ($Z=-6.45$, $p<0.05$, $r=0.68$) in the repeat than in the historical data in all habitats (Figure 1), other than in coastal salt spray ($Z=0.22$, $p>0.05$, $r=0.01$; Figure 2). The most pronounced increase in total vegetation cover (by ca 18%±9%) occurred in fellfield (Figure 2; Appendix S3). The overall increase in total cover was largely due to the higher cover of pteridophyte ($Z=-5.10$, $p<0.05$, $r=0.63$), epiphytic graminoid ($Z=-3.01$, $p>0.05$, $r=0.33$), alien grass ($Z=-3.62$, $p<0.05$, $r=0.47$), alien herb ($Z=-3.30$, $p<0.05$, $r=0.43$) and bryophyte ($Z=-4.30$, $p<0.05$, $r=0.51$) guilds in the repeat compared to the historical data (Figure 2; Appendix S3). Bare ground ($Z=6.51$, $p<0.05$, $r=0.64$), cushion dicot ($Z=3.91$, $p<0.05$, $r=0.38$), tussock graminoid ($Z=2.21$, $p<0.05$, $r=0.35$) and suffrutescent herb cover ($Z=2.29$, $p<0.05$, $r=0.15$) were significantly lower in the repeat than in the historical data (Figure 2; Appendix S3). The remaining guilds (mire graminoid, mat dicot, rosette dicot and erect dicot) did not differ significantly ($p>0.05$) between years in the combined data (Appendix S3; Figure 2).

In fellfield vegetation, bare ground ($Z=3.18$, $p<0.05$, $r=0.88$) and cushion dicot ($Z=2.40$, $p<0.05$, $r=0.64$) cover were significantly lower in the repeat than in the historical data, whereas epiphytic graminoid cover ($Z=-2.97$, $p<0.05$, $r=0.82$) was higher in the repeat data (Figure 2). No other plant guilds differed significantly between the years in fellfield ($p>0.05$; Figure 2; Appendix S3). On slopes, pteridophyte cover ($Z=-3.55$, $p<0.05$, $r=0.85$) was significantly higher and tussock graminoid ($Z=2.80$, $p<0.05$, $r=0.73$), bryophyte ($Z=-2.32$, $p<0.05$, $r=0.56$), suffrutescent herb ($Z=2.90$, $p<0.05$, $r=0.66$), cushion dicot ($Z=2.04$, $p<0.05$, $r=0.46$) and bare ground ($Z=2.64$, $p<0.05$, $r=0.64$)

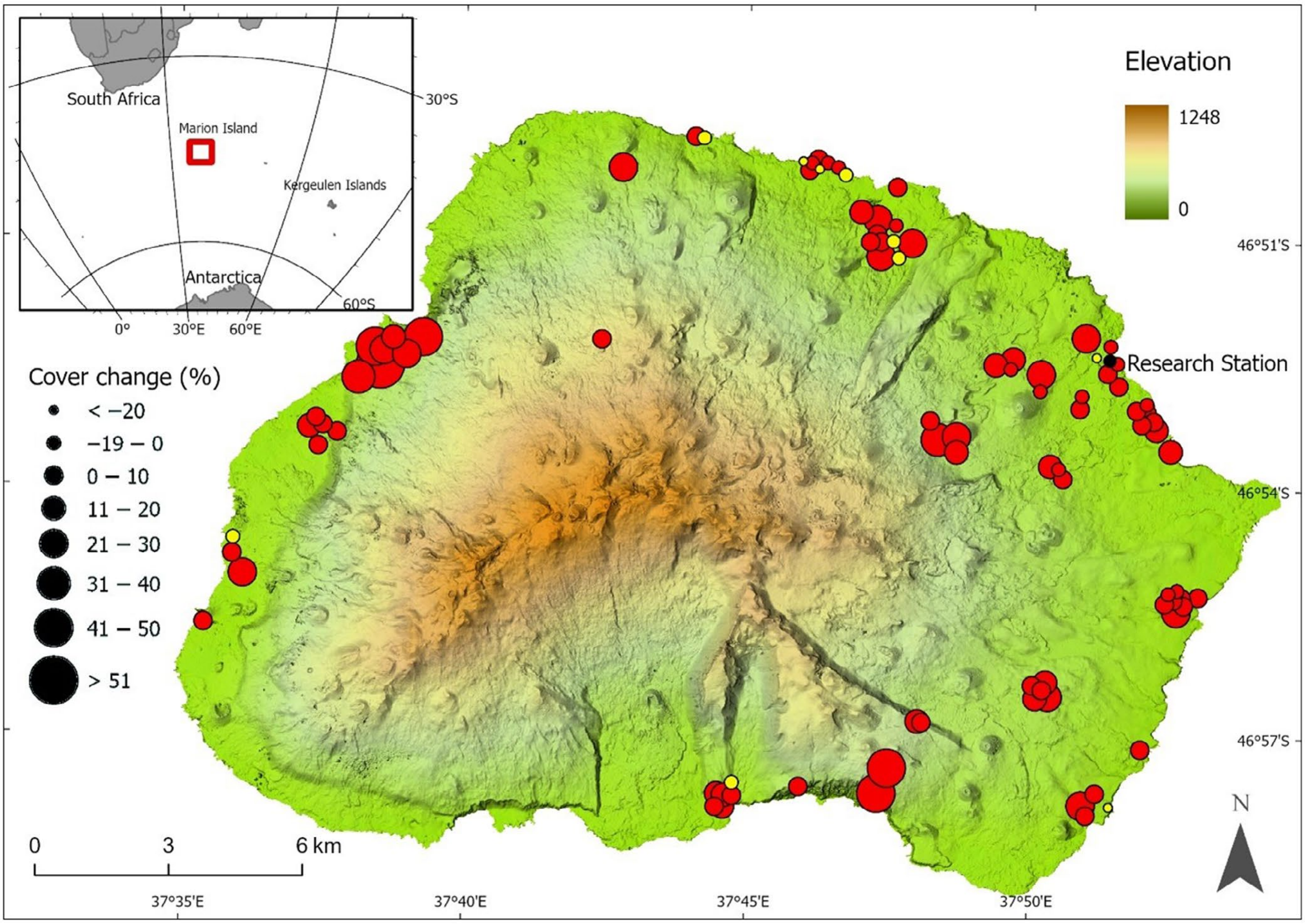

FIGURE 1 Percentage change in total vegetation cover at each photograph location of the repeat photography analysis across Marion Island between 1965 and 2020. The embedded map shows the geographic location of the study site. Graduated symbols indicate percentage change from decreasing to increasing total vegetation cover. Yellow indicates the sites with a decrease in cover and red indicates sites with an increase in plant cover. The position of some site symbols has been jittered to improve visibility at this map scale.

