



# Vegetation Change on subantarctic Macquarie Island



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## Abstract

Macquarie Island has a high diversity of vascular plant species and vegetation communities compared to other subantarctic islands. The severe impact of feral rabbits on the tundra vegetation of this island over many decades has been well documented. The native vegetation is changing rapidly following the removal of rabbits, rats and mice in 2011, in one of the largest island eradication projects undertaken. In the absence of native vertebrate herbivores, plant species distribution and vegetation structure are largely determined by abiotic factors such as climate. Recent responses to climate change are evident in the changing abundance and dieback of vascular plant species in grassland and feldmark vegetation.

This thesis aims to determine how topography, climate and release from grazing pressure influence the distribution of plants and vegetation communities on Macquarie Island by investigating the climatic, topographic and historical factors influencing the dominant vascular plant components of the vegetation.

Climatic factors such as wind exposure, air temperature and cloud cover were investigated using field data, image interpretation and spatial modelling to better understand topographic variation in these factors, which may influence plant species distributions. Changes in vegetation preceding and following pest eradication were observed from a 34-year series of repeat photographs and a temporally equivalent vegetation monitoring sites dataset. Spatial analysis of these changes and of satellite imagery from before and after eradication revealed geographic variation in vegetation trends. The total range and core range of key plant species constituting different vegetation communities were predicted using species distribution models.

South-westerly winds were more damaging to plants than the prevailing westerly and north-westerly winds on Macquarie Island. Air temperature lapse rates on Macquarie Island are steep and have limited diurnal and seasonal variation and are not related to the frequent presence of fog at higher elevations. Tussock grass and megaherbs present in 1980 were reduced or absent in 2009, but in most cases had subsequently increased by 2014, following three growing seasons without grazing pressure. Other floristic elements showed mixed trajectories, including high elevation feldmark vegetation which did not show directional trends consistent with rabbit impacts or climate change. Generalist plant species with a wide



geographic range occur as subdominants over much of their range, with a smaller modelled 'core range' where they have the potential to be dominant species.

The lowland vegetation of Macquarie Island has changed rapidly since the successful pest eradication project in 2011. This ecosystem recovery will continue as the shifting distributions and abundance of individual plant species adjusts to the absence of grazing and a changing climate.





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## Chapter One: Introduction

Ecosystems respond dynamically to internal and external drivers. Most ecosystems on Earth have been substantially altered by anthropogenic processes (Watson *et al.* 2016). Current rates of global change are considerably greater than typical background rates for ecological factors at the biosphere scale (Gaffney & Steffen 2017; Rockström *et al.* 2009). In particular, anthropogenic climate change is altering the structure, function and distribution of ecosystems across the Earth. Climate change in the present century and beyond is likely to have dramatic impacts on ecosystems.

Terrestrial environments at high elevations and high latitudes are among the least disturbed by human agency but are also highly susceptible to ecological impacts of anthropogenic global change (Callaghan *et al.* 2011; Watson *et al.* 2016; Wookey *et al.* 2009). The flora and vegetation of alpine and subpolar environments is relictual, having contracted in distribution since the last glacial maximum (Birks 2008). In the Southern Hemisphere these cool-climate habitats are small and fragmented and therefore highly vulnerable to further contraction and loss in a warming climate (Hodgson 2009; Venn *et al.* 2017).

These cool-climate ecosystems are often well-defined spatially and simple in structure and function (Convey 2007), making them more amenable to study the effects of environmental impacts and global change than more complex ecosystems (Chown *et al.* 1998). Improved knowledge of these ecosystems will aid land managers of these environments, which are covered by management plans in most cases (Whinam *et al.* 2006). Invasive species and climate change are key threats to the persistence and integrity of cool-climate terrestrial environments (Bergstrom & Chown 1999; Lembrechts *et al.* 2016; McDougall & Walsh 2007; Venn *et al.* 2017; Whinam *et al.* 2006).

In this thesis, I investigate how topography, climate and release from grazing pressure influence the distribution of plants and vegetation communities on Macquarie Island.

This Introduction chapter comprises an overview of the subantarctic islands and environment, followed by a review of the vegetation, climate and environmental history of Macquarie island within the context of the subantarctic tundra biome. The subantarctic zone is briefly described with a particular focus on the terrestrial vegetation, followed by a review of Macquarie Island flora, vegetation and plant ecology. Key characteristics of the subantarctic climate are outlined,

followed by a review of meteorological and bioclimatic studies relevant to the ecology of Macquarie Island. The impact of feral mammals on subantarctic islands, particularly rabbits on Macquarie Island, is summarised. The role of climate and grazing in determining past and present spatial patterns of plant species and vegetation communities is discussed prior to considering future vegetation patterns in response to climate change and grazing cessation. Finally, this chapter presents the research aims and thesis structure.

## The subantarctic

Although the subantarctic region has been variously defined, a widely used definition includes those islands beyond the limit of tree growth but supporting abundant vascular plant vegetation, i.e. South Georgia, Marion and Prince Edward Islands, Îles Crozet, Îles Kerguelen, Heard and McDonald Islands and Macquarie Island (Smith & Lewis Smith 1987). Warmest monthly mean temperatures are around 7–8°C and for most subantarctic islands no monthly minimum is below 0°C at sea level (Convey 2007), though temperatures can be substantially lower at higher elevations.

The tundra biome comprises ecosystems where tree growth is prevented due to low temperatures or high winds and precipitation (French & Smith 1985). The subantarctic islands are a distinct subset of the tundra biome, with a highly oceanic climate making them more closely related to the cool temperate environment than the Antarctic (French & Smith 1985). Compared to the Northern Hemisphere, subantarctic tundra occurs at relatively low latitudes (Bergstrom & Chown 1999). This is likely to be due to the effect of strong winds at subantarctic latitudes (French & Smith 1985) counteracting the oceanic influence on air temperature, which ameliorates the subantarctic climate compared to equivalent continental latitudes (Meurk 1984). The oceanic climate results in a long growing season (from around 170 to 300 days per year, depending on latitude) near sea level with consequently high annual net productivity (Smith 1987).

In near coastal environments, the climate is warm enough to support high levels of primary productivity but too cool for corresponding rates of organic decomposition. Consequently, deep organic soils develop near the coast and gradually decrease, along with vegetation cover, with elevation (Smith & French 1988; Whinam *et al.* 2006). High elevation, inland environments typically have mineral soils, periglacial landforms and sparse vegetation characteristic of feldmark ecosystems (Boelhouwers *et al.* 2003; Smith & Steenkamp 2001).



The most extreme subantarctic environments are polar desert, ice caps and glaciers, which occur beyond the tundra zone on Marion, Heard, South Georgia and Kerguelen islands (Bergstrom & Selkirk 2000; Smith & Lewis-Smith 1987; Smith & Mucina 2006).

Although they differ geologically (Quilty 2007) and are separated by large distances, the subantarctic islands share many vascular plant species and have similar vegetation communities (Smith & French 1988). Vegetation on subantarctic islands reflects a consistent suite of environmental influences: cool temperatures, strong winds, substrate instability, salt deposition and high inputs of biotic nutrients from seabirds and marine mammals (Bergstrom & Selkirk 2000; French & Smith 1985; Jenkin 1997; Smith & French 1988; Smith & Mucina 2006; Smith & Steenkamp 2001).

Unlike the subarctic and temperate zones, the subantarctic islands lack large native herbivores. Few of the invertebrate species are herbivores (Convey 2007). Despite having relatively low diversity and abundance, invertebrates are important for terrestrial nutrient cycling (Bergstrom & Pedersen 1999) along with fungi and bacteria (Smith & Lewis-Smith 1987). Away from animal sources of nutrients, decomposition and cycling of plant litter and peat are the main sources of plant nutrients (Smith 2008).

Subantarctic terrestrial ecosystems are therefore influenced by the highly oceanic climate, isolation from other landmasses and lack of disturbance by fire and herbivores, at least in the pre-human era. The unique characteristics of subantarctic terrestrial ecosystems, which differ notably from polar and alpine ecosystems, and their small spatial extent makes them important for conservation (Selkirk 2007).

In recognition of their outstanding universal value, both of Australia's subantarctic territories are listed properties under the UNESCO World Heritage Convention. Heard and McDonald islands and Macquarie Island are both recognised for their geological processes and abundance of wildlife. Macquarie Island is also listed for aesthetic values, combining a wild and spectacular landscape with dramatic vegetation and large congregations of wildlife.

### Macquarie Island vegetation

Macquarie Island has a greater diversity of native vascular plant species than other subantarctic islands (Chown *et al.* 1998; Convey 2007; Smith 1984; Van der Putten *et al.* 2010); yet with 42 indigenous species it is a very modest flora compared to less isolated and extreme

environments. Characteristics of some of the dominant vascular plant species are summarized in Table 1. Non-vascular plants are more diverse, with some 200 species (Smith 1984) and in some situations mosses are dominant. In the absence of woody plants, the vegetation is dominated by forbs, graminoids, ferns and mosses (the mat-forming *Coprosma perpusilla* has been considered a shrub by some authors but is non-woody). Vegetation types on the island are mire, grasslands, herbfelds and feldmark (Selkirk *et al.* 1990; Venn *et al.* 2017; see Bricher 2012 for a review of classification schemes). Grassland and *Acaena* or *Stilbocarpa* herbfield typically occur on slopes, with *Pleurophyllum* herbfield and mires on flatter sites where the water table is high, and feldmark on higher ground subject to strong winds (Taylor 1955).

Pollen profiles from peat cores are similar to extant plant assemblages over the past few thousand years, but it is not possible to differentiate Poaceae species (Bergstrom *et al.* 2002; Selkirk *et al.* 1983). The pollen record, therefore, does not indicate the extent and abundance of the tussock grass *Poa foliosa* relative to the shorter grasses that are presently widespread, such as *Agrostis magellanica* and *Festuca contracta*. Megaherbs are prominent in pollen cores, with *Stilbocarpa polaris* abundant near the coast and *Pleurophyllum hookeri* a dominant species further inland (Bergstrom *et al.* 2002).

Most of the present-day dominants of Macquarie Island vegetation have a long history on the island as evidenced by pollen from the base of peat cores, suggesting that the megaherbs *P. hookeri* and *S. polaris*, the cushion plant genus *Azorella*, *Acaena* species and grasses were established at least 7000—8000 years bp (Bergstrom *et al.* 2002). The subantarctic palaeoendemic genus *Pleurophyllum* appears to have survived the last glacial maximum on the cool temperate islands south of New Zealand (Wagstaff *et al.* 2011), probably including Macquarie Island, which was not glaciated (Adamson *et al.* 1996). Other subantarctic islands also show no major changes in their flowering plant floras in the palaeo-ecological record, suggesting a relatively stable environment and infrequent immigration (Van der Putten *et al.* 2010). Genetic studies show multiple immigration events have occurred in some subantarctic flowering plants, but these events are rare and gene flow between islands is very limited (Moon *et al.* 2017). Similarities in the bryophyte, lichen and pteridophyte floras between Macquarie Island and distant locations at similar latitudes suggests that the Southern Hemisphere westerlies are an important long-distance dispersal vector for these wind-dispersed plants (Muñoz *et al.* 2004).

**Table 1.** Characteristics of some key vascular plant species of Macquarie Island. Summarised from George *et al.* (1993).

Scientific name	Family	Common name	Growth form	Size	Global Distribution	Habitat/Distribution on Macquarie Island
<i>Acaena magellanica</i>	Rosaceae	Subantarctic buzzy	Mat forming herb	To 12 cm tall	Macquarie Is., Patagonia, most subantarctic islands	Widespread
<i>Acaena minor</i>	Rosaceae		Mat forming herb	To 5 cm tall	Macquarie Is., Auckland Is., Campbell Is.	Widespread, generally on drier sites than <i>A. magellanica</i>
<i>Agrostis magellanica</i>	Poaceae	Subantarctic bentgrass	Tufted grass	To 45 cm tall	Macquarie Is., New Zealand (including subantarctic islands), Patagonia, several subantarctic islands	Widespread
<i>Azorella macquariensis</i>	Apiaceae	Macquarie Island cushionplant	Cushion herb	Cushions reach c. 0.3 m tall and 2 m wide	Macquarie Island endemic	Largely confined to feldmark habitats with skeletal soils and wind exposure
<i>Deschampsia cespitosa</i>	Poaceae		Tufted grass	To 30 cm tall	Cosmopolitan in temperate and arctic zones	Mid-altitude slopes and mires
<i>Festuca contracta</i>	Poaceae		Tufted grass	To 40 cm tall	Macquarie Is., Patagonia, Kerguelen Is., South Georgia, Falkland Is.	Widespread
<i>Luzula crinita</i>	Juncaceae		Tufted graminoid	To 45 cm tall	Macquarie Is., Auckland Is., Campbell Is., Antipodes Is.	Widespread, except waterlogged sites
<i>Poa foliosa</i>	Poaceae	Leafy tussockgrass	Tussock grass	To 1.5 m tall	Macquarie Is., Auckland Is., Campbell Is., Antipodes Is.	Widespread, all habitats except very wind exposed or waterlogged
<i>Polystichum vestitum</i>	Dryopteridaceae		Fern	To c. 0.8 m tall	Macquarie Is., New Zealand (including subantarctic islands)	Confined to relatively sheltered slopes and creeks in the east
<i>Pleurophyllum hookeri</i>	Asteraceae	Macquarie megadaisy	Rosette megaherb	To c. 0.5 m tall and 1 m wide	Macquarie Is., Auckland Is., Campbell Is.	Widespread, usually on sites with poor drainage
<i>Stilbocarpa polaris</i>	Apiaceae	Macquarie Island cabbage	Megaherb	To 2 m tall	Macquarie Is., Auckland Is., Campbell Is., Antipodes Is.	Widespread, all habitats except very wind exposed

Long-distance dispersal appears to be a major filter limiting Macquarie Island's flora since many plants from the neighbouring but distant landmasses of Australia and New Zealand could survive in the subantarctic climate (Duffy *et al.* 2017). Lack of suitable pollinating insects appears to be another selective filter for the Macquarie Island flora (Shrestha *et al.* 2016). Some plant species have established following long-distance dispersal in recent times, notably *Carex trifida* and *Poa litorosa* (Bergstrom *et al.* 2005). Macquarie Island shares a number of species with its nearest neighbours, Campbell and Auckland Islands, which have a slightly warmer climate and support a much higher diversity of vascular plants including some shrubs (Meurk 1982; Meurk *et al.* 1994).

Compared to continental habitats and extreme polar environments, the subantarctic environment presents an unusual set of limitations on the growth and survival of plants. On Macquarie Island, plant growth is limited by nutrients, air temperature and low levels of radiation (Jenkin 1975; Tweedie 2000). Water stress is not a limiting factor (Jenkin 1975), although changed rainfall patterns may be leading to water stress in field environments (Bergstrom *et al.* 2015). There is considerable spatial variation in the availability of plant nutrients related to the variable influences of geology, sea spray and animal manure and redistribution by wind and water (Erskine *et al.* 1998; French & Smith 1985; Smith 2007).

Large leaves are effective for capturing solar radiation and airborne nutrients and heating plant tissues above ambient air temperature, all of which are potentially advantageous in the subantarctic environment (Little *et al.* 2016). These factors, and the physical size to suppress competition from smaller plants, may explain the convergent evolution and ecological success of megaherbs on some subantarctic islands (Hnatiuk 1975; Little *et al.* 2016; Mitchell *et al.* 1999; Nicholls & Rapson 1999; Wagstaff *et al.* 2011). Large tussock-forming grasses are successful probably for similar reasons. Tussock grassland is characteristic of the cool maritime climates of the Southern Hemisphere that lack large herbivores and fire (Wace 1960).

In grassland and herbfield, particularly at lower elevations, the uniformly cool temperatures are generally not cold enough to limit metabolism (Jenkin 1975; Tweedie 2000). Consequently, the native plants adapted to efficient photosynthesis at low irradiances and low temperature experience a growing season of 8–10 months, resulting in high productivity and biomass (Jenkin 1975; Tweedie 2000). Day length is the major seasonal climatic variable, ranging from

7 to 17 hours (Bergstrom *et al.* 1997), though sunshine hours are considerably less due to cloud cover. These bioclimatic conditions reflect the characteristic subantarctic climate.

### The subantarctic climate

The Southern Hemisphere cool temperate zone, which sits between around 35 and 66.5°S, differs from similar latitudes of the Northern Hemisphere in its predominantly oceanic climates (French & Smith 1985). The most oceanic climates on Earth occur in the more southerly subantarctic part of this zone (Currey 1974), where terrestrial environments account for a tiny proportion of the Earth's surface, in the vast Southern Ocean. Extremes of temperature and droughts are typically absent (Boelhouwers *et al.* 2003; Pendlebury & Barnes-Keoghan 2007).

The Southern Hemisphere storm track, a regular procession of Southern Ocean cyclones circling the Antarctic continent, dominate the subantarctic weather year-round and reach as far north as Tasmania (40–43.5°S) in the austral winter months. The eastward path of these persistent cyclones results in predominantly westerly winds, with the highest annually-averaged oceanic wind speeds on Earth (Hande *et al.* 2012). Macquarie Island's oceanic location and perpendicular alignment to the almost constant westerlies result in a high mean wind speed with little diurnal or seasonal variation (Tweedie 2000).