were significantly lower in the repeat than in the historical data (Figure 2; Appendix S3). In mires, pteridophyte ($Z = -2.80$, $p < 0.05$, $r = 0.83$) and bryophyte cover ($Z = -2.20$, $p < 0.05$, $r = 0.62$) were significantly higher in the repeat than in the historical data (Figure 2; Appendix S3). Mire graminoid ($Z = 2.22$, $p < 0.05$, $r = 0.58$) and bare ground ($Z = 2.32$, $p < 0.05$, $r = 0.66$) were significantly lower in the repeat than in the historical data (Figure 2; Appendix S3). In biotic sites, pteridophyte ($p = 0.02$), bryophyte ($p = 0.02$), mire graminoid ($p = 0.03$), alien grass cover ($p < 0.05$) and alien herb ($p = 0.01$) were significantly higher in the repeat than in the historical data, with lower bare ground cover ($p < 0.05$) in the repeat data (Figure 2; Appendix S3). In coastal saltspray habitat, only cushion dicot differed significantly ($Z = 2.37$, $p < 0.05$, $r = 0.70$), being lower in the repeat than in the historical data (Figure 2). Examples of the most prominent guild cover changes in each habitat are shown in Figure 3.

3.2 | Climate data

Mean annual temperature increased significantly ($p < 0.05$, deviance explained = 74.6%) over the study period from ca 5.8°C in 1949 to ca 6.3°C in 2020 (Figure 4). Mean annual temperatures increased up to ca 1999, decreased until ca 2009 and increased again thereafter (Figures 4 and 5). The annual mean monthly maximum temperatures did not change significantly ($p > 0.05$) between 1949 and 2020 (Figures 4 and 5). Annual mean monthly minimum temperatures increased significantly from ca −2.2°C (1949) to ca −1.2°C (2020), although a negligible amount of variation (12.0%) was explained by the model.

The total rainfall decreased significantly from ca 2585 mm p.a. in 1960 to ca 1640 mm p.a. in 2020 ($p < 0.05$, $R^2 = 70.4\%$; Figure 6), with a general decrease in rainfall in all months, especially in the past two decades (Figure 5). Total number of rain-free days increased significantly ($p < 0.05$, deviance explained = 14.7%) from the 1960s to 1990s, then decreased until ca 2010 and increased again thereafter (Figure 6). The maximum number of consecutive rain-free days (i.e., dry spells) decreased significantly over the study period (Figure 6), although a negligible amount of variation (8.10%) was explained by the model. Wind direction changed significantly ($p < 0.05$; deviance explained = 68.3%) from being predominantly NW to predominantly SW (Figure 7). Wind speed increased until the 1990s, then decreased

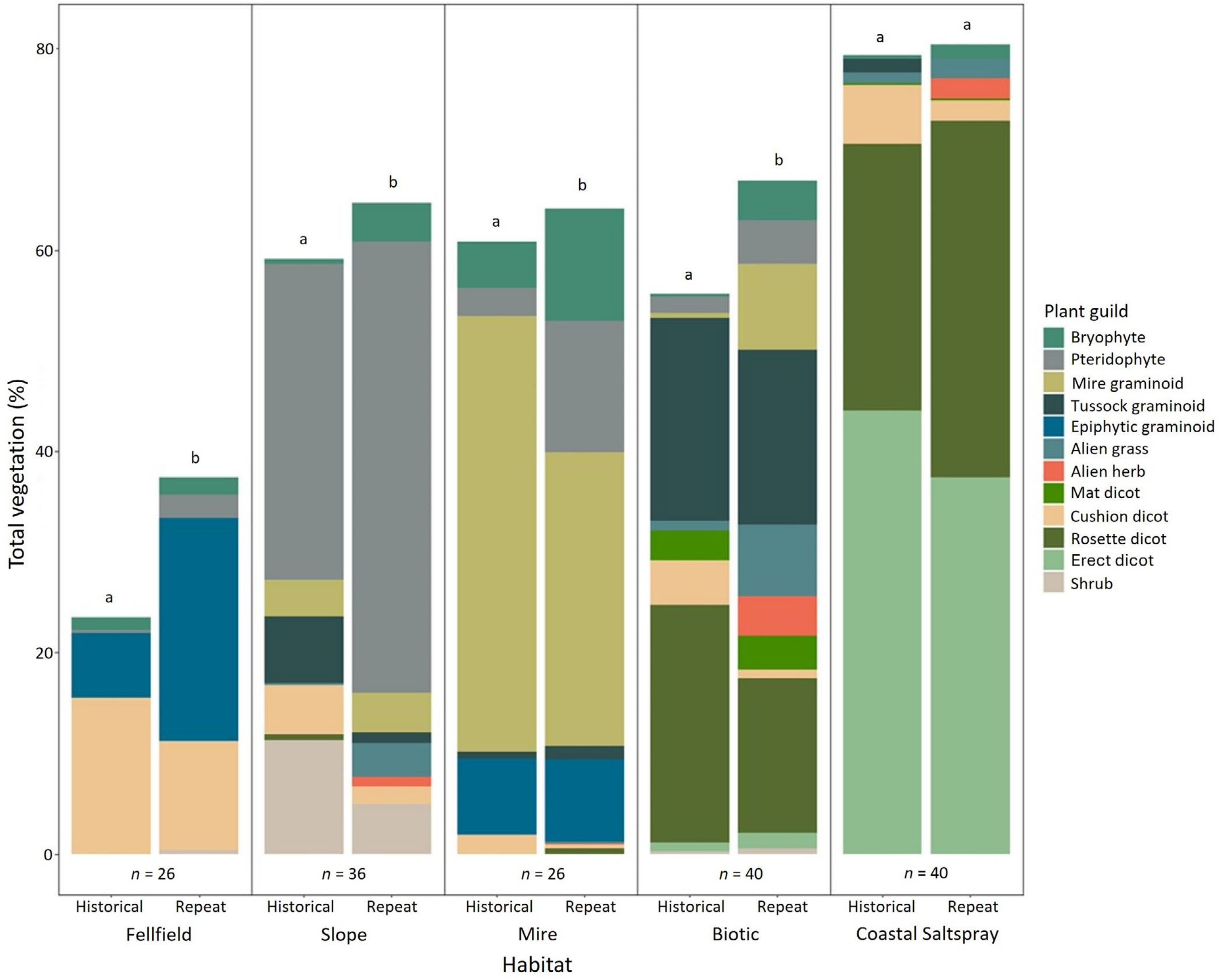

FIGURE 2 Stacked bar charts showing percentage vegetation cover across habitats on Marion Island between 1965 or 1980 ('Historical') and 2019 or 2020 ('Repeat'). Bars are stacked by mean percentage of each plant guild that made up the total vegetation cover. Bare ground and water estimates were removed to display only vegetation cover. Significant differences ($p < 0.05$) between historical and repeat data for total vegetation cover are indicated by letters.

from the late 1990s, although this was not significant ($p > 0.05$; deviance explained = 68.0%; Figure 7).