Inter-annual variation in Southern Ocean climate is largely driven by latitudinal shifts in the path of the storm track, which is quantified by the Southern Annular Mode (SAM) (Turner *et al.* 2013). The SAM is currently in its most positive phase for at least the past 1000 years, partly due to stratospheric ozone depletion, with increasing greenhouse gas concentrations expected to continue this trend (Abram *et al.* 2014). The SAM is also correlated with centennial scale climatic and ecological changes in the middle latitudes of the Southern Hemisphere, including Southern Australia and South America (Fletcher *et al.* 2018; Villalba *et al.* 2012).

Increased wind speeds in the Southern Ocean region, including Macquarie Island, since the 1970s are consistent with the positive SAM, which indicates a greater air pressure gradient between mid and high latitudes (Convey *et al.* 2009; Hande *et al.* 2012). More intense and greater total rainfall at Macquarie Island in recent decades appears to be related to the positive SAM phase (Jovanovic *et al.* 2012; Pendlebury & Barnes-Keoghan 2007). However, warming trends at subantarctic latitudes appear to be independent of the SAM and are stronger in the

Indian Ocean sector of the subantarctic than at Macquarie Island (Richard *et al.* 2013). For example, Marion Island experienced around 1.0°C warming in the second half of last century (le Roux & McGeoch 2008a), the Kerguelen Archipelago warmed by 1.3°C over 40 years (Chapuis *et al.* 2004), while an increase of 0.3°C occurred on Macquarie Island after 1948 (Tweedie & Bergstrom 2000). The total warming during the previous century on Macquarie Island is estimated at 0.6°C (Tweedie & Bergstrom 2000), having been limited due to a slight cooling trend since 1980 (Turney *et al.* 2017).

As a driver of subantarctic climate, current and future changes in the depth, frequency and latitudinal position of circumpolar cyclones will influence the rainfall and winds experienced at Macquarie Island. Modelling suggests that a significant decline in the number of subantarctic cyclones (between 40°S and 60°S) that occurred during the past century will continue (Fyfe 2003). Complex interactions between natural modes of variability, such as SAM, and anthropogenic forcing could lead to major and rapid shifts in the Southern Hemisphere westerlies this century (Mayewski *et al.* 2015).

Air temperature at Macquarie Island is tightly coupled to sea surface temperature, displaying a general trend of increasing inter-annual variability and warming over the past century (Turney *et al.* 2017). Sea surface temperatures near Macquarie Island are projected to warm by around 1°C during the present century according to global climate models (Turner *et al.* 2009).

Projections based on trends in climatic variables observed last century indicate that Macquarie Island is likely to become warmer, windier, less sunny, less humid and receive more precipitation (Tweedie 2000). The highest forecast rate of change among these extrapolations is for an increase in mean monthly vapour pressure deficit (Tweedie 2000). However, in most cases inter-annual variation is greater than the forecast change over the period 1948—2030 (Tweedie 2000).

Macquarie Island's small size (128 km<sup>2</sup>) and oceanic situation means the entire island is subject to the same synoptic conditions with limited influence of continental processes such as thermal convection or cold air drainage. Consequently, spatial variation in climate on the island is a result of the influence of topography on moving air masses and incident solar radiation. Air and soil temperatures decrease with elevation, but not linearly (Tweedie 2000). Precipitation varies spatially across the island, with highest levels on the lee side of the plateau (Wang *et al.* 2016). Fog is a frequent phenomenon (Streten



1988) and is likely to influence several climatic parameters relevant to plant growth, including incident solar radiation, precipitation and air temperature.

### Meteorological data and bioclimatic studies

The only long-term climate data for Macquarie Island come from a Commonwealth Bureau of Meteorology (BOM) station near sea level on the isthmus at the northern end of the island, established in 1948. These data are possibly not representative of the climate experienced across most of the island (Davies & Melbourne 1999; Jenkin 1972; Tweedie 2000; Wang *et al.* 2016). Meteorological observations from sites other than the BOM station are very limited in space, time and weather variables (e.g. Davies & Melbourne 1999; Jenkin 1972; Löffler 1983; Tweedie 2000).

Tweedie (2000) observed and calculated numerous climatic and bioclimatic variables on an altitudinal transect on Macquarie Island. The resulting 13-month dataset represents the only comprehensive meteorological dataset from Macquarie Island apart from long-term records of the BOM. Strong positive correlations were found between air and soil temperatures and precipitation at all elevations but the BOM observations were not good predictors of wind speed, relative humidity or evapotranspiration on the transect, particularly at higher elevations (Tweedie 2000).

Jenkin (1972) noted the difficulty of accurately quantifying precipitation in the field due to the influence of strong winds (horizontal rain) and frequent snow and fog which may not be accurately captured by a rain gauge. Fog interception is likely to be an important contribution to the hydrology of Macquarie Island. While data are lacking for Macquarie Island, in the maritime climate highlands of New Zealand for interception can add up to 22% of the recorded rainfall amount (Fahey *et al.* 2011; Ingraham & Mark 2000).

Climatic variables can be useful for explaining and predicting the distribution of plant species if the relevant variables are available at sufficient spatial resolution. However, microclimates experienced by vegetation can be substantially different from the climate recorded by standard meteorological observations. For example, differences of 15°C have been observed between subantarctic grassland and ambient air (Walton 1984).

Given the low amplitude of climatic conditions experienced by the subantarctic flora, even relatively modest global climate change is expected to shift conditions outside of the Holocene

climatic envelope. Subantarctic endemics such as *Azorella macquariensis* are potentially highly sensitive to climate change (Bergstrom *et al.* 2015). Due to the small number of vascular plant species, the vegetation is particularly vulnerable to disturbances (Jenkin 1975). This may be due to a lack of functional redundancy which allows exotic species, such as ruderal weeds, to invade unoccupied niches or outcompete native species (Convey 2007). Decline or loss of a dominant species, for example, can have ecosystem-transforming effects (Bergstrom *et al.* 2015).

Wind speed has a strong influence on bioclimatic indices such as net precipitation, evapotranspiration and wind chill (Tweedie 2000), and therefore changes in wind regimes could have substantial impacts on plant growth and species distributions (Bergstrom *et al.* 2015; le Roux *et al.* 2005; Pammenter *et al.* 1986). Such interactions between climatic variables and between climate and biotic stressors such as introduced herbivores make predictions about climate change impacts difficult.

### Impacts of feral mammals

Invasive fauna species are widespread on the subantarctic islands and have had considerable impact on the native biota and ecosystems (Chapuis *et al.* 1994; Convey & Lebouvier 2009; Greve *et al.* 2017; Whinam *et al.* 2006). In particular, cats (*Felis catus*) have preyed on birds (Smith 2007), and the megaherb communities on several islands have been seriously impacted by feral herbivores (Convey 2007). Several successful eradication projects have alleviated these impacts (Broome 2009; Convey & Lebouvier 2009). Control and eradication of feral animals has been an important management strategy on Macquarie Island, which is a managed as a Nature Reserve, Biosphere Reserve and World Heritage Area (Carmichael 2007).

Since their introduction by humans around 1880, European rabbits (*Oryctolagus cuniculus*) transformed the structure and composition of the native vegetation across much of Macquarie Island (e.g. Carmichael 2008; Copson & Whinam 1998; Costin & Moore 1960; Jenkin 1972; Saunders *et al.* 2014; Scott 1988; Scott & Kirkpatrick 2012; Taylor 1955; Whinam *et al.* 2014a). Feldmark communities and some steep coastal slopes in the far south of the island were less affected due to lower rabbit populations (Copson *et al.* 1981; Scott 1988). Less accessible sites such as rock stacks and cliffs were little impacted (Copson & Whinam 1998). In favourable habitats, population density could exceed 8 rabbits per hectare (Copson *et al.* 1981).

Besides rabbits, the other long-established alien mammals on Macquarie Island were the domestic cat (*Felis catus*), black rat or ship rat (*Rattus rattus*) and the house mouse (*Mus musculus*) (Springer 2016). Eradication of cats in 2000 (Robinson & Copson 2014) may have contributed to an increase in rabbit population (Bergstrom *et al.* 2009), along with other factors (Brothers & Bone 2008; Dowding *et al.* 2009; Kirkpatrick 2009). The rabbit population in 2006 was the highest in 25 years (Terauds *et al.* 2014), with severe impacts on vegetation (Scott & Kirkpatrick 2012; Whinam *et al.* 2014a). For example, the magnitude of damage to tall tussock vegetation at this time may have been unprecedented (Carmichael 2008).

Rats and mice had some negative impacts on the vegetation. These impacts were less widespread and severe than that of rabbit grazing and digging (Brothers & Bone 2008; Pye *et al.* 1999; Raymond *et al.* 2011; Shaw *et al.* 2005). Furthermore, rodents do alter the ecosystem at other levels. Mice have been associated with a significant negative impact on invertebrate populations on subantarctic islands (McClelland *et al.* 2018) with consequent reduction in nutrient cycling (Smith 2008). Rats preyed on several seabird species nesting on Macquarie Island (Brothers & Bone 2008), which may have reduced nutrient inputs to the soils. Eradication of feral mammals is considered successful, since no rabbits, rats or mice have been detected on Macquarie Island since 2011 (Springer 2016). Globally, eradication of rabbits from islands results in increased vegetation cover and plant species richness, with increased percentage cover of most native and exotic plant species occurring across a wide geographic range of islands (Schweizer *et al.* 2016).

### Present and future vegetation patterns

While it is clear that substantial changes in vegetation followed rabbit establishment, the natural composition, structure and distribution of vegetation on Macquarie Island prior to rabbits is poorly known. Observers in the late 19th century, soon after rabbit introduction, noted extensive *P. foliosa* tussocks, along with *S. polaris* and patches of *P. hookeri*, and at higher elevations, mosses and *A. macquariensis* (Kirkpatrick 2009).

Since the major perturbation of Macquarie Island's vegetation (Hodgson 2009) has ceased with the eradication of rabbits, the system is expected to revert to a pre-rabbit state, subject to modification by climate change and possibly persistent long-term ecosystem impacts from rabbit grazing. There is also potential for ecological change due to the establishment of new

plant species, following either natural or human-mediated migration, or the expansion of recent colonists such as *C. trifida*.

To understand the vegetation recovery process and future changes in vegetation it is necessary to understand past rabbit impacts on the vegetation and current environmental determinants of plant species distributions. Since rabbit eradication, vegetation disturbance is localized on Macquarie Island, with no broad-scale disturbances such as fire and grazing. Therefore, key influences on vegetation distribution are some combination of localized disturbance, edaphic, climatic and interspecific factors.

Climatic factors such as air temperature and wind exposure are related to the distribution and abundance of vascular plants on subantarctic islands (le Roux & McGeoch 2008a, Smith & French 1988; Smith & Steenkamp 1990). Despite their isolation and geological differences, the subantarctic islands are broadly similar ecologically with several plant species occurring on more than one island and analogous vegetation communities. This ecological similarity reflects a climatic similarity: they all share a cold maritime climate.

Persistent winds are a notable feature of alpine and subantarctic climates, with a variety of physiological and ecological effects on plants (Gardiner *et al.* 2016; Grace 1977). Strong winds are potentially a limiting factor for the growth and survival of plant species in wind-exposed locations (Gardiner *et al.* 2016; Pammenter *et al.* 1986). Feldmark communities, for example, comprise a subset of alpine or subantarctic plants found in neighbouring communities.

Wind speed and direction vary with topography, particularly in mountainous terrain. To understand the relative wind exposure experienced by plants in the environment it is necessary to determine the direction of damaging winds. Studies of wind impacts on natural ecosystems are mostly confined to trees and forest in the Northern Hemisphere, with little research on shrubs and non-woody plants (Gardiner *et al.* 2016).

Many species are widely distributed across Macquarie Island (Copson 1984). The extent and abundance of these widespread generalist plant species is likely to be influenced by interspecific interactions, such as competition for light and nutrients. Some plant species have very limited distributions indicative of either a narrow fundamental niche or barriers to occupying their niche. Coastal species such as *Puccinellia macquariensis*, *Crassula moschata* and *Colobanthus muscoides* are probably limited to the sparsely vegetated sea spray zone by an

inability to compete with other species (Taylor 1955). In contrast, there is no obvious explanation for the disjunct and localized distribution of *Poa litorosa* (Williams *et al.* 2016) or the very rare *Galium australe*.

Taylor (1955) mapped the Macquarie Island vegetation using three structural vegetation types: tussock grassland, herbfield and feldmark. He also described seven floristic associations. Later vegetation mapping by Selkirk and Adamson (1998) used a similar structural scheme with three vegetation types (closed tall herb, closed and complex vegetation) because the six floristic communities described by Selkirk *et al.* (1990) were not distinguishable from satellite imagery and aerial photography. Bricher (2012) reviewed the phytosociological and vegetation mapping schemes previously applied to Macquarie Island and considered the determination of vegetation communities or mapping units to be arbitrary and inconsistent. Instead, Bricher (2012) focussed on the distribution of key plant species as a method for monitoring vegetation change.

Previous research on Macquarie Island vegetation has described an environment altered by alien herbivores. To understand and monitor the emerging threat of climate change it is important to determine the distribution of plant species in the present environment, which is without macroherbivores.

The observed impact of rabbits on Macquarie Island vegetation and the early stages of post-eradication ecosystem recovery can provide an insight into the prehuman vegetation distribution and dynamics of a subantarctic ecosystem.

## Research Aims

The primary research question of this thesis is:

How do topography, climate and release from grazing pressure influence the distribution of plants and vegetation communities on Macquarie Island?

The following questions help address the primary question:

How does the topography and climate shape vegetation communities on Macquarie Island?

How will plant species occupy the landscape following release from grazing pressure?

This is the first comprehensive investigation of the response of Macquarie Island flora and vegetation to a total release from all grazing pressure.

## Thesis structure

Relationships between the four research chapters are presented in Fig. 1.

### *Chapter 2: Wind distortion in alpine and subantarctic plants*

Previous researchers have noted that wind speed and direction observations from the meteorological station on Macquarie Island's isthmus may not be representative of the wind conditions experienced across most of the island, particularly the exposed plateau region. Wind can be a limiting factor for plant growth in exposed environments, influencing vegetation structure and species composition. Wind speed and direction has changed on Macquarie Island over recent decades and is projected to continue changing. Growth distortions in woody plants have been shown to provide an indication of predominant wind direction in various environments.

This chapter explores the utility of this method in environments lacking woody plants, such as Macquarie Island, by firstly examining patterns of wind distortion in graminoids and cushion plants where they co-occur with shrubs in wind-exposed alpine vegetation in Tasmania. Secondly, wind damage and distortion were inferred from asymmetry in Macquarie Island plant growth. Examining the characteristics of wind frequency, intensity and associated weather variables provides inferences about the ecological role of winds in shaping vegetation.

### *Chapter 3: Air temperature lapse rates and cloud cover in a hyper-oceanic climate*

Air temperature is a key factor controlling the performance and limits of plant species. Understanding how air temperature changes with elevation (i.e. environmental lapse rates) is important for understanding the present distributions of species and vegetation, which often show altitudinal zonation, and for predicting and monitoring the ecological effects of climate change. This chapter examines diurnal and seasonal patterns in lapse rates on both the western (windward) and eastern (leeward) sides of Macquarie Island. A feature of Macquarie Island's subantarctic climate that is likely to have a considerable influence on the vegetation is frequent cloud cover. This chapter investigates diurnal and seasonal patterns in the vertical coverage of cloud on the island and its relationship to lapse rates.



#### *Chapter 4: Patterns of vegetation and landscape change before and after rabbit eradication on subantarctic Macquarie Island*

To examine the negative impacts of rabbits on the vegetation of Macquarie Island and the subsequent ecosystem recovery this research project examined a time series of photographs from 109 locations across the island. Each scene was photographed in 1980 when rabbit numbers were low; in 2009 when rabbit numbers were moderate after a population peak; and in 2014, 2.5 years following rabbit eradication. Qualitative differences in vegetation were recorded for each scene and the observations geolocated to examine spatial and topographic patterns in vegetation trajectories associated with rabbit grazing and release from grazing.

A time series of floristic data from six vegetation monitoring sites established in 1981 provided data on the abundance of plant species with more detail but less spatial coverage than the rephotography. Satellite image change detection was also used to investigate vegetation change for the latter period in the northern part of the island. Using approaches with different coverage and precision makes up for the strengths and weaknesses of individual methods when quantitative data are not available at sufficient temporal or spatial scales to examine long-term change at the landscape scale.

#### *Chapter 5: Using species distribution models to predict floristic assemblages in herbaceous vegetation following grazing release*

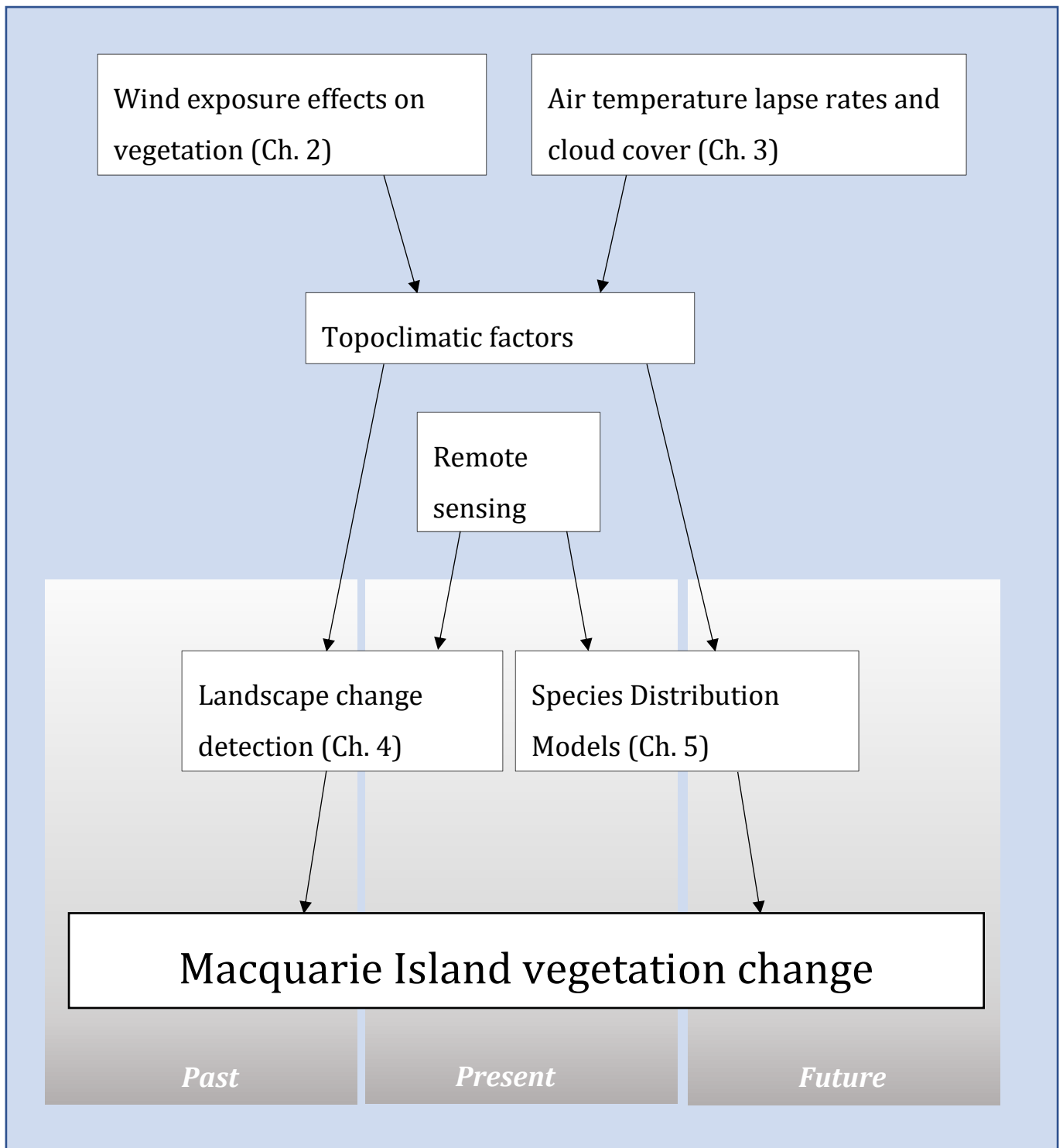
Vegetation classification and mapping is a key tool for understanding and monitoring ecosystem change but is plagued by theoretical and practical problems. Mapping vegetation using traditional remote sensing interpretation can discriminate only three vegetation structural types on Macquarie Island, much fewer than the described floristic communities. Where sufficient species location data are available, mapping species using species distribution models (SDMs) can reduce the uncertainty and assumptions involved in delineating communities.

A typical SDM approach using only presence records would not be very informative on Macquarie Island where many dominant plant species are widespread generalists. Using three classes (absent, not-dominant, dominant) for SDMs allows more useful inferences about vegetation communities. This chapter demonstrates a method for modelling the core range of

dominant species and using these core ranges to predict present and near-future vegetation community spatial patterns.

### *Chapter 6: General discussion*

The final chapter is a synthesis of the results from the preceding chapters, discussing how topography, climate and release from grazing pressure influences the distribution of plants and vegetation communities on Macquarie Island. Gaps in knowledge and future research directions are identified.



**Fig. 1.** Schematic representation of research process and thesis structure.

## Chapter Two: Wind distortion in alpine and subantarctic plants

This chapter examines wind as one of the climatic factors that may be significant in determining the distribution of plant species and consequently the structure and composition of vegetation communities in alpine and subantarctic environments.

This chapter uses observations of plant growth form to infer the characteristics of winds which influence plant growth in wind-exposed environments. If wind is a significant factor in determining the distribution of plant species and vegetation communities in high-wind environments, such as the subantarctic, we would expect the relevant wind characteristics to be useful predictive variables in spatial modelling of vegetation distribution and temporal change (Chapter Four) and in modelling the spatial distribution of key plant species (Chapter Five). This chapter establishes the likely most ecologically important wind direction and speed on Macquarie Island in order to spatially model wind exposure across the island in Chapters Four and Five.

The research contained in this chapter has been published as:

Fitzgerald NB, Kirkpatrick JB (2017) Wind distortion in alpine and subantarctic plants is constant among life forms but does not necessarily reflect prevailing wind direction. *Arctic, Antarctic, and Alpine Research* **49**, 521–535.

## Abstract

Woody plants in windy environments have been used as indicators of prevailing wind direction, since wind can influence plant growth form. We investigated whether non-woody plants also display consistent prevailing wind deformation by observing the direction of asymmetry in growth form of cushion plants, graminoids and prostrate shrubs growing in highly wind-exposed treeless environments in alpine Tasmania and subantarctic Macquarie Island. Wind distortion of individual plants was inferred from vertical photographs of fieldmark and alpine heath vegetation. High correspondence in growth direction between plants of different types suggests a uniform wind influence on plants at the local scale (within < 2 m). Dominant wind direction inferred from plant distortion was not consistent with the strongest and most frequent winds. On a relatively dry mountain with shallow soils the plants responded to strong northwest winds in an apparent desiccation response. Elsewhere, they responded to strong southwest winds in an apparent ice abrasion response. This study shows that, in maritime alpine and subantarctic environments, the direction of wind distortion can be measured using any of shrubs, graminoids or cushions plants. However, this direction is not necessarily a response to the prevailing strongest winds, rather winds that most damage foliage, the cause of damage varying with environmental context.

## Introduction

An influence of wind on plant growth form is observable in many plants, including tropical trees (Noguchi 1979), subalpine conifers (Wooldridge *et al.* 1996) and grasses (Aston & Bradshaw 1966). Deformation of trees and shrubs in windy environments is used as an indicator of prevailing wind direction and wind speeds, providing a useful proxy measure in areas lacking in meteorological data or where winds are spatially variable due to complex topography (Noguchi 1979; Wooldridge *et al.* 1996). However, it is not clear whether non-woody plants give the same indication of variation in wind speed and direction as woody plants, or whether the relationship of distortion to particular parameters of wind regimes is constant between environments.

The local wind regime (frequency, magnitude, duration, direction, seasonality), small scale differences in airflow due to topography and vegetation, other climatic factors, plant morphology and plant ecophysiology can all influence patterns of plant growth (Anten *et al.* 2010; Gardiner *et al.* 2016; Holtmeier & Broll 2010). Asymmetry in trees exposed to strong winds can occur by physical damage (wind or wind-blown particles) or asymmetric growth due to biomechanical properties of wood under stress (Telewski 2012). Asymmetry in trees is related to persistent or repeated winds over a certain threshold speed during infrequent synoptic scale weather (Bonnesoeur *et al.* 2016; Robertson 1994).

In many cases, high wind speeds reduce transpiration and evaporation by cooling the leaf surface and thus reducing the leaf to air vapour pressure deficit (Dixon and Grace 1984). While wind is unlikely to contribute directly to desiccation, other mechanisms of drought damage are evident in cold climate plants, including cuticular damage caused by windblown particles which can lead to water loss from the leaf. Where water availability is limited, desiccation can lead to foliage loss or mortality. For example, winter water deficits are associated with some northern hemisphere alpine treelines (Holtmeier & Broll 2010). Cold dry southwest winds, rather than the stronger moister northwest winds, are associated with drought damage to cushion plants on subantarctic Marion Island (le Roux *et al.* 2005). Subantarctic cushion plants (*Azorella* spp.) are predisposed to desiccation due to a simple vascular system, shallow roots and a structural reliance on turgidity (Bergstrom *et al.* 2015).

Physical asymmetry in the vegetation drives migration or cyclic succession as plants grow preferentially in the direction of the prevailing wind, with erosion or leaf mortality on the



windward side (Ashton and Gill 1965; Barrow *et al.* 1968; Mark and Bliss 1970; Morgan *et al.* 2010). Wind damage in plants can occur at the patch or landscape scale as distinctive vegetation patterns, such as ‘fir wave’ forest (Foster 1988), ‘ribbon forest’ (Holtmeier and Broll 2010), dynamic feldmark (Barrow *et al.* 1968) and vegetated stripes in arid shrublands (Okin and Gillette 2001). Wind exposure can influence alpine tree-lines, with woody vegetation limited to lower elevations on slopes subject to stronger winds (Wagemann *et al.* 2015).

Morphological responses of non-woody plants to wind may be useful as an indicator of wind regimes in areas lacking both meteorological instrumentation and woody vegetation, such as the subantarctic islands. The way in which wind influences plant growth is also of ecological interest, particularly in a rapidly changing climate.

In locations where wind is a key environmental stress we expect that graminoids and cushion plants will display a morphological response to wind by directional growth away from the direction of the strongest winds, as is known to occur in woody plants. Alpine sites in Tasmania where woody plants co-occur with graminoids and/or cushion plants allowed us to investigate whether these three different life-forms displayed a consistent directional response within and between sites.

Based on the response of Tasmanian alpine plants, we extend this method beyond the limits of woody plants in the high latitudes of the subantarctic by investigating cushion plants and graminoids on Macquarie Island. We consider the use of non-woody plants as a proxy for wind exposure and their relationship to wind regimes in mid to high latitude oceanic climates. To explain the apparent wind response in plants we consider wind characteristics including frequency, intensity, seasonality, air temperature and relative humidity.

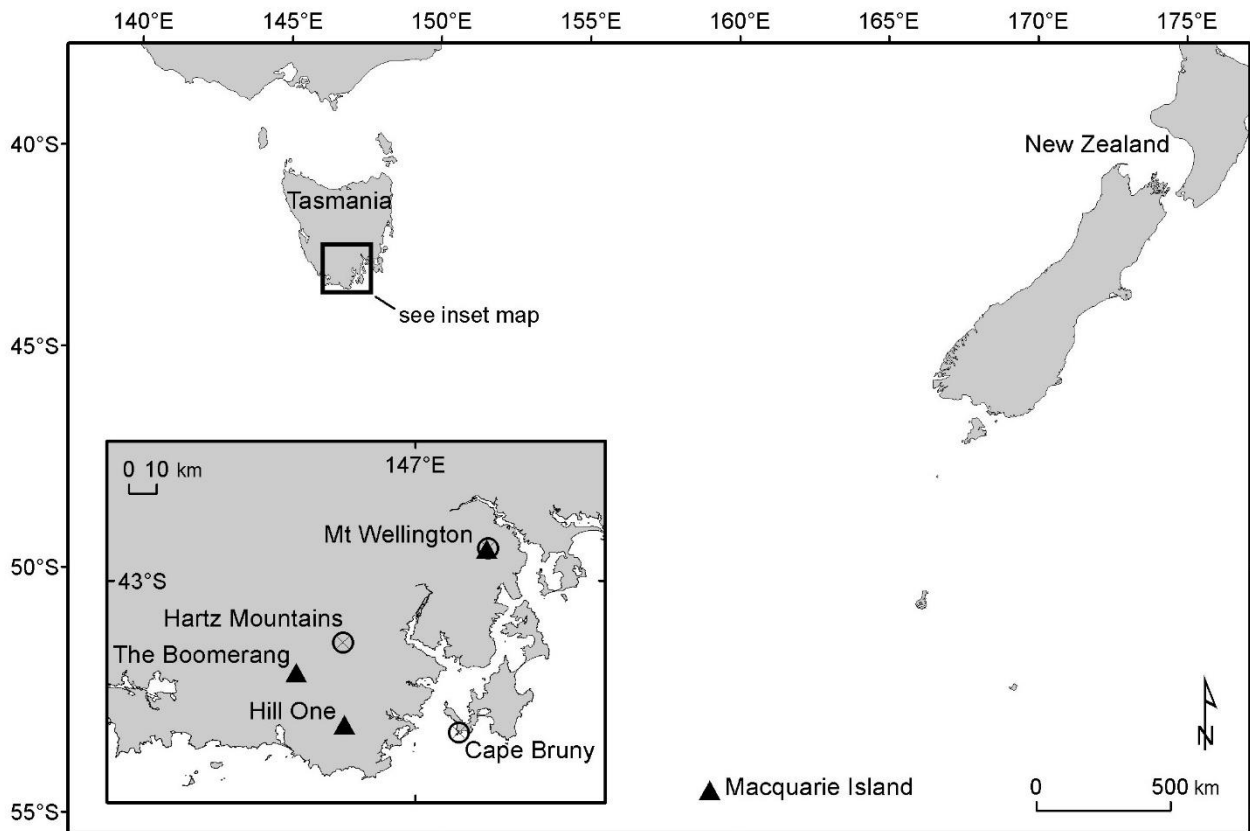
### Methods

Three alpine locations in southern Tasmania, Australia, and one study site on the Australian subantarctic territory of Macquarie Island (Fig. 1; Table 1) were examined using vertical photography with a handheld camera. The Mount Wellington site was rephotographed monthly over one year to test for seasonal changes in plant distortion, while the other locations utilized photography from a single time period. Nomenclature follows de Salas and Baker (2016).

**Table 1.** Study site details. Annual mean air temperature is from a BIOCLIM model for Tasmania (Landscape Logic 2008) and, for Macquarie Island, from a global BIOCLIM dataset (Hijmans *et al.* 2005). Modelled annual rainfall is derived from Nunez *et al.* (1996) for Tasmania and Hijmans *et al.* (2005) for Macquarie Island.

Site	Elevation (m.a.s.l.)	Latitude/ Longitude	Number of quadrats	Quadrat size (m)	Modelled annual rainfall (mm)	Mean min. temp coldest month (°C)	Mean max. temp warmest month (°C)
Mt Wellington	1250–1255	42°54'S 147°14'E	12	1 x 1	925	-1	12
Hill One	990–1010	43°28'S 146°46'E	31	1 x 1.5	1915	0	13
The Boomerang	1030–1081	43°18'S 146°37'E	62	1 x 1	2100	-1	13
Macquarie Island	170–340	54°32'S 158°54'E	35	2 x 2	960– 1040	0	7

This study derives new data by reanalysis of photographs from previous photo-monitoring studies, plus a new site at Mount Wellington. Consequently, the sampling methods and quadrat sizes vary between sites. However, the quantitative data used here is not area based and therefore not influenced by quadrat size, rather it is the relative proportion of quadrats at each site with plants present in each wind distortion class. Quadrat sizes (range: 1–4m<sup>2</sup>) are appropriate for the low alpine vegetation.



**Fig. 1.** Location of the four study sites with the three Tasmanian alpine sites shown in inset map (triangles). Australian Bureau of Meteorology (BOM) weather stations used for wind data also shown for Tasmania (circles). Macquarie Island BOM station not shown due to map scale.

In cushion plants, the wind response is evident as foliage death and erosion of the cushion on a particular side of the cushion, typically resulting in a crescent shape (Fig. 2a). Cushion plants are variable in shape due to endogenous processes of coalescence and senescence (e.g. Cerfonteyn *et al.* 2011) as well as environmental factors. We focused only on physical damage consistent with wind impacts. In shrubs there is often wind damage evident as stripped bark but the key feature is the strongly linear orientation of branches and foliage (Fig. 2b). Graminoids which would have a circular or spherical form in sheltered sites can display an asymmetric form indicative of wind distortion, or the leaves and culms are consistently aligned in one direction (Fig. 2b).



**Fig. 2a** Cushion plant *Donatia novae-zealandiae* displaying crescent shape due to wind erosion by southerly winds, The Boomerang. Measuring tape aligned north-south with north at top. Quadrat measures 1 x 1 m. Photograph by Micah Visoiu. **Fig. 2b** Graminoid *Carpha alpina* showing distortion attributed to westerly winds, Mt Wellington. The shrubs *Epacris serpyllifolia* and *Leptospermum rupestre* display similar orientation. Top of image is north. Quadrat measures 1 x 1 m

Twelve 1 x 1 metre quadrats were established on a slightly elevated rocky area near the summit of Mount Wellington, chosen because it is exposed to winds from all directions. Quadrats placed at a randomly located northwest corner point were aligned to magnetic north. Random quadrats were excluded if they did not contain both woody plants and graminoids with at least one individual of either displaying directional distortion until 12 quadrats meeting these criteria were established. Each quadrat was photographed vertically (from above) with a wide-angle lens.