4 | DISCUSSION

Following decades of speculation that the vegetation has been changing on MI (Smith & Steenkamp, 1990; Chown & Smith, 1993; Smith et al., 2001), this study provides the first vegetation-level, circum-island demonstration that this is indeed the case (see also le Roux & McGeoch, 2008b who focussed more on individual species). Vegetation cover has generally increased across the island, suggesting vegetation biomass has also increased, with invasive plants contributing to the overall cover increase on the island. This biomass increase is consistent with global greening trends (Piao et al., 2020), especially in cold environments, such as the Arctic tundra (Tape et al., 2006; Hudson & Henry, 2009), and the evidence here suggests that the sub-Antarctic may be following a similar trend. Increase in biomass is commonly related to climate change and rising global CO_2 concentrations, which is thought to increase carbon availability to plants (Elbasiouny et al., 2022), and increased photosynthetic rates, especially when combined with warming in cold environments (Marchand et al., 2005; Campioli et al., 2013; Piao et al., 2020). In Antarctic tundra, warming experiments similarly showed greater above-ground biomass and C concentrations in sites that were warmer than the ambient controls (Day et al., 2008). However, these responses are context-specific and complex (Körner, 2006), thus we cannot reach firm conclusions on its role in the observed biomass increase on MI without experimental data. However, concurrent with the increase in vegetation cover was a rapid change in climate, as well as an increase in invasive plant species' cover and abundance and density of invasive mice. These are thus likely major factors driving vegetation change.

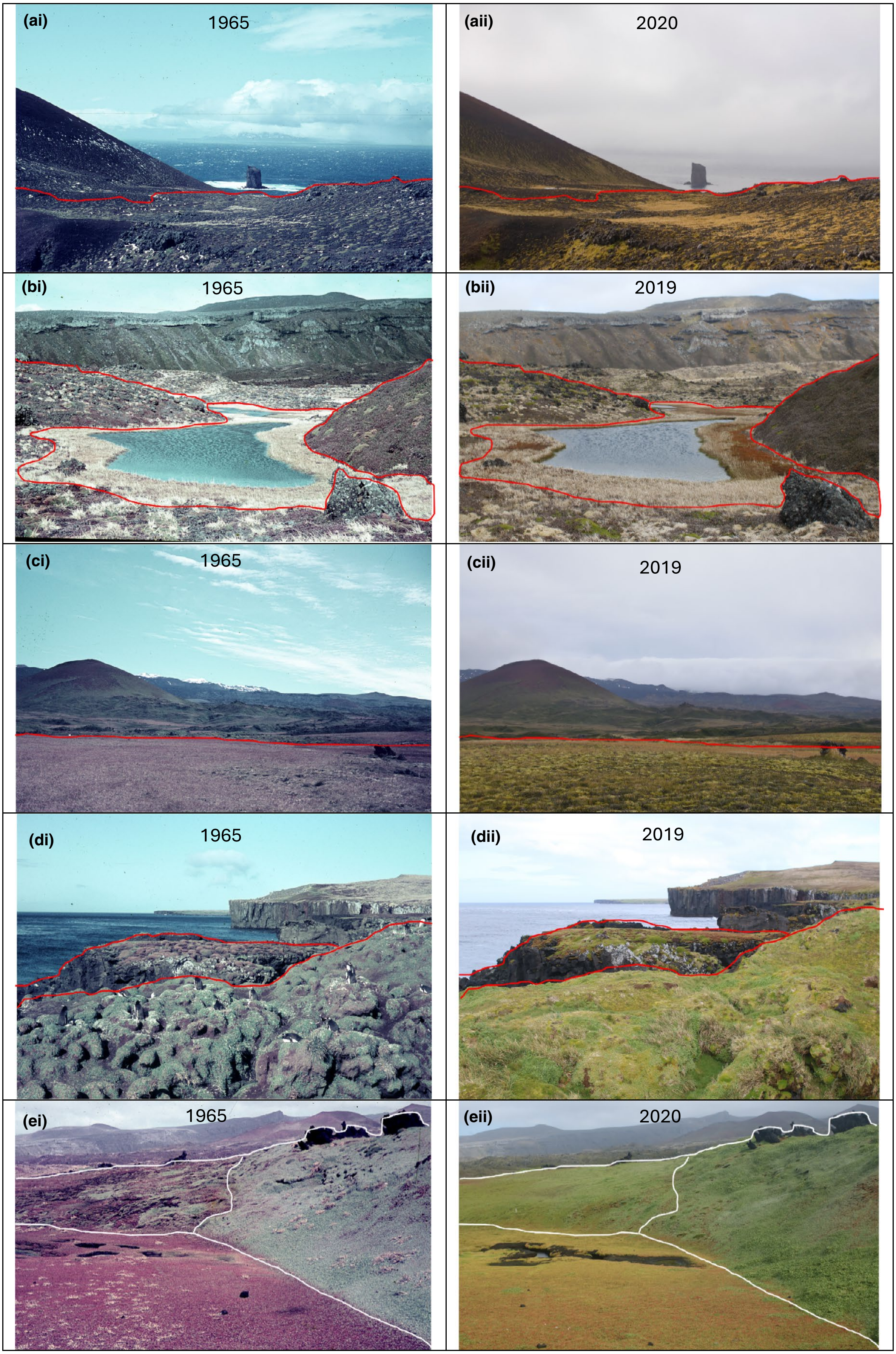
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FIGURE 3 Matched photograph examples showing the most prominent vegetation change within each habitat on Marion Island. Historical photographs from 1965 are on the left and repeat photographs captured in 2019/2020 are on the right. Plant guilds were estimated within each polygon. These are examples of (a) epiphytic graminoid expansion onto cushion dicots and bare ground in fellfield; (b) pteridophyte cover increase and cushion dicot decrease or shading on slopes (on the right). In the mire (centre), bryophytes have expanded where a new foot path was created on the right; (c) mire graminoid decrease and bryophyte and pteridophyte increase in mires; (d) species compositional shift, with mat dicot, alien grass and herb cover increase in the biotic habitat. Non-native plant species are present in the repeat photographs, where they were previously absent in the historical photograph; (e) slight cushion dicot decrease and rosette dicot increase in coastal saltspray, although the cover changes in coastal saltspray were not significant. Anecdotal microtopographical changes can also be seen in (e).