This site is located on Jurassic dolerite with regosols (Kirkpatrick and Dickinson 1984) and includes rock outcrops where soil is confined to joints in the rock. Vegetation is alpine heath with an open shrub layer and a mix of graminoids (principally *Carpha alpina*), bryophytes and forbs. Prostrate and semi-prostrate shrubs include *Leptospermum rupestre* and *Epacris serpyllifolia*, while *Richea scoparia* and *Orites acicularis* grow as erect shrubs to around 0.8 m tall.

Individual plants of both shrubs and graminoids were selected from the photographs for analysis if they displayed signs of directional growth, or in quadrats with one or fewer individuals of either shrubs or graminoids displaying distortion, other individuals with no distortion were randomly selected to be included in the analysis.

Photographs were rectified to remove lens distortion using GIMP 2.0 ([www.gimp.org](http://www.gimp.org)). ScreenScales software ([www.littlearea.com](http://www.littlearea.com)) was used to measure the dominant compass direction of growth in each graminoid and shrub and these angles were converted to true north prior to statistical analysis. Each photograph in the time series was visually compared with the original quadrat photograph to determine any change in growth direction for the selected shrubs and graminoids over time.

The second study area was The Boomerang, an extensive sedimentary peak with well-formed stone steps supporting one of the largest feldmarks in Tasmania (Kirkpatrick & Harwood 1980; Visoiu 2014). A total of 62 quadrats (each 1 x 1 m) were placed at five metre intervals (or at vegetation boundaries) along five transects in January 2013 (Visoiu 2014). Transects were oriented both along the major axes of the summit plateau, capturing the highest and flattest parts of the peak, and perpendicular to these to sample different aspects of the higher slopes.

All plants evidently deformed by wind were classified according to which of the eight ordinal and cardinal compass directions describe the directional response. Because of difficulties determining what is an individual in cushion plants, graminoids and prostrate shrubs the number of plants was not quantified, rather a presence/absence of plants in each combination of growth form category (shrub/graminoid/cushion) and wind distortion category (eight compass sectors) was recorded for the quadrat. Where a quadrat contained life-forms displaying more than one distortion direction (e.g. cushion plants with both southerly and southwesterly responses and shrubs with southerly and northwesterly responses), we recorded all categories that were present.

Hill One is a terraced sedimentary outcrop in the Southern Range, where feldmark vegetation on the most wind-exposed sites grades into bolster heath and alpine heath (Lynch and Kirkpatrick 1995). Hill One is a rounded peak with exposure to winds from all directions. One by 1.5 m quadrats were located along north-south and east-west transects and photographed in 1989 and 1998 (Lynch and Kirkpatrick 1995; Kirkpatrick *et al.* 2002a). This design samples the highest slopes of the peak with transects radiating in four directions from the summit.



Photographs of the 32 quadrats which contained plants with distortion in 2013 were examined and recorded as for the Boomerang site.

Wind damage to *Azorella macquariensis* cushion plants on subantarctic Macquarie Island was recorded by Whinam *et al.* (2014b). These data provide counts of the incidence of directional damage for 234 individual cushions within 30 2 x 2 m quadrats located in feldmark vegetation on mineral soils developed on igneous geology. In the present study, photographs of the quadrats were re-examined to record presence of wind-distorted grass (*Agrostis magellanica*), in addition to cushion plants, in the eight compass directions, as for the Hill One and Boomerang sites.

Given the potential mechanistic link between snow weather and plant distortion (windblown ice and snow as abrasive agents, breakage of frozen leaves and stems; and conversely protection afforded by snow cover) we sought relevant data on snow cover, with no success. To address this data gap, satellite images of Tasmania from the Landsat archive (1983–2014) were inspected and where widespread snow cover was visible in an image the synoptic weather pattern was inferred if possible (determined as the direction of cirrus clouds or perpendicular to the orientation of rows of lenticular clouds associated with mountain waves).

### Statistical methods

Meteorological data from the Commonwealth Bureau of Meteorology were obtained for stations relevant to each site (Table 2). To characterize wind regimes, seasonal and directional variation in wind speed, air temperature and relative humidity were examined using ANOVA. All statistical analyses were performed in R 3.2 (R Core Team 2014).

For the Mt Wellington data, the mean distortion direction of the distorted plants was calculated using circular statistics. Watson's two sample test of homogeneity for circular data was used to compare the shrub and graminoid populations using the 'circular' package for R (Agostinelli & Lund 2013). Within each quadrat, individual graminoids and shrubs were randomly selected and paired for a paired t-test to compare differences in growth direction between shrubs and graminoids (growth direction data were taken from the first month of the time series since there was little difference between months).

To test whether directionality in plants differed between life-forms at each site we tabulated the frequency of quadrats by the presence of plants in the eight directional distortion classes

for each of the two or three life-forms present. We used the chi-squared statistic, with Monte Carlo simulation (10 000 replicates) for datasets where small expected values occur. Similarly, we tested for independence between quadrat aspect and plant distortion by tabulating frequency of quadrats by quadrat aspect (east/south/west) and presence of distorted plants (all life-forms) for the Hill One site where each of the three transects (excluding the north transect which comprises only two quadrats) has a distinct aspect. No aspect was recorded or analysed for Mt Wellington quadrats because these were located on flat ground.

**Table 2.** Weather station details.

Weather Station	Elevation (m.a.s.l)	Latitude/ Longitude	Distance from study site	Mean max. temperature warmest month (°C)	Mean min. temperature coolest month (°C)	Mean daily wind run (km)
Mount Wellington	1260	42.90°S 147.24°E	<1 km	13.7	-1.7	759
Hartz Mountains	831	43.20°S 146.77°E	Boomerang 16 km Hill One 29 km	17.7	1.4	570
Cape Bruny	55	43.49°S 147.14°E	Boomerang 48 km Hill One 30 km	18.6	6.2	510
Macquarie Island	6	54.50°S 158.94°E	2–16 km	8.8	1.5	749

Binary logistic regression was used to test whether the aspect of each quadrat predicted the presence/absence of plants in a particular distortion class for the Boomerang and Macquarie Island datasets. To avoid using a circular variable we converted aspect in degrees to radians and calculate the sine and cosine to generate two indices ('eastness' and 'northness', respectively) to use as independent variables for each quadrat. Macquarie Island quadrats were geographically widely distributed so we used slope angle and elevation (derived from a 25 m DEM using ArcGIS 10.1) as additional explanatory variables in the model. This test was repeated for each of the distortion directions for each life-form (provided there were a minimum of three quadrats with distorted plants).

The frequency of quadrats (classified into eight compass sectors by quadrat aspect) was tabulated by the presence of *Azorella* plants within each of the distortion classes (also classified into eight compass sectors). After excluding rows or columns totalling zero, this

contingency table was used to perform a chi-squared test with simulated  $p$  value to investigate whether directional wind damage is independent of quadrat aspect. The same test was performed for *Agrostis* plants. Similarly, a chi-squared test was used to compare the frequency of damage to individual cushion plants with the frequency of wind using the same eight compass sectors.

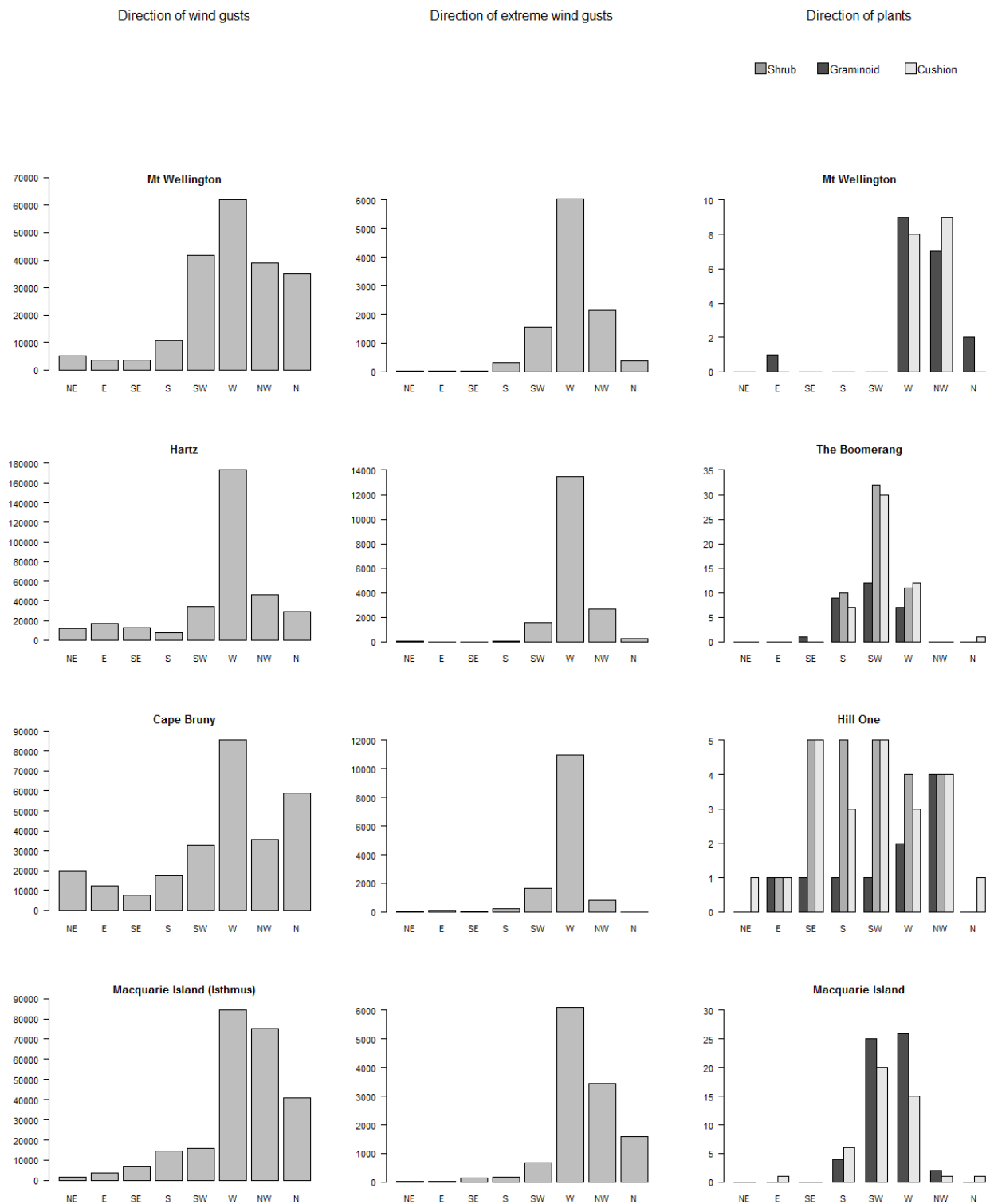
## Results

The prevailing winds on Mount Wellington are from southwest to northwest with westerly winds the most frequent and strongest (Fig. 3). Strong warm winds are associated with northwesterly airflows, while southwest winds are slightly colder than other directions at moderately high speeds. Relative humidity varies with wind direction and month (ANOVA,  $p < 0.001$ ) with drying winds typically northwest (Fig. 4) and in the summer months. High temperatures combined with low humidity occur with airflows from the west through north between December and February.

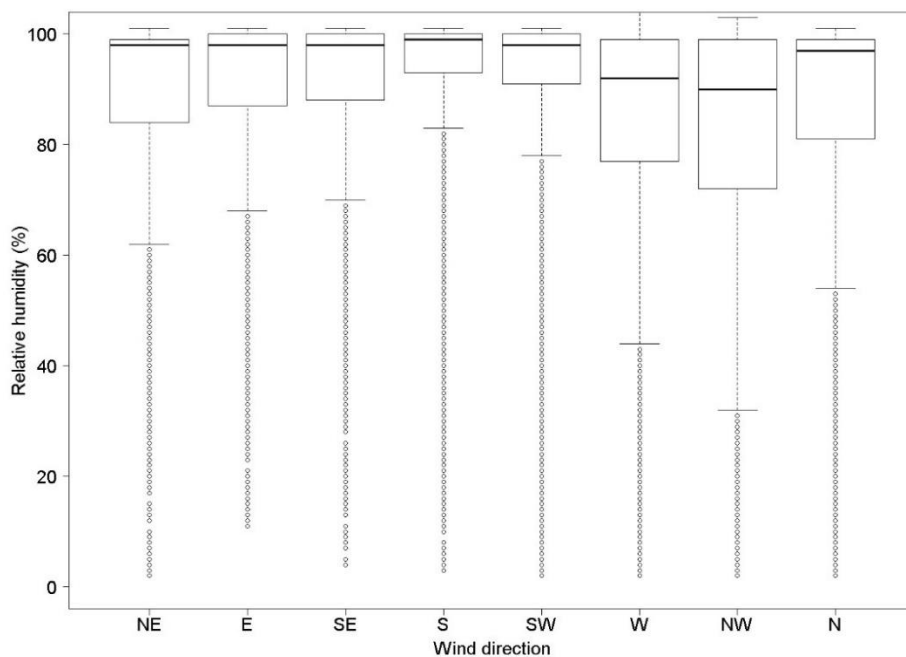
Statistically significant variation in air temperature, relative humidity and wind speed occurs with changes in wind direction and month at all meteorological stations. Of the 93 Landsat images in which snow was visible, the prevailing wind direction was clearly apparent in 40 cases (see Appendix). Southwest winds accounted for the majority of clearly apparent wind patterns where snow cover was present (25 out of 40 images). We therefore surmise that the prevailing winds during periods of widespread alpine snow cover are from the southwest.

On Mt Wellington, both shrubs and graminoids appear to be influenced by west and northwest winds, but not southwest winds (Fig. 3). Mean values for growth direction are similar for shrubs (circular mean =  $293^\circ$ , circular SD = 0.429,  $n = 22$ ) and graminoids (circular mean =  $296^\circ$ , circular SD = 0.541,  $n = 33$ ), with graminoids being more variable. The growth direction for the two groups, shrubs and graminoids, are not significantly different (Watson's  $U_2 = 0.128$ ,  $p > 0.1$ ). The mean difference between 19 shrub/graminoid pairs of  $5.7^\circ$  at the initial survey suggests the two life-forms are not significantly different in orientation (paired t-test,  $p = 0.35$ ).





**Fig. 3.** Frequency of ten-minute highest wind gusts grouped by wind direction for the four weather stations. Extreme wind gusts are the highest 5% of recorded wind speeds for each station. Direction of plants: number of quadrats at four study sites with shrubs, graminoids and cushion plants orientated in response to winds from a particular direction (i.e. with plants growing away from that compass direction).



**Fig. 4.** Relative humidity at Mt Wellington, 1990–2014. Box and whiskers are quartiles, black line is median, outliers shown as points where they are less than the lower quartile minus 1.5 times the interquartile range. Note that it is possible for relative humidity to exceed 100% when supersaturation occurs.

Of the 33 graminoid individuals with a distinct orientation at the first survey: 19 remained unchanged throughout the 12 months, 4 changed orientation slightly (but remained within the same compass sector), 9 became indistinct, and one became obscured by a shrub. In some cases changes in orientation were temporary. Shrubs displayed no change in orientation over this period.

Winds at Hartz and Cape Bruny are predominantly from the west, particularly the strongest winds (Fig. 3). Given this consistent trend between weather stations at different locations and elevations it is likely to be representative of the wind regimes experienced at The Boomerang and Hill One. This is supported by wind data recorded at Hill One by Lynch and Kirkpatrick (1995) over a relatively short period (April–October 1989) in which west winds were the most frequent and strongest.

Most plants of all three life-forms which displayed wind influence at The Boomerang were within the westerly through southerly range, with southwesterly being most frequent (Fig. 3). Of the 62 quadrats, ten had very little or no vegetation, eight had vegetation with no apparent wind influence and 16 had only one life-form displaying wind distortion. The remaining 28 quadrats, which contained more than one life-form with obvious wind distortion, showed consistency between two or three life-forms in all but four cases (Table 3). We did not detect a significant relationship between quadrat aspect and the orientation of plants (chi-squared test,

$p = 0.177$ ). Shrubs with southwesterly distortion were the only subset of plants to display a statistically significant relationship with site aspect (binary logistic regression, eastness  $p = 0.034$ ), reflecting the relative abundance of southwesterly-distorted shrubs on west-facing slopes.

**Table 3.** Frequency of wind distortion congruence across life-forms within 62 quadrats at The Boomerang. Bold numerals are total number of quadrats where the life-forms display the same orientation (in at least some individuals), italic numerals are number of quadrats where different lifeforms display different orientations (no congruence present). 15 quadrats which did not contain more than one life-form with wind distortion were not scored.

	Shrub	Graminoid	Cushion
Shrub		<b>19</b>	<b>6</b>
Graminoid	<i>3</i>		<b>18</b>
Cushion	<i>0</i>	<i>1</i>	

Orientation of plants at Hill One was more variable and had a more southerly bias, largely ranging from northwest to southeast (Fig. 3). In all but one of the quadrats in which more than one life-form displayed wind distortion, the distortion direction was consistent between the two or three life-forms (note that distorted graminoids are less frequent than the other life-forms in most quadrats). The relationship between quadrat aspect and plant distortion direction was just significant (chi-squared test with Monte Carlo simulation, average  $p \sim 0.05$ ).

At Macquarie Island the dominant winds are from the west through to north, with strong winds typically from the west (Fig.3). Most quadrats contained cushion plants with southwesterly or westerly damage (Fig. 3). Counts of damage to *Azorella* cushions show that most damage occurs in the southwest sector, not reflecting the frequencies of maximum wind gust direction (Table 4; chi-squared test,  $p < 0.001$ ). Hail does not appear to be important since 83% of hail events occur on days with west or northwest airflows.

Comparison of total numbers of wind distorted *Azorella* and *Agrostis* in the eight principal compass directions shows similar trends between the life-forms (chi-squared test with simulated  $p$  value,  $p = 0.278$ ). Both *Azorella* and *Agrostis* orientation appears to be independent of the quadrat aspect (chi-squared tests with simulated  $p$  value,  $p > 0.8$ ). Individual exceptions to this are *Agrostis* with westerly distortion (logistic regression, northness  $p = 0.047$ ) and

*Azorella* with southwest distortion (northness  $p = 0.024$ ). Quadrat slope and elevation were not statistically significant in predicted presence/absence of plant distortion.

**Table 4.** Frequency of damage to 234 *Azorella* cushions on Macquarie Island by section of cushion affected (excluding damage in the centre). Some cushions have damage in multiple sectors. Data from Whinam *et al.* (2014). Frequency of daily maximum wind gusts for Macquarie Island is shown classified in the same eight directional classes. Extreme wind gusts are the highest 5% of daily maxima.

Compass sector	Damage count	%	Daily max. wind gust frequency	%	Extreme wind gust frequency	%
NE	21	6.7	189	1.0	0	0.0
E	16	5.1	210	1.1	0	0.0
SE	18	5.8	614	3.1	4	0.4
S	51	16.3	1090	5.5	18	1.8
SW	111	35.6	693	3.5	28	2.7
W	60	19.2	7334	37.0	620	60.4
NW	19	6.1	6264	31.6	281	27.4
N	16	5.1	3421	17.3	75	7.3
Total	312	100	19815	100	1026	100

## Discussion

### *Congruence between life-forms in direction of distortion*

The Mount Wellington, Boomerang and Hill One data show that shrubs and graminoids have a similar growth response in a windy environment, indicating that graminoids have potential for use as indicators of wind direction. Distortion of graminoids was generally less distinct than that of shrubs and varied seasonally, becoming most obvious when mature culms were present. Graminoids were less effective than shrubs as indicators of wind regime due to a greater variation in their orientation and, in some instances, temporal variation in individuals. However, with a sufficient sample size they provide similar orientation results to woody vegetation.

The data from The Boomerang, Hill One and Macquarie Island show that cushions and graminoids also have a similar response in a windy environment. Therefore, in the absence of woody plants, either cushions or graminoids can be used to indicate spatial patterns of wind direction. While the likely mechanical processes and morphology of wind distortion varies between the three distinct life-forms examined here, their directional responses to damaging winds were consistent.

Wind direction as indicated by vegetation is largely consistent between quadrats at each site. However, the quadrats which do display different wind direction tend to be internally consistent, in that there is congruence in apparent wind response between life forms, suggesting local differences in wind flow related to topography. Several quadrats on flat ground or a variety of aspects provided a signal of prevailing wind direction even if there was some small-scale variability due to topography or vegetation.

### *Correspondence of distortion to wind regimes*

Our data suggest patterns of distortion in alpine and subantarctic plants, regardless of growth form, do not simply relate to the most frequent strong winds, as is generally the case in other environments (Noguchi 1979; Robertson 1986; Wooldridge *et al.* 1996), with some exceptions, such as seasonality of winds (Holtmeier 2009).

One possible explanation for this discrepancy is the locations of meteorological stations. The Mt Wellington station is located near the summit with a clear line of view in all directions, so may be reliable. Wind data from the Tasmanian weather stations examined in this study consistently indicate prevailing westerly winds, even at Hartz Mountains where the weather station is located east of a prominent ridge and therefore might be somewhat sheltered.

The weather station at Macquarie Island is located at 6 m.a.s.l. and is not directly exposed to southwest winds due to the 200–300 metre high adjacent plateau. Nevertheless, wind speed at the meteorological station predicts that at other locations on the island, including at high elevations, where the winds are much stronger than at sea level (Davies & Melbourne 1999; Jenkin 1972; Tweedie 2000; Selkirk & Saffigna 1999). Jenkin (1972) interpreted an increase in the difference between sea level and plateau wind speeds in October to a high frequency of S and SW winds during this period, suggesting that the meteorological station is not representative of winds from these sectors. Selkirk and Saffigna (1999) found that wind direction on the plateau was very similar to that observed at the meteorological station over the course of one month but recorded no wind speed data.

In rugged mountain topography we would expect very localized variation in winds but such variation is unlikely to occur at our Tasmanian study sites. Strong westerly winds were consistently recorded from Tasmanian stations. Short-term wind data from the Hill One site (Lynch & Kirkpatrick 1995) is consistent with data for wind speed and direction from both

weather stations used in our analysis for this site. Given the similar topography of The Boomerang, we expect the wind regimes from these stations to also be representative of this site. However, the wind experienced by low-growing plants at the ground surface may differ from the wind direction in the free atmosphere, particularly in mountainous terrain. Therefore, meteorological observations may not be representative of the vegetation microenvironment.

The data presented here from the quadrats at Hill One show much more variable responses of cushion plants and shrubs to wind than the less systematic observations of Lynch and Kirkpatrick (1995, Fig. 12) who reported distorted cushion plants and shrubs overwhelmingly displaying a distinct southwest to northeast trend in growth.

Since southwesterly winds are neither strongest nor most frequent in either the Hill One or BOM climate data, this growth response is potentially related to low temperature events, where southwesterlies tend to be stronger than other winds (Lynch and Kirkpatrick 1995). However the southwesterly winds are only slightly stronger than other wind directions associated with low temperatures.

In the Tasmanian feldmark sites, the congruence in apparent wind response between shrubs and graminoids or shrubs and cushion plants within individual quadrats suggests that the different vegetation orientation between quadrats is due to localized differences in wind flow on different aspects of the summit combined with microtopographic effects. Patterns in feldmark may be reinforced by a feedback whereby vegetation modifies surface airflow (Barrow *et al.* 1968; Selkirk-Bell and Selkirk 2013).

The major discrepancy in direction of distortion is between our Mt Wellington site and the others. As with our plants at the other sites, the trees in the subalpine forest on Mt Wellington lean away from the southwest (Gilfedder 1988), whereas, in our quadrats near the summit, the plants lean away from the northwest. Leaf damage from wind-blown ice is greater on the windward (southwest) side of treeline eucalypts, which combined with the asymmetric crown form suggests ice-bearing southwesterly winds are the controlling factor (Gilfedder 1988).

Gilfedder (1988) presents evidence that the upper altitudinal limit of trees on Mt Wellington is related to drought. Hot dry north-westerly winds occur during the summer growing season. Unlike other Tasmanian alpine regions, Mount Wellington may be subject to the warm dry fohn winds which can occur in south-eastern Tasmania during north-westerly weather (Fox-Hughes

2012; Kirkpatrick *et al.* 2002b; Sharples 2009). Mt Wellington has lower average rainfall than other alpine areas (Nunez *et al.* 1996) and has shallow soils compared to the other sites, therefore the alpine vegetation is more likely to be subject to water stress. Further exploration of this water stress theory would require ecophysiological studies of alpine plants at Mt Wellington to measure water potentials.

These northwesterly winds are implicated as a drying force in the complex patterning of migrating *Sphagnum* mires on the Tasmanian Central Plateau (Morgan *et al.* 2010). We suggest that the direction of asymmetry reflects greater damage from desiccation during northwesterly winds than ice abrasion during southwesterly weather. Our other sites have higher precipitation and deeper soils than those on Mount Wellington (Table 1), making desiccation an unlikely cause of asymmetry.

The lack of a match between the southwesterly trend in wind damage on Macquarie Island, Hill One and The Boomerang, and the dominant westerly and northwesterly winds may reflect the frontal synoptic patterns associated with the potential for ice abrasion. Cold fronts bearing snow move in from the west, followed by increasingly southerly cold air as the pressure becomes higher (Jones 2003). Our satellite image interpretation suggests that snow cover in Tasmania's alpine zone typically coincides with southwesterly weather. Under clear conditions, snow becomes icy as it is transported locally to the northeast, the location of most snow patches. Apart from these snow patches, which usually are filled with snow through winter and early spring, the vegetation is mostly exposed to wind (Kirkpatrick 1997). We suggest the correspondence of icy snow with low snow cover and strong winds is maximised with southwesterlies.

While studies of asymmetry in trees typically implicate prevailing winds, cold winds have a greater influence than warm winds (Grace 1977). Asymmetry in tree crowns can be produced by physical damage on the windward side (such as ice abrasion during glazing storms), but there may also be a microclimatic effect whereby growth rates are higher on the lee side (Foster 1988).

Wind-blown ice, snow, soil and salt spray often have a greater influence on plant form than wind *per se* (Ennos 1997; Grace 1977). Similar processes are likely to be involved in the growth of prostrate shrubs in alpine environments, in that a combination of physical damage, differential growth rates and thigmotropism drive a directional response which may be

confounded by factors other than wind speed. Salt spray may be implicated in foliar damage in coastal environments but is unlikely to be a contributing factor in the Tasmanian sites given the distance and elevation from the coast. On Macquarie Island salt spray does not substantially affect higher elevations (Mallis 1988).

Studies of the subantarctic cushion plant *Azorella selago* Hook. f. (closely related and morphologically similar to the allopatric Macquarie Island endemic *A. macquariensis*) report asymmetry in microclimates and wind damage. Microclimatic differences in soil moisture and temperature are evident, with greater variation in these factors on the windward (western) side of *A. selago* cushions, apparently due to increased evaporation and less snow accumulation (Hausmann *et al.* 2009).

In a field experiment with *A. selago* subjected to reduced rainfall, greater senescence on the southwest side of cushions suggests cold dry southwesterly winds have a desiccating effect under drought conditions (le Roux *et al.* 2005). In contrast to the leeward migration typically observed in feldmark plants, Boelhouwers *et al.* (2003) report *A. selago* cushions migrating toward the prevailing wind due to decay of the cushions on the leeward side where needle ice forms. On Marion Island, frost events are predominantly associated with southwesterly airflows (Nel *et al.* 2009). Macquarie Island is likely to experience a similar regime given the similarities in synoptic weather patterns and soil temperatures between it and Marion Island and thus windblown ice is likely associated with southwesterly winds.

Cold air is dense and more effective at moving particles than warm wind (Selkirk and Saffigna 1999), which may accentuate the abrasive effects of ice and soil particles, particularly near ground level. The dynamic stress experienced by plants is a function of wind speed and air density (Wagemann *et al.* 2015) so relatively low elevation locations such as Macquarie Island will experience more damaging winds for a given wind speed.

Active wind erosion of mineral soils on Macquarie Island (Selkirk & Saffigna 1999) under conditions of frequent strong winds and rare snow cover provides suitable conditions for sand-blasting of vegetation, both on the coast and plateau. Hence Macquarie Island vegetation might be more predisposed to wind damage than typical high latitude and alpine environments where extensive snow cover provides protection from wind for a large part of the year, or Tasmanian alpine vegetation which almost exclusively occurs on dolerite or quartzite peaks with very little sand and gravel. Hill One and The Boomerang are rare examples of sedimentary



geology in the Tasmanian alpine zone, which explains the well-developed feldmark on these peaks. Spatial modelling of extreme wind gusts suggests that Hill One is subject to some of the most damaging winds in Tasmania (Cechet *et al.* 2012).

### *Conclusion*

We conclude that, at least in maritime alpine and subantarctic environments, the direction of wind distortion can be measured using any of shrubs, graminoids or cushions, but that these directions are not related to any consistent attribute of the local climate. We identify desiccation and ice abrasion as the likely causes of asymmetry at our sites, with the former only on a relatively dry mountain with shallow soils and responding to strong northwesterly winds, and the latter elsewhere, responding to strong southwesterly winds. Thus, plant distortions do not reflect the most frequent strong winds, but rather the most frequent damaging strong winds. The novel use of graminoids to indicate ecologically important wind direction has applications in environments lacking woody vegetation.

## **Chapter Three: Air temperature lapse rates and cloud cover in a hyper-oceanic climate**

This chapter examines air temperature and fog as two of the climatic factors that may be significant in determining the distribution of plant species and consequently the structure and composition of vegetation communities on Macquarie Island.

Altitudinal variation in vegetation on Macquarie Island is likely to be influenced by air temperature, cloud cover and wind exposure. Chapter One examined wind exposure. This chapter investigates daily and seasonal altitudinal variation in air temperature (lapse rates) on Macquarie Island using temperature loggers on altitudinal transects. Photographs from a webcam are used to determine cloud level in order to investigate relationships between low cloud (fog) and air temperature.

Altitudinal patterns in air temperature and cloud cover determined in this chapter inform the selection of environmental variables for spatial models of flora species and vegetation communities in Chapters Four and Five, including the interpretation of these models.

The research contained in this chapter has been accepted for publication, subject to minor revision, in *Antarctic Science*.

## Abstract

Air temperature lapse rates vary geographically and temporally. Subantarctic Macquarie Island provides an opportunity to compare lapse rates between windward and leeward slopes in a hyper-oceanic climate. Lapse rates were steep by global standards, typically close to the dry adiabatic lapse rate despite the near-constant high humidity. Limited diurnal and seasonal variation occurs in lapse rates on Macquarie Island. High variability of lapse rates on the eastern (lee slope) in summer months and in the midday hours appears to be driven by solar radiation. No diurnal or seasonal pattern was evident on the western slope. Development of orographic cloud is expected to modify lapse rates, given the theoretical shift between dry and saturated adiabatic lapse rates which occurs with condensation of water vapour. Cloud cover was frequent, with higher elevations under cloud 50% of the time, with no seasonal variation. However, cloud base level did not explain variation in lapse rates. Low cloud is likely to be of ecological importance because it influences fog precipitation, solar radiation and evapotranspiration. Year-round dominance of westerly airflows and limited seasonal variation in air temperature and humidity explain the limited seasonal variation in cloud cover and lapse rates on Macquarie Island.

## Introduction

Changes in air temperature with elevation due to adiabatic processes driven by vertical movement of parcels of air are described by air temperature lapse rates. Lapse rates vary spatially and temporally due to differences in relative humidity and vertical stability of air masses. Local lapse rates are determined by a combination of regional synoptic conditions and landscape-scale physiography (Dobrowski *et al.* 2009). Since air temperature is a fundamental variable in meteorology and bioclimatology, understanding lapse rates is important for interpolation of air temperature between meteorological stations, particularly in areas of complex terrain, and for spatial modelling of biological phenomena such as species distributions, phenology and growing seasons. Lapse rates are also important for hydrological modelling and for downscaling global climate models (Dobrowski *et al.* 2009). The present study examines lapse rates and cloud base levels on Macquarie Island as part of a broader project investigating the spatial distribution of plant species on the island.

Subantarctic Macquarie Island (54.50°S 158.94°E) is 34 km long and 3—5 km wide. It has an undulating plateau with peaks reaching 420 m a.s.l. surrounded by steep slopes arising from narrow coastal plains. The climate of the island is at the extreme end of the oceanicity scale, being one of the few terrestrial environments on Earth with a continentality index  $< 0$  (Currey 1974). The climate is dominated by the Southern Ocean storm track with regular fronts accounting for at least 60% of precipitation (Wang *et al.* 2015). High humidity (mean 86%) and strong winds (mean 35 km/hr) occur year-round. Mean annual daily minimum and maximum temperatures are 3.1°C and 6.6°C. Rainfall at sea level typically occurs on 317 days per year with an annual mean 1033 mm (1980-2010) increasing at around 65 mm/decade (Jovanovic *et al.* 2012).

Cloud cover exceeds 80% over the Southern Ocean, mostly comprising boundary layer cloud, while the less frequent frontal clouds (10-12% of cloud cover) are associated with higher precipitation intensity and hence higher total precipitation (Mace 2010, Catto *et al.* 2012, 2013). Occult precipitation (i.e. fog deposition) is likely to be very important to the hydrology and ecology of Macquarie Island (Tweedie 2000), where the tundra vegetation is dominated by large-leafed megaherbs, except in feldmark (Selkirk *et al.* 1990).

Cloud base levels have not been directly measured on Macquarie Island, although Tweedie (2000) estimated cloud base levels using lapse rates and dew point temperature from an altitudinal sequence of automatic weather stations and Huang *et al.* (2012) estimated frequency of cloud cover in altitude bands using sonde-derived relative humidity data.

Environmental lapse rates (air temperature lapse rates) are variable between locations (Table 1) due to effects of continentality, topography, synoptic weather patterns and localised phenomena such as cold air drainage, snow cover and sea breezes (Nunez & Colhoun 1986, Pepin 2001). Snow cover and cloud cover can also influence environmental lapse rates (Oke 1987; Pepin & Norris 2005). For saturated air, the moist adiabatic lapse rate becomes steeper with decreasing air temperature (Barry 1992). For example, the moist adiabatic lapse rate is around  $0.55^{\circ}\text{C } 100 \text{ m}^{-1}$  at  $10^{\circ}\text{C}$  and around  $0.6^{\circ}\text{C } 100 \text{ m}^{-1}$  at  $5^{\circ}\text{C}$ .