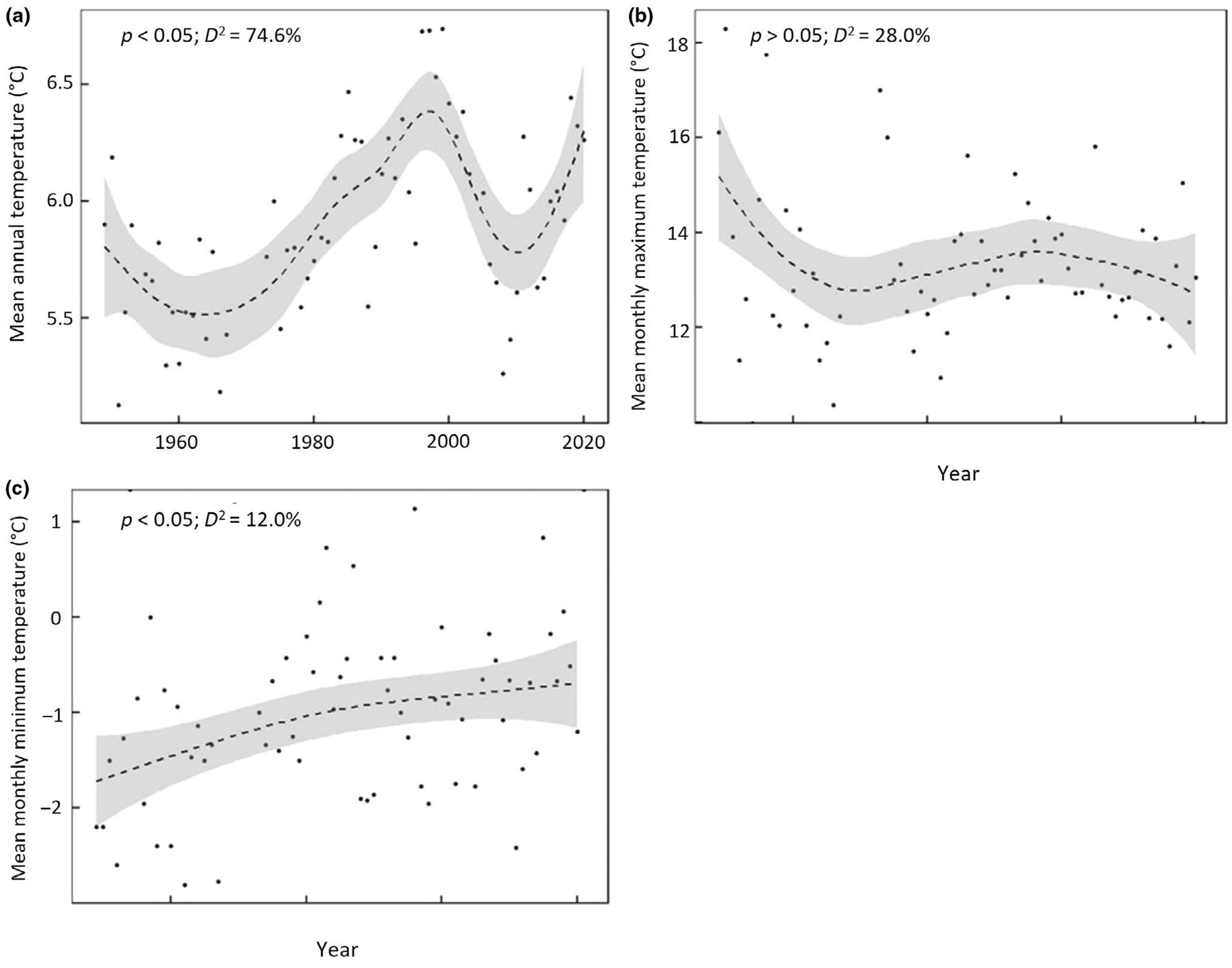

FIGURE 4 Air temperature change (± SE) on Marion Island from 1949 to 2020: (a) mean annual temperature, (b) mean monthly maximum temperature and (c) mean monthly minimum temperature. General additive models were used to illustrate trends.

A key limitation of a repeat photography approach is that correlating vegetation change to a specific driver is particularly challenging. However, on MI, direct anthropogenic influence is limited to the research station, overnight huts and footpaths around the island, thus typical continental drivers of vegetation change, such as habitat loss and land-use change, are absent. Other non-anthropogenic change drivers such as fire and herbivory are also mostly absent, as indigenous insects do include herbivorous species, but their impacts are low (Crafford & Chown, 1991), and mice feed mostly on invertebrates on MI (Smith et al., 2002). Therefore, many typical drivers of change can be ruled out. Because we do not have exact dates for the 1965 photographs, comparisons may be influenced by season. This was compensated for by firstly deducing the season from the vegetation in the photographs, secondly, by focussing on the perennial aspects of vegetation and thirdly, by comparing the climate in years preceding those in which the photographs were taken to detect any unusually warm or cold years. In terms of the last point, we did not find atypical climate patterns