Macquarie Island provides a simple model environment for studying lapse rates at the oceanic extreme given the presumed lack of importance of confounding factors such as cold air drainage and sea breezes. The equable oceanic climate and strong persistent influence of synoptic winds means that lapse rates should be driven by airflow over the relatively simple but prominent topography, which is oriented more or less perpendicular to the prevailing winds (90.2% of winds at the meteorological station are from the westerly sector  $180\text{--}360^{\circ}$ ). Low-level atmospheric stability due to the effects of topography on wind speed and air temperature may be important since it will determine the magnitude of orographic lifting (Sarmadi *et al.* 2017).

The only detailed study of lapse rates on Macquarie Island examined the eastern (lee) slope of the island and suggested that western slope lapse rates are likely to be less steep since the strong prevailing westerly winds create a pronounced föhn effect on the eastern slopes (Tweedie 2000). We therefore expect a difference in lapse rates between opposite sides of the island due to adiabatic processes associated with orographic cloud and precipitation as the prevailing westerly airmass passes over the island's plateau.

**Table 1.** Lapse rates reported from other studies.

Location	Region	Annual mean lapse rate (°C 100 m <sup>-1</sup> )	Daily minimum temperature lapse rate (°C 100 m <sup>-1</sup> )	Daily maximum temperature lapse rate (°C 100 m <sup>-1</sup> )	Winter lapse rate (°C 100 m <sup>-1</sup> )	Summer lapse rate (°C 100 m <sup>-1</sup> )	Reference
Macquarie Island	Maritime subantarctic	0.79 (slope segments range 0.19 – 1.4)					Davies and Melbourne (1999)
Macquarie Island	Maritime subantarctic	~ 1.0					Jenkin (1972)
Macquarie Island	Maritime subantarctic	~ 1.0					Taylor (1955)
Macquarie Island	Maritime subantarctic	0.6 (eastern slope)					Tweedie (2000)
Heard Island	Maritime subantarctic				0.89 (eastern (lee) slope)	0.54 (eastern (lee) slope)	Thost and Allison (2006)
South Georgia	Maritime subantarctic					0.98 (on glacier)	Smith (1960)
Marion Island	Maritime subantarctic	0.5					Holness (2001) cited in Hedding (2006)
Mt Wellington	Maritime temperate	0.63	0.5	0.75			Nunez and Colhoun (1986)
Pennines	Maritime temperate		0.55	0.86			Pepin (2001)
Cascade Mountains	Maritime temperate	0.39					Minder <i>et al.</i> (2010)
Taiwan	Maritime subtropical	0.52			0.49	0.55	Chiu <i>et al.</i> 2014
Rocky Mountains (southern Canada)	Continental	0.4					Diaz and Bradley (1997)
European Alps	Continental	0.54 - 0.58					Rolland (2003)
European Alps	Continental	0.3 - 0.4					Kollas <i>et al.</i> (2014)
Central China	Continental	0.34 (southern slope), 0.5 (northern slope)			0.14 (S slope), 0.29 (N slope)	0.43 (S slope), 0.63 (N slope)	Tang and Fang (2006)

Condensation associated with cloud or fog formation releases latent heat (Severini, *et al.* 1986) which warms the surrounding air, reducing the environmental lapse rate. Therefore, we expect to see a signal in the air temperature elevation profile to indicate the presence of low cloud or fog. Lapse rates should be gentler under conditions of low cloud (Pepin *et al.* 1999). Previous studies on the relationship between cloud base level and lapse rates have derived an estimated height of cloud base from observed dew point data (Pepin *et al.* 1999, Tweedie 2000). In the present study we utilize an archive of webcam images to provide observational data for cloud base level.

We examine lapse rates on a transect across Macquarie Island to determine spatial and temporal patterns in air temperature and four possible drivers of these: solar radiation; synoptic weather systems; cloud cover; and, low-level atmospheric stability. We also test whether free air lapse rates from radiosonde data can be used as a proxy for terrestrial lapse rates. Furthermore, we investigate whether an altitudinal series of air temperature observations can predict cloud cover.

## Methods

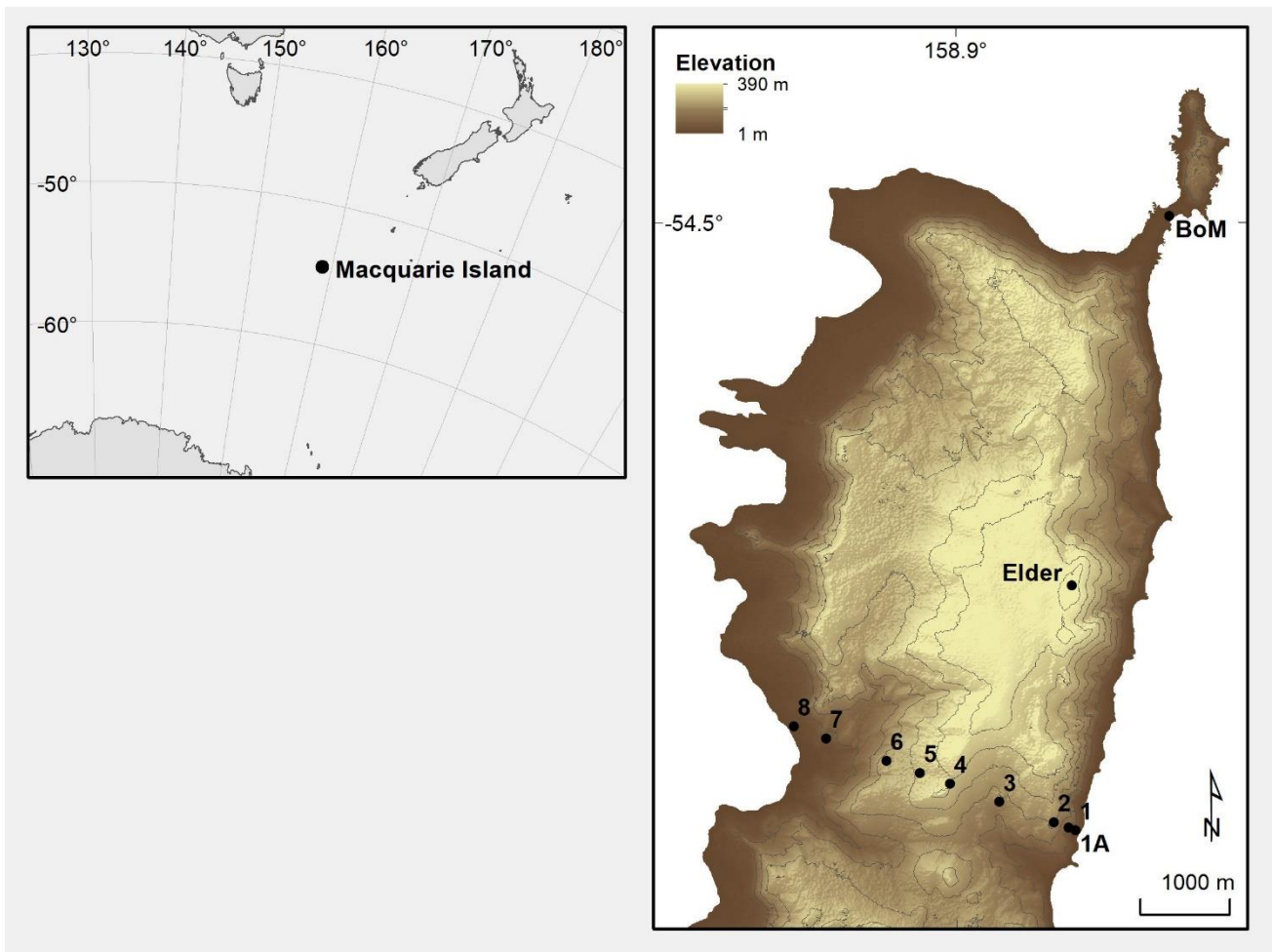
### *Air temperature*

We used LogTag temperature loggers (model TRIX-16, LogTag Recorders Ltd, Auckland) placed inside waterproof polycarbonate cases (LogTag Recorders Ltd, Auckland) mounted on posts at a height of one metre above ground level, with no solar radiation screening. The loggers were located along a transect crossing the main axis of Macquarie Island from the west to east coasts (Fig. 1, 2). This transect has been used for previous studies of wind exposure, vegetation communities and geomorphology (Peterson and Scott 1988, Jenny Scott and Michael Comfort, unpublished data 2016). One logger was located 2 km north of the transect at the highest point in the northern half of Macquarie Island, the summit of Mt Elder (385 m a.s.l.), because this location provides a higher elevation than the transect and replicates a site used in a previous study of lapse rates (Tweedie 2000).

Loggers were synchronized to record temperature hourly. Prior to field deployment in August 2014 all 11 loggers were stored together for 8 weeks to determine variation in temperature readings between individual loggers. Loggers were retrieved in March 2016. During the study

period, the logger at site 2 fell off its post and the site 1A logger malfunctioned. These anomalous data were omitted from analyses.

A dataset of hourly observations of meteorological data from the Macquarie Island station of the Commonwealth Bureau of Meteorology (BoM) was obtained. One logger was placed in the Bureau of Meteorology instrument enclosure, mounted without a screen and at the same height as our other loggers, to allow comparison between the logger record of temperature and the official meteorological data.

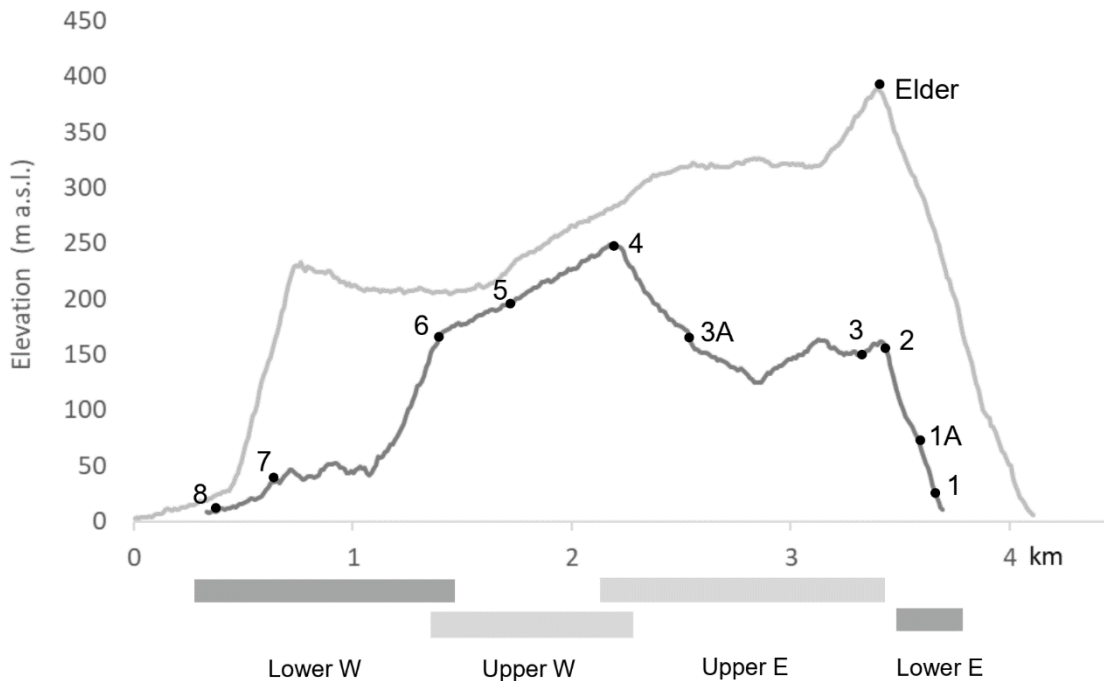


**Fig. 1.** Location of temperature logger sites at the northern end of Macquarie Island. 50 m contours shown.

The BoM provided a dataset comprising atmospheric observations at various elevations from radiosondes launched twice daily, at 09:00 and 21:00 Macquarie Island time (UTC +10 h). For each radiosonde flight during the period in which temperature loggers were deployed we



calculated the environmental lapse rate at Macquarie Island, using all air temperature observations below 400 m a.s.l., to compare with the logger data.



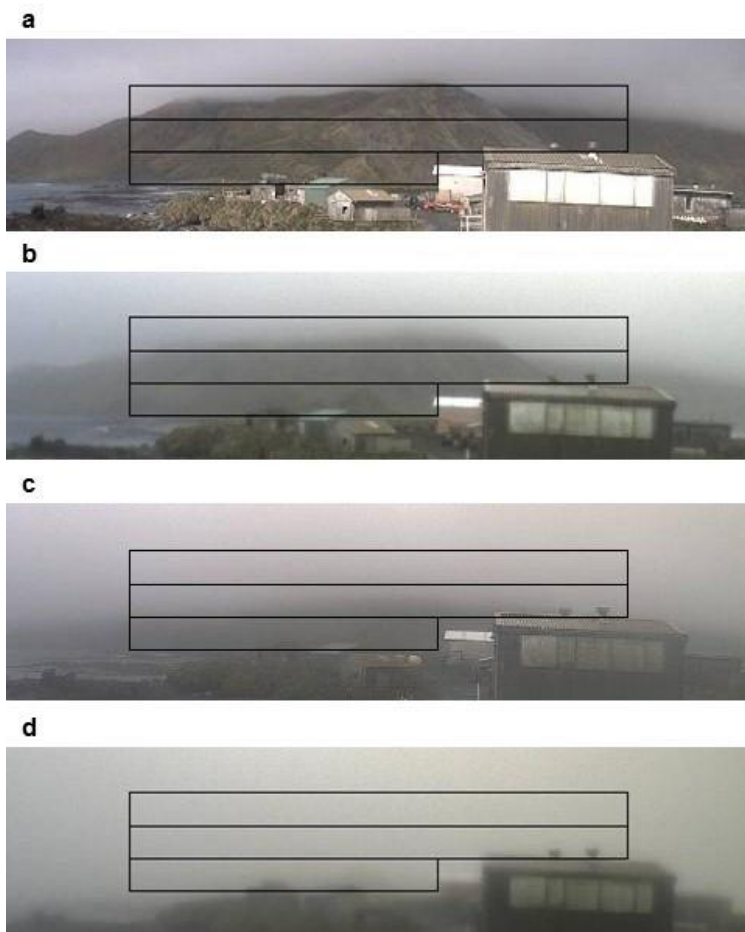
**Fig. 2.** Elevation profile of Macquarie Island transect (see Fig. 1) with temperature logger locations. Pale grey profile shows location of Mt Elder logger. Slope segments shown below profile.

### Cloud base level

The Australian Antarctic Division maintains a webcam at Macquarie Island Station facing south and capturing a profile image of the northern end of the island's plateau at five minute intervals. Archived webcam images were obtained for the period in which LogTag data were collected to determine cloud base levels relative to the topography of the island.

Highly variable lighting, and confounding factors such as moisture on the camera lens, made automated image analysis using histogram comparison methods impractical. Instead, manual analysis of a random sample of images from the study period was undertaken. To enable comparison with temperature data we selected only those images captured within 2 minutes of the hourly temperature logger observations, then analysed a random sample of this subset (50 random samples per month,  $n = 600$ ). Using a graticule superimposed on the images we

manually classified each image using four categories of cloud base level (Fig. 3). The lowest level of cloud was consistent with the meteorological definition of fog (i.e. visibility less than 1 km) at sea level. Images too dark or blurry to classify were excluded. We continued to randomly sample and manually classify images until we had at least 50 images scored for cloud base level in each month. This random sampling stratified by month provided a final dataset of 600 images (50 per month).



**Fig. 3.** Examples of webcam images from Macquarie Island Station looking south toward Perseverance Bluff. (a) high cloud (cap or crest clouds), (b) medium cloud base level, (c) low cloud base level, (d) sea level cloud (i.e. fog).

### *Data Analysis*

We identified outliers in the LogTag data using median absolute deviation (MAD) and accounted for the asymmetric distribution of outliers (i.e. mostly high temperatures) by calculating MAD separately for values lower and higher than the median. Since the median temperature varies seasonally we applied MAD monthly to each logger dataset. Outliers, defined as those values greater than two deviations from the median, were replaced with no

data ( $n = 5833$  or 4.9 % of data). Datasets with outliers removed showed little difference in median values to the original datasets.

The 12 month period with the most complete data (August 2013 to August 2014), which has missing data from one logger (site 1A) for the last two months, was used for most lapse rate calculations.

Annual average lapse rates were calculated for each of the western and eastern slopes. Although not on the transect, Mt Elder was included as a data point in each slope series to extend the elevation sequence to one of the highest points on the island.

Hourly lapse rates were calculated for the western and eastern slopes. To investigate differences in lapse rates between upper and lower slopes, since these may be related to cloud level, we calculated four different lapse rates for each hourly temperature observation using 3-4 data points for each (but not including Mt Elder): lower west slope (5-165 m a.s.l.), upper west (165-260 m a.s.l.), lower east (10-150 m a.s.l.) and upper east (130-260 m a.s.l.) (see Fig. 2).

Monthly lapse rates were calculated for the 18 months in which recording took place (with missing data for two loggers in the latter months). Diurnal patterns were investigated by calculating lapse rates for daytime (10:00-15:00 local time) and night time (22:00-03:00). To investigate seasonal difference in lapse rates we plotted air temperature and elevation for January (austral summer) and July (austral winter). ANOVA was used to test for differences between monthly lapse rates and spatial differences between eastern and western slopes. Multiple linear regression and Pearson correlation coefficient were used to examine the relationship between each pair of eastern, western and free air (radiosonde) lapse rates.

To investigate seasonal variation in air temperature with location we determined the difference between lowest and highest mean monthly temperature for each logger over a 12-month period (excluding Site 1A which had incomplete data) and performed linear regression with elevation as explanatory variable for all sites and east and west slopes independently.

To examine potential synoptic scale drivers of lapse rates we classified weather patterns based on sonde data. Sonde-recorded air temperature, air pressure, relative humidity, wind speed and wind direction were binned into two altitude classes, representing the lower and upper

elevations of Macquarie Island: 8–200 m and 201–400 m. Mean values were calculated where more than one observation occurred within an altitude class, while sonde flights in which no data were recorded within an altitude class were excluded from further analysis. Hierarchical clustering using Ward's method identified three distinct groups which were tested for independence based on each of the eastern and western slope lapse rates where simultaneous data were available.

Weather conditions and daily and annual cycles might influence cloud base level so we tested time of day (1–24 hours), month and meteorological variables from the BoM station (air temperature, dew point, relative humidity, wind speed, wind direction, MSLP) as predictors for the five categories of cloud base level (including no cloud) using Linear Discriminant Analysis (LDA), which incorporates potential interactions between variables. The relationship between each individual meteorological and time variable with cloud base level was tested using ANOVA (with a circular statistics implementation of ANOVA for time and month; Agostinelli and Lund 2013).

To quantify low-level atmospheric stability we calculated the Froude number using radiosonde-derived lapse rates, since these are representative of free air conditions. Observed air temperature and windspeed at launch (6 m.a.s.l.) and temperature lapse rate below 400 m.a.s.l. were used to calculate Brunt-Väisälä frequency, natural wavelength and, subsequently, Froude number (Stull 2000). Pearson correlation coefficient was computed to assess the correlation between Froude number and each of east and west slope lapse rates. ANOVA was used to test for independence between Froude number and cloud level classes, since atmospheric stability influences the formation of orographic cloud. Data analysis and statistics were performed in R v.3.4.1 (R Core Team 2017).

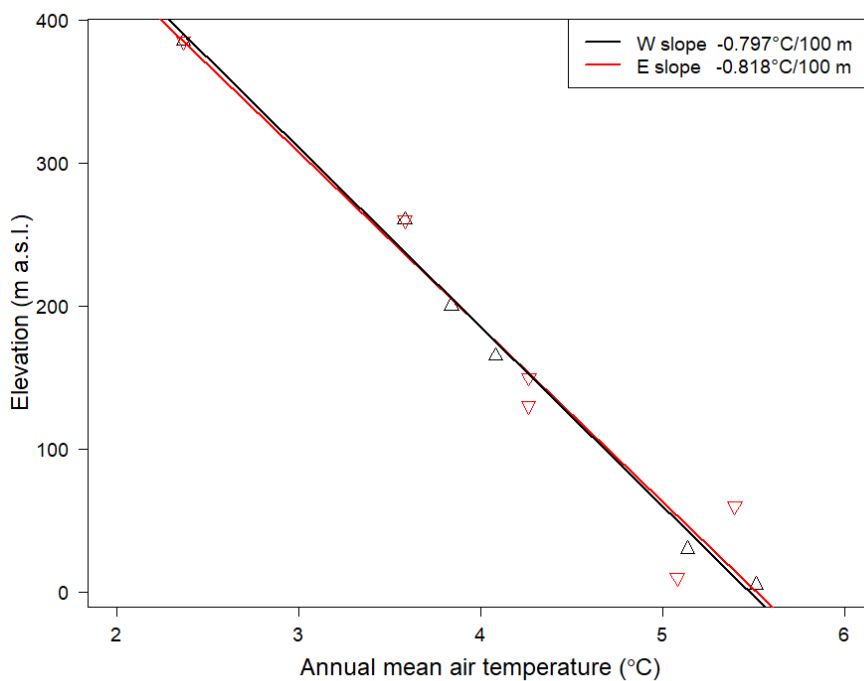
## Results

### *Lapse rates*

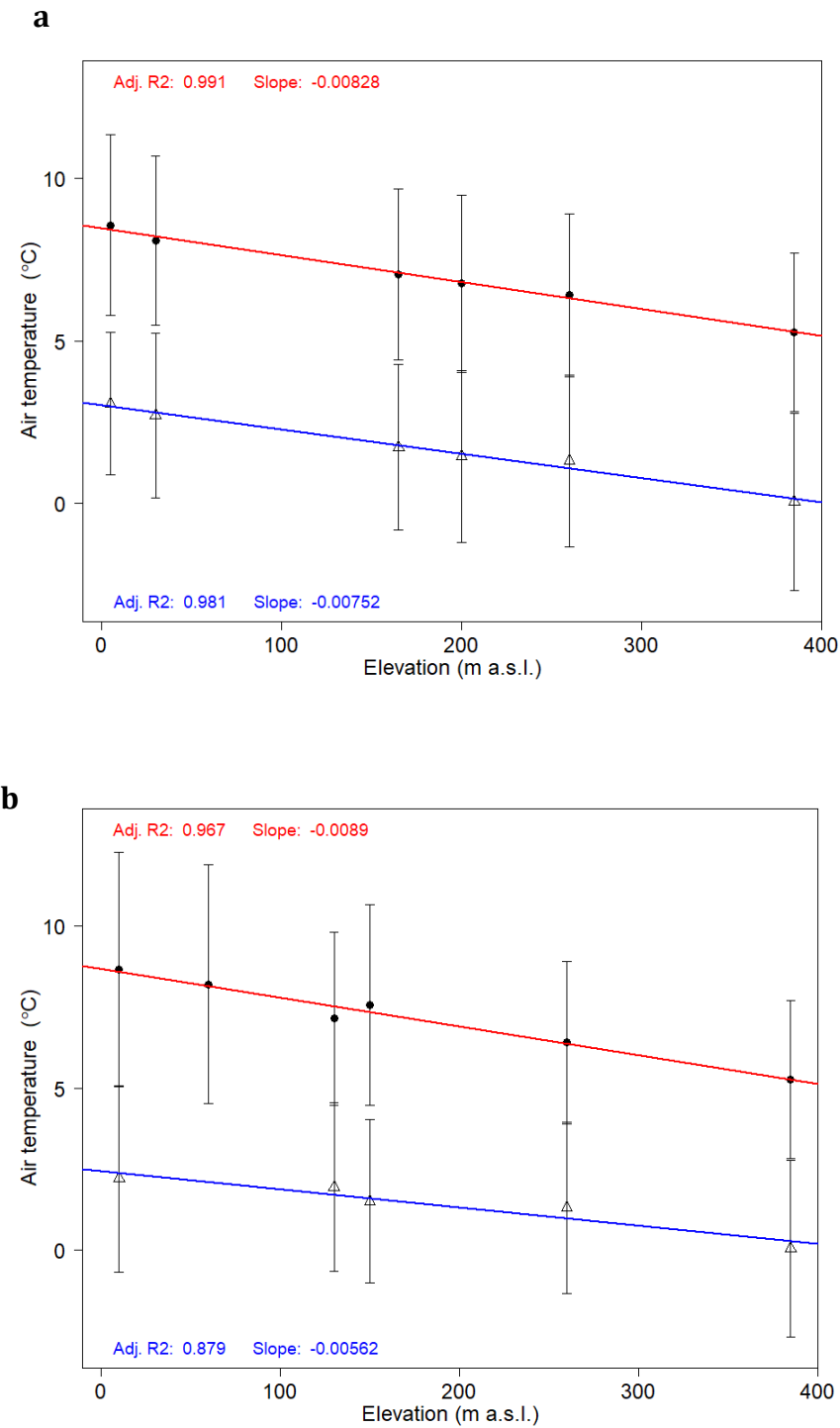
Correlation coefficients for all possible pairs of LogTags during the 8-week calibration period were  $> 0.998$ , with mean temperature  $\pm 0.67^{\circ}\text{C}$ . The LogTag recorder located at the BoM weather station had a median air temperature of  $5.4^{\circ}\text{C}$  compared to the BoM median of  $5.1^{\circ}\text{C}$  for the same period. LogTag data were consistent with the station at lower air temperatures but show some deviation at higher temperatures at which the logger frequently had higher

readings than the BoM temperature probe. LogTag readings which notably exceeded synchronous BoM readings occurred in daytime in summer, most often when cloud cover (measured in oktas at the BoM station) was low, which suggests the LogTag unit was heated above ambient air temperature by direct solar radiation.

A linear fit approximated lapse rates for the western slope and eastern slope (Fig. 4). Including the data from Mt Elder improved the fit marginally for the western slope and notably for the eastern slope (Table 2). On the western slope, the annual range of mean daily temperature was approximately 6°C between January and July throughout the elevation profile, resulting in similar lapse rates in January and July (Fig. 5a), while January lapse rates were steeper than July on the eastern slope (Fig 5b).



**Fig. 4.** Mean annual temperature for ten data loggers on a transect across Macquarie Island. Fitted lines are mean annual lapse rates for eastern (adj.  $R^2 = 0.8155$ ) and western slopes (adj.  $R^2 = 0.9771$ ). Note that the two highest loggers were shared by both slopes.



**Fig. 5.** January 2015 (filled circles) and July 2015 (triangles) mean monthly air temperature ( $\pm$ SE) recorded at each logger with lapse rates plotted as a linear regression: (a) western slope; (b) eastern slope.

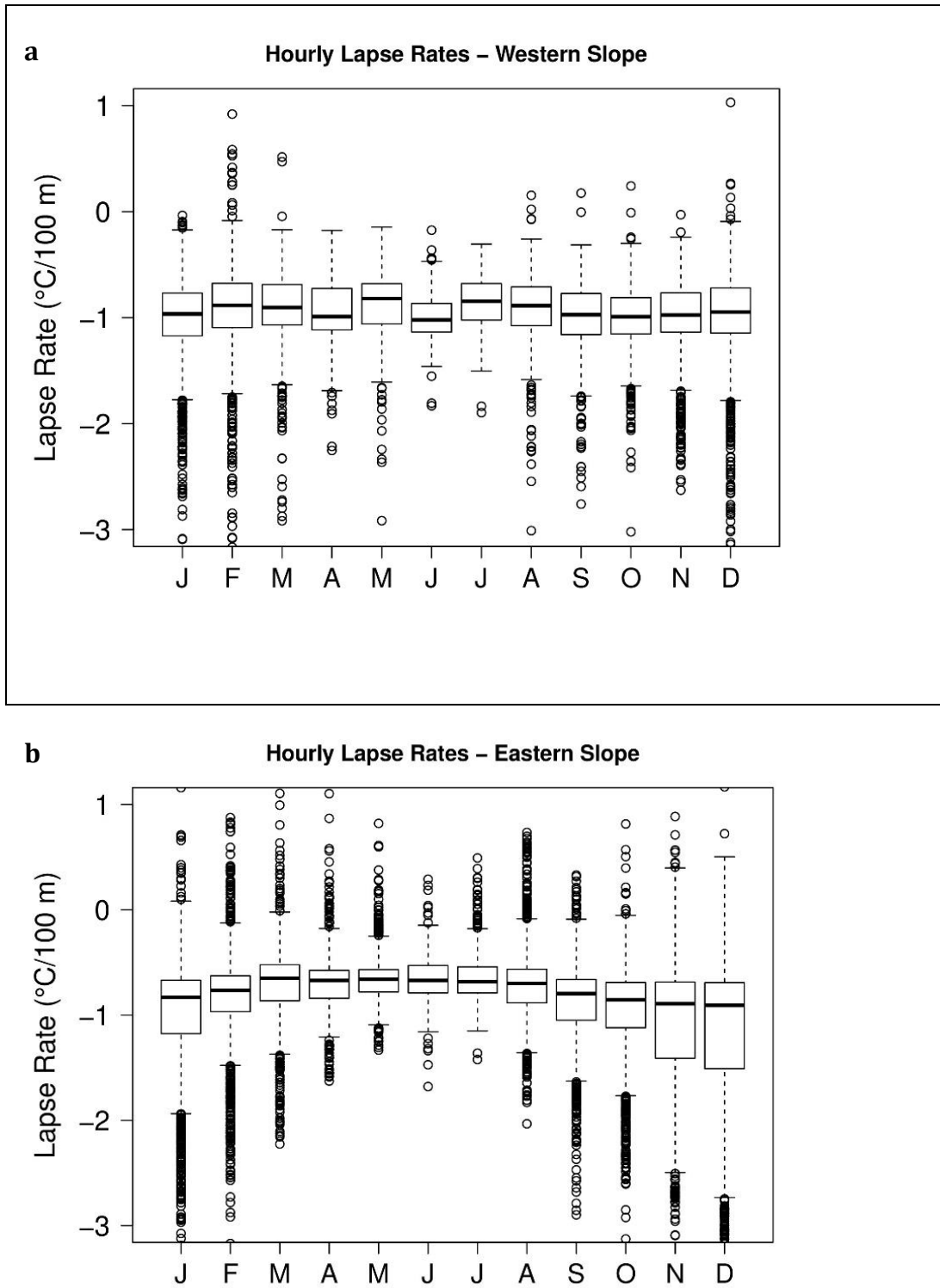
**Table 2.** Lapse rates determined from mean air temperature over 18 months along altitudinal transect (with and without the highest logger at Mt Elder), showing  $R^2$  for the linear relationship between altitude and air temperature.

Location	Lapse rate (°C 100 m <sup>-1</sup> )	$R^2$
Eastern slope including Mt Elder	0.818	0.9332
Eastern slope excluding Mt Elder	0.818	0.8155
Western slope including Mt Elder	0.797	0.9889
Western slope excluding Mt Elder	0.774	0.9771

The highest and lowest monthly mean rates for the western slope lapse rate ( $W_{LR}$ ) both occurred in December, with  $0.91^\circ\text{C } 100 \text{ m}^{-1}$  in December 2014 and  $0.69^\circ\text{C } 100 \text{ m}^{-1}$  in December 2015 (equal to the February 2016 rate). The eastern slope lapse rate ( $E_{LR}$ ) had a summer maximum of  $1.15^\circ\text{C } 100 \text{ m}^{-1}$  in December 2014, and a winter minimum of  $0.478^\circ\text{C } 100 \text{ m}^{-1}$  in August 2015.

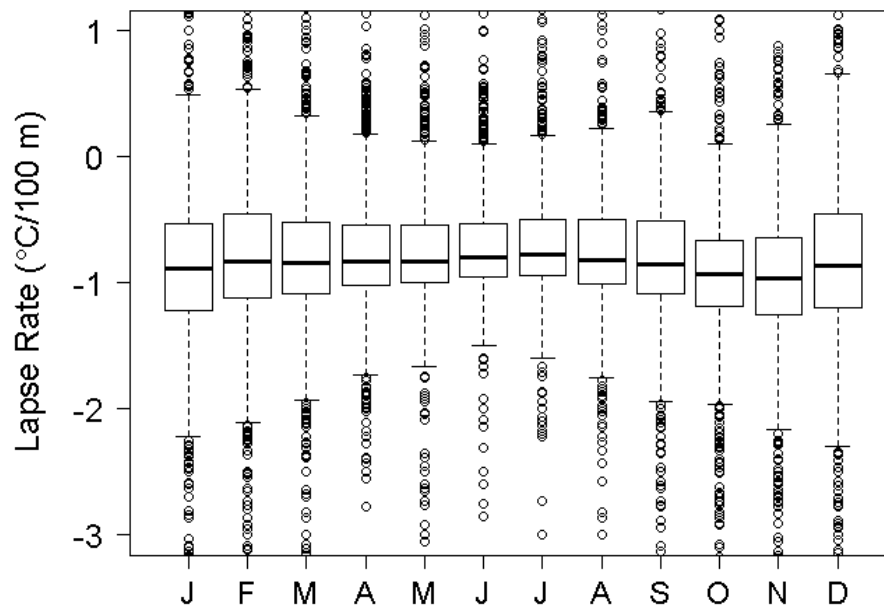
**Table 3.** Relationship between lapse rate variables and predictors (ANOVA results).