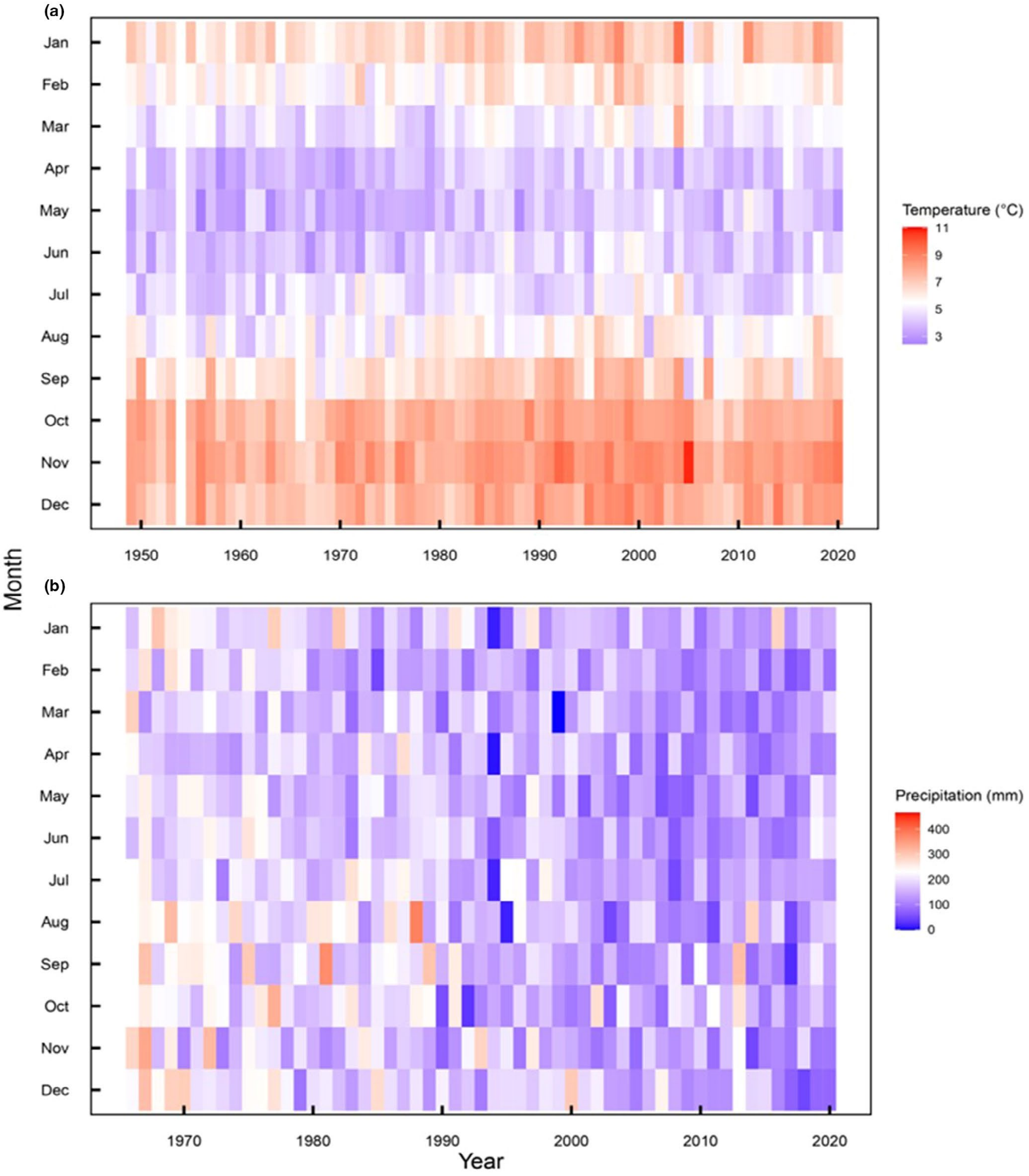

FIGURE 5 Graph showing seasonal variation and trends over time. Monthly changes are shown in (a) mean air temperatures from 1949 to 2020 and (b) total precipitation from 1960 to 2020.

in the 1964/1965, 1979/1980 or 2019/2020 growing seasons that would particularly have influenced the vegetation growth in either year. Furthermore, seasonal differences are not pronounced in sub-Antarctic tundra due to the oceanic climate (Bergstrom & Chown, 1999; Convey, 2020) and thus likely would not lead to the pronounced increases in cover observed here. The increase in total cover observed here is not typically indicative of the short-lived changes associated with seasonality in tundra systems, such as sudden increases in flowering heads during summer. Rather, our observations reflect island-wide increases in plant cover, regardless

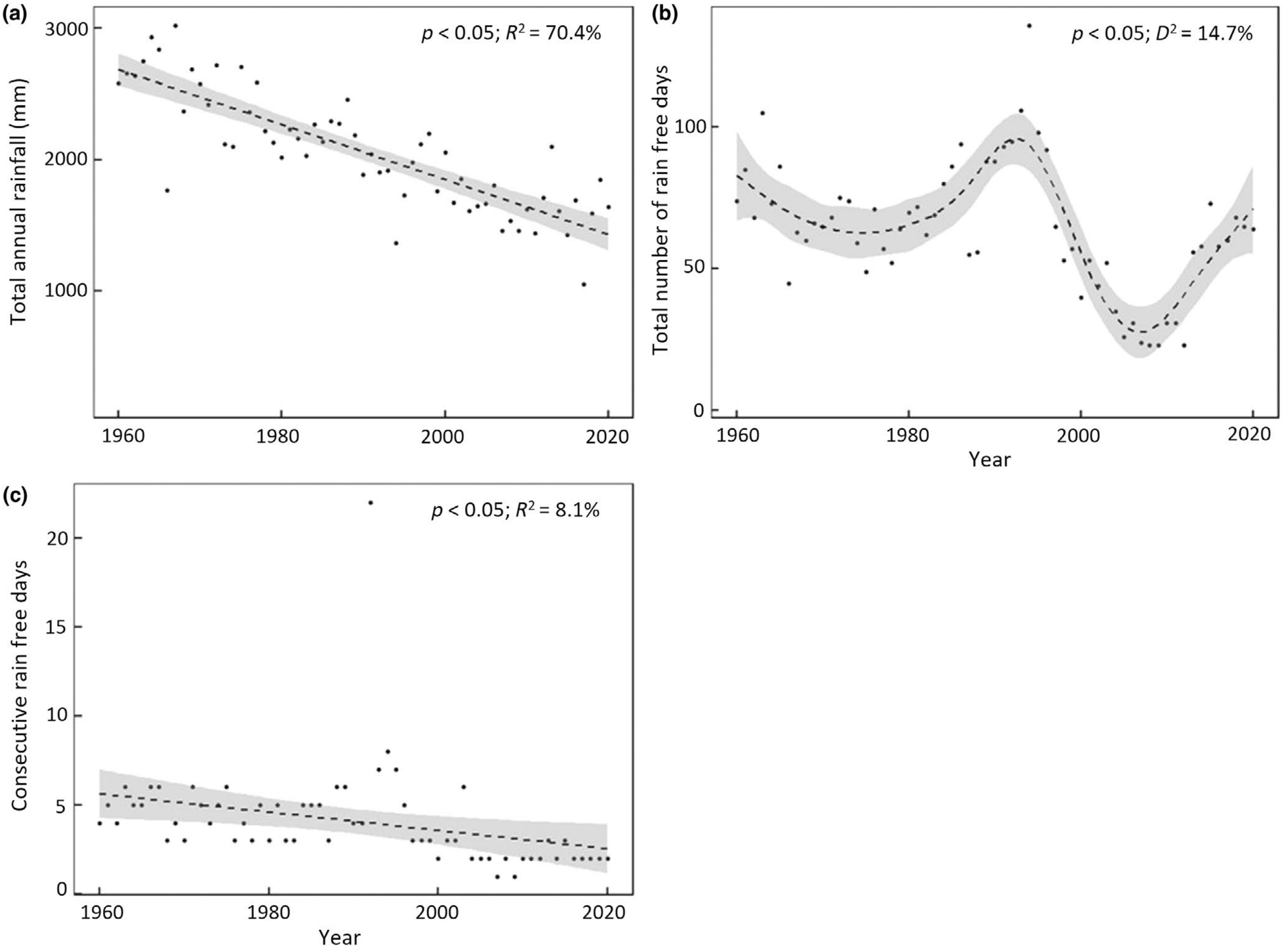

FIGURE 6 Change (±SE) in (a) total annual rainfall; (b) total number of rain free days; and (c) maximum number of consecutive rain-free days, that is, dry spells, between 1960 and 2020. A general linear model has been fitted to the graph in (a) and (c) and a general additive model was fitted to (b).

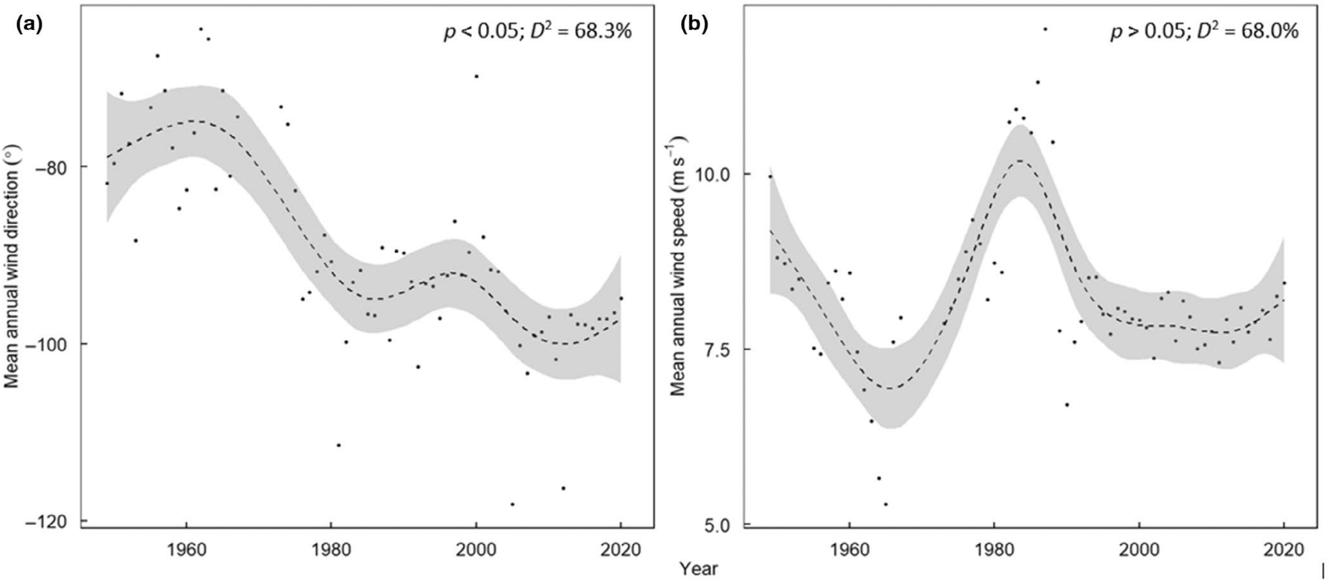

FIGURE 7 Changes in wind conditions (±SE) between 1949 and 2020: (a) mean annual wind direction shown as degrees from 360° and (b) mean annual wind speed. General additive models were fitted to the graphs.

of season, consistent with findings in both northern (Marchand et al., 2005; Hudson & Henry, 2009; Piao et al., 2020) and some southern (Day et al., 2008) hemisphere tundra systems.

While climate change is likely contributing significantly to vegetation change, a more nuanced understanding emerges when considering the climate data over a longer period, revealing fluctuations in the trends since the last in-depth climate study was conducted on MI in 2003 (le Roux & McGeoch, 2008a). Between the 1960s and 1990s, mean air temperatures increased rapidly, surpassing the mean global warming trends (Rantanen et al., 2022). However, this rapid warming slowed in ca 2000, with temperature cooling until the early 2010s, after which a warming trend resumed. Although mean minimum temperatures increased by ca 1°C between 1949 and 2020, high variation around the mean resulted in negligible explained variance. Nonetheless, despite the warming trend slowing between 2000 and 2010, overall air temperatures continued to rise over the long term on MI. For instance, the mean temperatures in 2020 were ca 0.5°C higher than those recorded in 1949, aligning with the increase in global mean air temperatures (Rantanen et al., 2022). Wind speed also did not follow a linear trend, increasing between the 1960s and 1990s, decreasing rapidly in the early 2000s and stabilising afterward, with annual windspeeds being similar in 1965 (ca $7.7\,\mathrm{m\,s^{-1}}$) and 2020 (ca $7.9\,\mathrm{m\,s^{-1}}$). Wind direction has also changed from more northwesterly winds to predominantly southwesterly winds. In contrast to the varying trends of temperature and wind, total rainfall has consistently and rapidly decreased over the entire study period, with 2020 experiencing around 1000 mm less rainfall per year compared to the 1960s. Therefore, while climate trends are more complex than previously understood, with cooler periods interrupting long-term warming, climate change, especially aridification, and invasive species likely remain the two key drivers of vegetation change, as found in studies at other islands in the sub-Antarctic (Frenot et al., 2005; Bergstrom et al., 2015; Hoffmann et al., 2019).

Globally, alien species are generally able to increase rapidly in distribution in response to warming on islands (Russell et al., 2017). In the historical photographs, there was no observable alien plant cover (although some alien plant species were present by then; Greve et al., 2017). In the repeat photographs, alien plant species were present in biotic sites, coastal saltspray and on slopes, suggesting that they are still spreading on MI and confirming predictions of increasing invasion (Smith et al., 2001; le Roux et al., 2013; Greve et al., 2017). There is no evidence that mice consume any part of the alien plants on MI (Smith et al., 2002). However, the disturbance of natural vegetation caused by mice may provide the opportunity for invasive species to spread. Alien species often establish in disturbed and nutrient-enriched environments (Vila et al., 2011). On MI, areas where fur seals occur particularly favour the production of invasive *Poa annua* lawns, due to nutrient enrichment and trampling of native species which creates disturbance sites for the establishment of non-native species (Haussmann et al., 2013). The range expansion of alien plants is thus likely due to the synergy between residence time, biotic disturbance and dispersal through seals (Haussmann et al., 2013), humans or seabirds (Ryan et al., 2003) and climatic changes.

While little is known about the impacts of alien plant species in the sub-Antarctic (see Gremmen et al., 1998), invasive plant species can more rapidly acquire resources (Mathakutha et al., 2019) and respond faster to disturbance as a result (Vila et al., 2011). Indeed, the photosynthetic rate of invasive grasses on MI increased in response to experimental warming, whereas native grasses did not (Ripley et al., 2020). The increase in cover of invasive plant guilds, comprised mainly of *Poa annua*, *Agrostis stolonifera* and *Sagina procumbens*, is thus of concern as these species may be more responsive than native species to the rapid changes occurring on the island. Indeed, in the biotic site studied here, where faunal disturbance is high, an increase in alien plants coincided with a decrease in native rosette dicots (*Leptinella plumosa*) and tussock grasses (*Poa cookii*), suggesting that aliens may play a role in displacing the native species. Similarly, some native *Poa cookii* grasslands were also replaced by *Poa annua* lawns in a study conducted between 1979 and 2011 on MI (McClelland et al., 2018). Furthermore, the invasive grass *Agrostis stolonifera* reaches dominance in some habitats where it displaces native species (Gremmen et al., 1998). This not only reduces diversity, but also effectively leads to changes in ecosystem functioning. The management of invasive plant species is thus necessary to avoid further impacts on native plant species, that are already undergoing change on MI due to climate change.

Globally, generalist species often capitalise on disturbance and changing environmental conditions, being able to respond more rapidly to change than specialist species, because of their broader niche preferences (Denelle et al., 2020). The guilds representing generalist species here, that is, pteridophyte, epiphytic and mire graminoid guilds, accounted for a large proportion of the increase in vegetation cover and thus biomass, indicating range expansion of these generalists. In particular, the cover of *Polypogon magellanicus* which occurs in two forms as epiphytic graminoid in fellfield and mire graminoid in mires and biotic sites, and *Austroblechnum penna-marina*, the dominant pteridophyte, expanded in all habitats where they occur. Pteridophytes in general are hypersensitive to environmental variation and are often used as indicators of change, since their distribution is independent of biotic vectors and thus rather a response to climate and other abiotic conditions (Abotsi et al., 2020). Indeed, mouse density and thus associated burrowing is low on *Austroblechnum penna-marina* slopes (McClelland et al., 2018) because mice do not eat *Austroblechnum penna-marina* (Smith et al., 2002), and alien plant species probably do not compete with the fern. Furthermore, *Austroblechnum penna-marina* is likely sensitive to temperature, reflected in its preference for warmer north-facing slopes (Huntley, 1971; Gremmen, 1981). Between the 1960s and early 2000s, *Austroblechnum penna-marina* shifted upslope by 147 meters, from an elevation limit of 275 meters above sea level, likely driven by a warmer climate (Huntley, 1971; le Roux & McGeoch, 2008b). It also prefers well-drained soils, never occurring in water-logged peat (i.e., mires; Huntley, 1971). The continued decrease in rainfall on MI may thus have contributed to the range expansion of *Austroblechnum penna-marina* into mires from 1965 to 2020, observed here. This also supports the prediction that mires may be drying out on MI (Hedding & Greve, 2018). Climate change is thus likely driving the range expansion in the generalist *Austroblechnum penna-marina*. Since it acts like a shrub at the study site, where this functional group is absent (Smith & Steenkamp, 1990), this expansion mimics that of the well-known shrub expansion that has occurred in Arctic tundra, also largely attributed to climate change (Tape et al., 2006; Myers-Smith et al., 2011; Campioli et al., 2013).

An important and often dominant vascular component of tundra systems are cushion plants (Cavieres et al., 2007), which act as ecosystem engineers and keystone species that facilitate a numerous biota within their canopies in the otherwise harsh habitats found in tundra (le Roux et al., 2005; McGeoch et al., 2006; Chau et al., 2019). The decreased cover of cushion plants in the repeat compared to the historical data may thus be significant as it could indicate a change in dominance to more responsive generalist species, such as *Polypogon magellanicus* (epiphytic graminoid) in the higher elevation fellfield and *Austroblechnum penna-marina* on lower elevation slopes, likely shading the very slow-growing cushion plants. Indeed, the interactive effects of shading by epiphytes, changes in wind and decreased rainfall have been shown to increase senescence of *Azorella selago* in a short-term experiment (le Roux et al., 2005). Similarly, the congeneric *Azorella macquariensis* is sensitive to drought and has experienced ongoing dieback likely as a result of an increase in drought periods and warming on Macquarie Island, with subsequent overgrowing of cushion remnants also by *Polypogon magellanicus* and lichens (Bergstrom et al., 2015; Dickson et al., 2019). In a longer-term cushion plant study on MI, *Polypogon magellanicus* also increased in cover on 58% of cushion plants studied, although there appeared to be no significant cost of epiphytic growth to the cushion plants (Raath-Krüger et al., 2023). However, on Kerguelen Island, also in the sub-Antarctic, the cushion plant *Lyallia kerguelensis* has been shown to exhibit necrosis related to water stress (Marchand et al., 2021). Therefore, the direct impacts of climate change on these cushion plant species in the sub-Antarctic may interact with indirect effects such as shading (le Roux et al., 2005; Dickson et al., 2019), along with the mechanical damage caused by mice on MI (Phiri et al., 2009), perhaps changing the dominance in vascular plant communities.

The specialist plant guilds (represented by tussock graminoid, rosette dicot, mat dicot) whose distribution is dependent on specific biotic or abiotic drivers, did not show marked change in cover, supporting our third hypothesis. The strong association of these plant guilds with particular habitat conditions, for example, high-nutrient soils that do not change rapidly with climate change, suggests that the ability of the specialists to respond to climate change may be constrained (Cramer et al., 2022). There was, however, a reduction of *Poa cookii* grasses (the only species in the tussock graminoid guild) in all biotically driven systems (i.e., where fauna occurs), although the decrease of *Poa cookii* cover was only significant on slopes between years in the current study. The distribution of *Poa cookii* is determined by manuring and trampling (Smith et al., 2001), and thus their reduced cover in relation to climate change may also be related to changes in these processes. Nevertheless, one important difference between 1965 and 2020 is the population changes of invasive cats and mice. Cats, which decimated seabird populations, eating up to 635,000 burrowing petrels and prions per year, had been present for 19 years at the time the historical photos were taken, but were eradicated by 1991 (Bester et al., 2002). *Poa cookii* only occurs inland on slopes where there is guano enrichment around bird burrows (Smith et al., 2001; Smith & Mucina, 2006) and thus cats were likely responsible for changes in its distribution, being replaced by *Austroblechnum penna-marina*. *Austroblechnum penna-marina* is sensitive to trampling by fauna (Smith & Steenkamp, 2001), thus its increase on slopes where *Poa cookii* decreased indicates reduced faunal activity. Fur seal populations have also increased considerably on MI (Haussmann et al., 2013), and could further reduce tussock grasses through trampling. While *Poa cookii* could potentially return to previously suitable inland slopes, burrow-nesting birds on slopes have not recovered as expected in the absence of cats (Dilley et al., 2017). This is likely due to continued predation on hatchlings by mice that have had to find other sources of protein after depleting invertebrate biomass and abundance (Dilley et al., 2017). Mice also eat *Poa cookii* seeds (Chown & Smith, 1993), perhaps reducing recruitment potential. While the decrease in *Poa cookii* cannot be explained with certainty, the indirect impacts of cats and then mice on burrowing birds and recruitment have likely led to reduced habitat suitability and the potential for more responsive species to dominate where *Poa cookii* cover declined.

The repeat photography results suggest that two predictions for specific plant species under changing climate on MI has been realised. First, mire graminoids that include the hygrophilous specialist species, of which the sedge *Carex dikei* was an important or even dominant component in the 1960s (Huntley, 1971), have decreased significantly in mires. Mice target *Carex dikei* seeds and can remove up to 75% of seed heads (Chown & Smith, 1993), reducing recruitment. The density of mice increased sixfold in mires specifically between 1980 and 2011, indicating diet switching (McClelland et al., 2018). The seed predation of *Carex dikei*, combined with the substantial decline in rainfall drying out the dominant habitat for hygrophilous species, mires, is highly likely the reason for the reduction of mire graminoids on the island, even though *Polypogon magellanicus*, also a mire graminoid, has increased. In fact, *Polypogon magellanicus* only occurs in drier mires (Huntley, 1971), thus its increase in cover could also indicate the drying out of mires. Second, *Pringlea antiscorbutica* (the Kergeulen Cabbage), a generally conspicuous plant in the 1960s, was not detected in the repeat photography analysis (although it still occurs on the island; pers. obs. SVDM). Similarly, van der Merwe et al. (2023) and Smith and Steenkamp (2001) did not detect *Pringlea antiscorbutica* in any of their sites considered for the vegetation classification on MI, even though in the 1970s it was prevalent across MI in most community complexes (Huntley, 1971; Gremmen, 1981). This species was previously used to indicate healthy vegetation and the only vascular species predicted to disappear from MI due to its intolerance to warming (Smith & Steenkamp, 1990). Invasive moths have also infested *Pringlea antiscorbutica*, likely causing further dieback (Smith & Steenkamp, 1990). On the sub-Antarctic Kerguelen Islands, *Pringlea antiscorbutica* has also been declining in abundance since the 1990s (Robin et al., 2011). In a species-poor system, the disappearance of even one vascular species may have far-reaching consequences for the indigenous biota. For example, the decline and potential local extinction of *Pringlea antiscorbutica* or *Carex dikei* may increase the available niche space for alien species.

Some of the vegetation changes observed here are mirrored on other sub-Antarctic islands, where plant biomass has also increased in some circumstances (Bazzichetto et al., 2021). However, each island group also has a unique topography and historical context that has impacted the vegetation differentially. For example, some islands have also reported plant cover decrease, such as on some of the Kerguelen Islands after removal of invasive rabbit (Robin et al., 2011). Nevertheless, the key threats of climate change and/or invasive species are shared by all islands in the sub-Antarctic (Bergstrom & Chown, 1999; Frenot et al., 2005; Convey & Lebouvier, 2009; Robin et al., 2011; Bazzichetto et al., 2021). Therefore, the study of their interactive impact on vegetation is generalisable across the region and should be contextualised by each island group's historical contingencies.

The reliability of using any type of so-called ‘snapshot resampling’, where historically sampled sites are resampled (Stuble et al., 2021), may be questioned by researchers, especially those who advocate for methodologies that allow long-term monitoring at regular intervals, such as is possible with satellite imagery (Magurran et al., 2010). This is because snapshot resampling, such as repeat photography, captures the vegetation properties at one moment in time in a particular season (Hoffman et al., 2020) and is subject to the vagaries of weather conditions (e.g., drought or flooding). Repeat photography also only captures the vegetation properties that are visible at the angle of the photo. However, the accuracy of the results of snapshot resampling increases when either the response variable has low intra-annual variability or the magnitude of change is substantial (Stuble et al., 2021). Both of these factors characterise MI, as is evident in the low seasonal variability together with the pronounced long-term observed climate change. Therefore, the paired data of repeated images still provide a comparison of the vegetation properties at the exact same location and at temporal scales not currently possible with other techniques (Hoffman et al., 2020) other than long-term permanent plots or palynological records. If a study site's history is well documented, such as on MI, plausible interpretations of vegetation change are still possible with resampling methods such as repeat photography and can contribute to a more complete understanding of global change impacts (Stuble et al., 2021).

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data supporting the article's results are archived in the South African Polar Research Infrastructure data repository (https://doi.org/10.15493/SAPRI.08352023).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Description of habitat complexes and their key plant characteristics.

Appendix S2. Overview of plant guilds used in the repeat photography analysis.

Appendix S3. Mean percentage change of plant guild cover across habitats between 1965/1980 and 2019/2020.

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