Independent variable	Dependent variable	F value	p value
Month	Eastern slope lapse rate	162.6	<0.0001
Month	Western slope lapse rate	25.26	<0.0001
Cloud base level	Eastern slope lapse rate	0.0572	0.8111
Cloud base level	Western slope lapse rate	3.5024	0.0618
Cloud base level	Lower eastern slope lapse rate	0.2744	0.6007
Cloud base level	Upper eastern slope lapse rate	0.1655	0.6844
Cloud base level	Lower western slope lapse rate	11.726	0.0007
Cloud base level	Upper western slope lapse rate	0.0397	0.8422
Cloud base level	Upper/lower slope lapse rate difference - eastern slope	0.4668	0.4949
Cloud base level	Upper/lower slope lapse rate difference - western slope	5.7612	0.0169



**Fig. 6.** (a) Western slope, and (b) eastern slope hourly lapse rates over 12 months. Extreme outliers not shown.

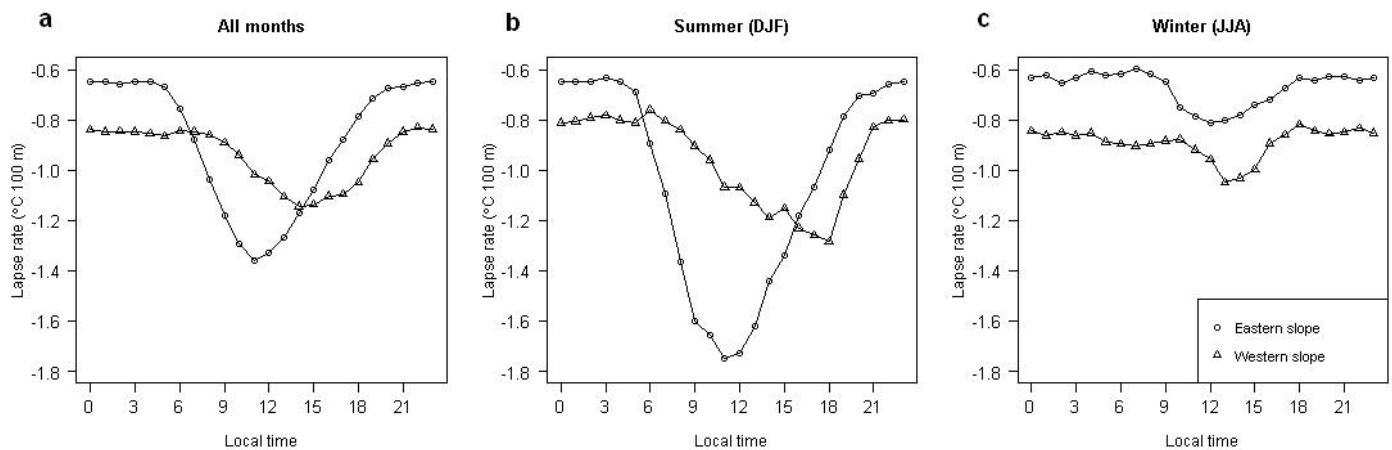




**Fig. 7.** Monthly free air lapse rates below 400 m.a.s.l. at Macquarie Island determined from twice-daily radiosonde data, 1995–2017. Extreme outliers not shown.

Differences between daily minimum and maximum temperature lapse rates were notable on the eastern slope, whereas western slope lapse rates showed little diurnal variation (Fig. 8). The diurnal lapse rate cycle for the eastern slope had a greater range in summer when daytime lapse rates were much steeper than at night, whereas in winter there was little difference (Fig. 8). Daily minimum and maximum temperature lapse rates averaged over 12 months were 0.495 and 1.029 for the eastern slope and 0.791 and 0.931 °C 100 m<sup>-1</sup> for the western slope, respectively.

Simultaneous hourly lapses were weakly correlated between all three elevation profiles:  $E_{LR}$ ,  $W_{LR}$  and the open air (linear regression,  $p$ -values < 0.0001; Pearson correlation coefficient 0.23–0.28). Although correlated, lapse rates differed between east and west slopes ( $t = 23.771$ ,  $p < 0.001$ ).  $E_{LR}$  generally exceeded  $W_{LR}$  during the middle of each day (Fig. 8).



**Fig. 8.** Mean hourly lapse rate for eastern and western slopes. (a) 12 months, (b) austral summer, (c) austral winter.

No significant trends in annual range of mean monthly air temperature with elevation were observed. Positive lapse rates, indicating temperature inversions, were very rare, accounting for 1.5% of hourly lapse rate observations for  $E_{LR}$  and 0.2% for  $W_{LR}$ .

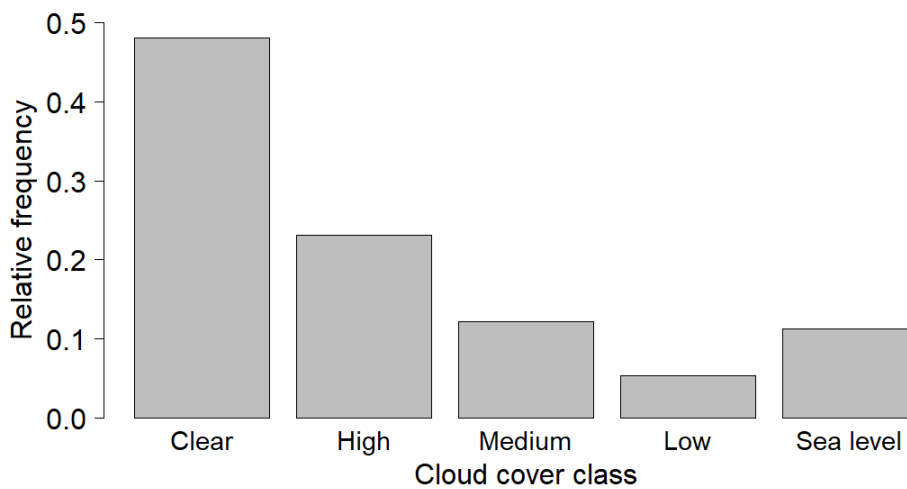
Clustering of sonde data ( $n = 2547$ ) revealed three broad meteorological conditions, based on visual inspection of the dendrogram: 1, north-westerly airflows with high windspeeds, air temperature and humidity (38% of observations); 2, westerly airflows with moderate windspeeds and lower air temperatures and humidity (49%); 3, airflows from other directions characterised by lower windspeeds and moderate air temperatures and humidity (13%). Lapse rates derived from logger data showed no significant difference between these three weather regimes (ANOVA, eastern slope  $F = 1.488$ ,  $p = 0.227$ ; western slope  $F = 2.21$ ,  $p = 0.142$ ;  $n = 76$ ).

Atmospheric stability (Froude number) was not strongly related to eastern slope (Pearson correlation coefficient = -0.292) or western slope (Pearson correlation coefficient = -0.133) lapse rates ( $n = 741$ ). In both cases, steeper lapse rates were associated with higher Froude numbers which indicate orographic lifting and leeward turbulence.

### Cloud base level

Cloud obscured at least part of Macquarie Island's topography in just over half the webcam images (Fig. 9). In around half of these instances of cloud at island level (approximately 25% of all images) cloud was confined to the higher plateau and peaks (around 250 m a.s.l. and higher).

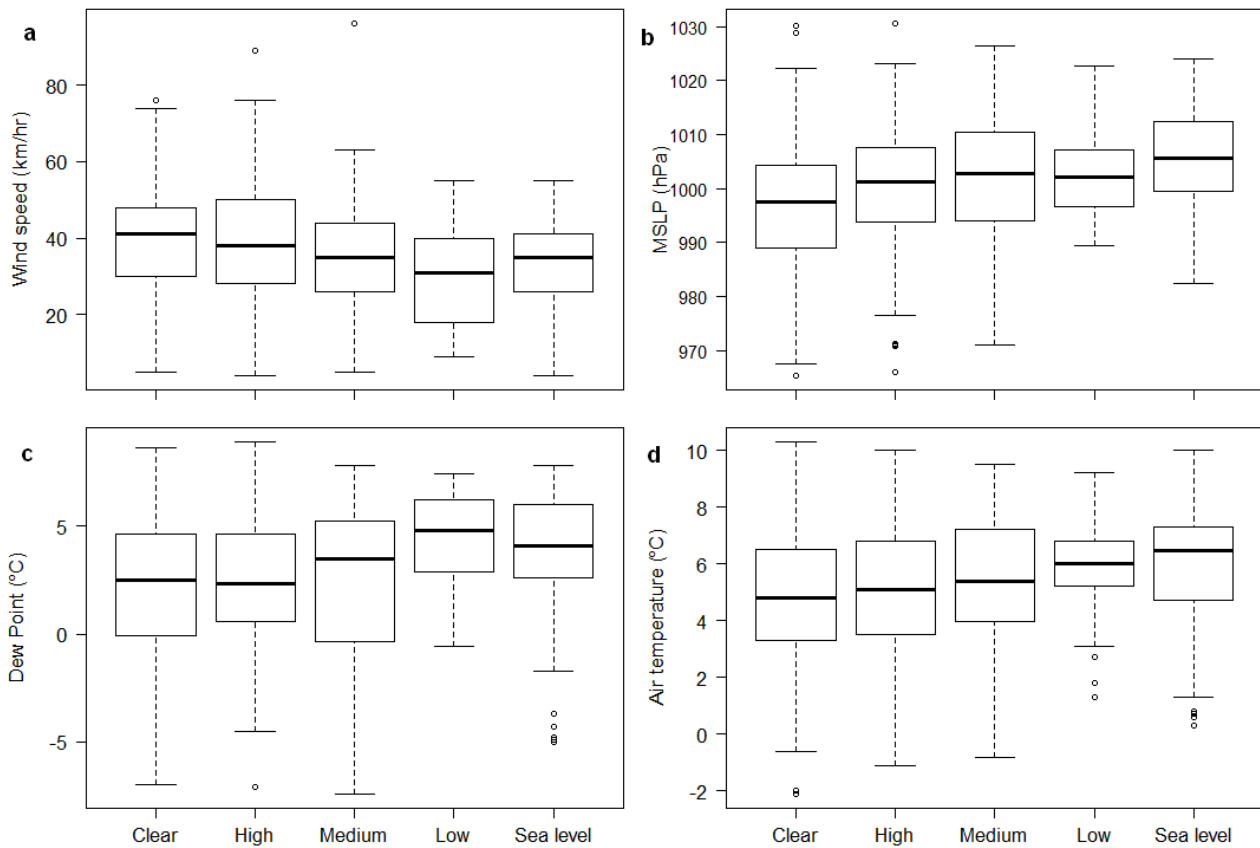
Cloud base level shows a relationship with all tested meteorological variables other than wind direction (Table 4, Fig. 10). Low cloud is generally associated with higher air pressure and air temperature and lower wind speeds (Fig. 10). Cloud base level varies between months, with no clear seasonal pattern (data not shown), and does not vary diurnally (Table 4). Linear Discriminant Analysis was unable to separate the cloud cover classes since they overlapped strongly in environmental space rather than reflecting discrete combinations of weather variables.



**Fig. 9.** Relative frequency of cloud cover on Macquarie Island classified from webcam images. Cloud higher than the island or absence of cloud is classified 'clear'. The four classes of cloud base level are cumulative since each class includes lower classes (e.g. medium cloud includes the lower two levels).

**Table 4.** Results of ANOVA tests for five classes of cloud base level. Variables are annual (month) and diurnal (hour) cycles and meteorological observations from BoM station at sea level.

Variable	F value	p-value
Mean sea level pressure	10.35	<0.001
Wind direction	5.048	0.001
Wind speed	4.341	0.002
Relative humidity	4.125	0.003
Dew point	4.038	0.003
Month	3.366	0.01
Air temperature	2.321	0.056
Hour	0.3974	0.811

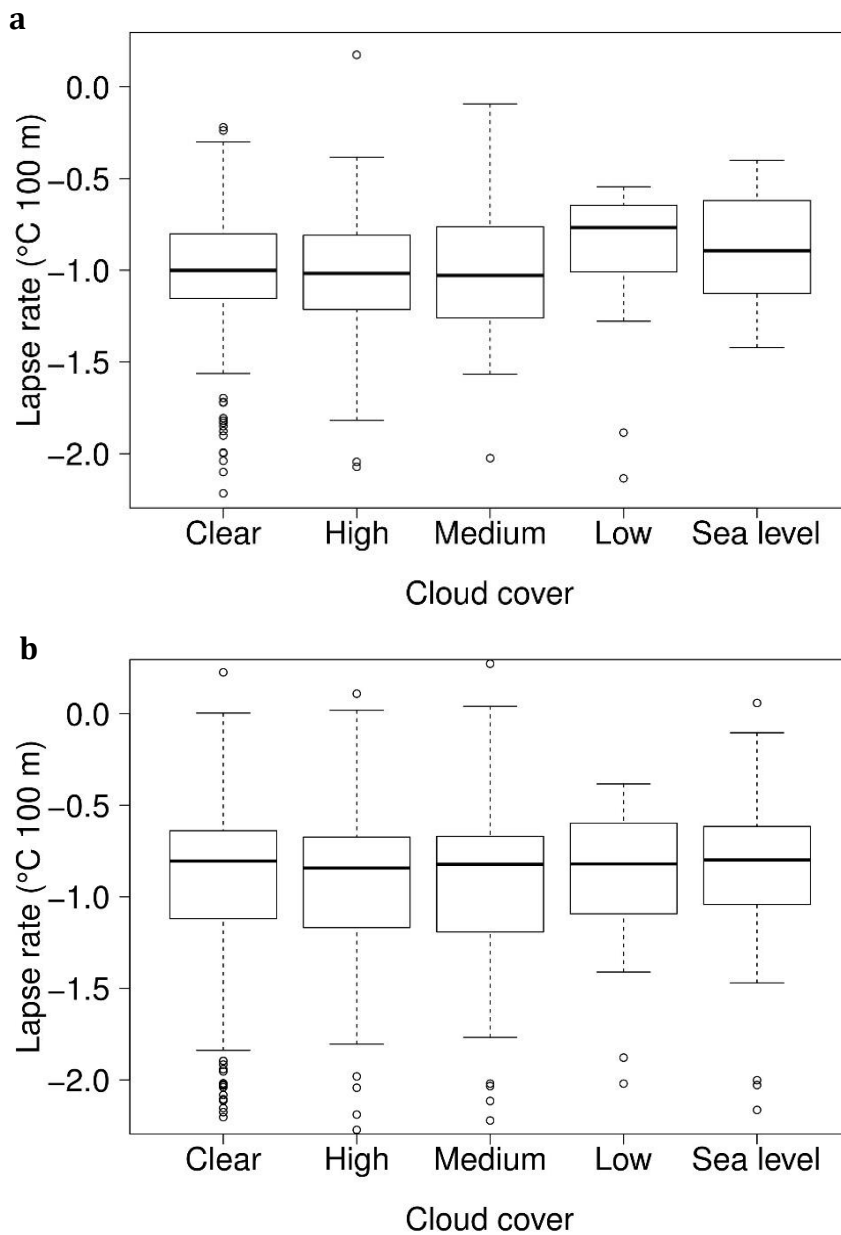


**Fig. 10.** Meteorological variables recorded at BOM under different cloud conditions. (a) wind speed (km/hr), (b) mean sea level pressure, (c) dew point, (d) air temperature.

Only the lower western slope lapse rate showed a significant relationship with cloud base level (Table 3). The difference between upper and lower slope lapse rates was also related to cloud cover classes on the western slope (Table 3). Lapse rates did not vary with cloud cover classes on the western slope (Fig. 11). Cloud base level appears to be independent of low-level atmospheric stability (ANOVA,  $F = 0.922$ ,  $p = 0.344$ ,  $n = 39$ ).

Observations of cloud base level from webcam imagery were necessarily limited to the period from dawn to dusk and therefore may be subject to bias associated with diurnal cycles. While there was no significant relationship between time of day (ANOVA,  $F = 2.677$ ,  $p = 0.102$ ) and cloud base level in our dataset we cannot be certain that our daylight observations are representative of cloud base levels during periods of darkness. In most cases we observed the presence of cloud at higher levels than the cloud base level and in no cases was a low cloud

base level observed in which cloud was visibly absent at a higher elevation. Consequently, where low cloud obscured visibility of the higher elevations of the island we assumed that cloud cover was present at all higher elevations but acknowledge that in rare cases the vertical extent of cloud cover may have been limited such that the higher elevations of the island were cloud free.



**Fig. 11.** (a) Eastern slope and (b) western slope lapse rates under different cloud conditions.  $N = 600$ . Cloud cover classes: Clear — no low cloud (cloud base approx.  $> 400 \text{ m.a.s.l.}$ ); High — cloud limited to higher peaks (cloud base approx.  $> 250 \text{ m.a.s.l.}$ ); Medium — most of plateau under cloud (cloud base approx.  $> 150 \text{ m.a.s.l.}$ ); Low — cloud covering most of vertical extent of island (cloud base approx.  $> 70 \text{ m.a.s.l.}$ ); Sea level — cloud at sea level. Extreme outliers not shown.

## Discussion

### *Lapse rates*

The observed mean lapse rates of around  $1.0^{\circ}\text{C } 100 \text{ m}^{-1}$  are similar to most previous estimates from Macquarie Island (Taylor 1955, Jenkin 1972, Davies & Melbourne 1999, see Table 1). However, Tweedie (2000) determined a mean eastern slope lapse rate of around  $0.6^{\circ}\text{C } 100 \text{ m}^{-1}$  and predicted a shallower rate on the (unmeasured) western slope due to a putative föhn effect on the eastern (lee) slope. While our results indicate steeper lapse rates on the eastern slope, the difference is very small ( $0.068^{\circ}\text{C } 100 \text{ m}^{-1}$ ). Temperature data and cloud formations indicate frequent and strong föhn winds on the eastern (lee) side of subantarctic Heard Island, which has more than five times the vertical relief of Macquarie Island (Thost and Allison 2006). Based on one month of observations on the eastern slope of Macquarie Island, Davies and Melbourne (1999) noted a much steeper lapse rate on the lower slope (below 150 m a.s.l.) than the upper slope, while our data show no such inflection.

Macquarie Island lapse rates are considerably steeper than those typically reported for mid-latitude oceanic climates, such as Mt Wellington in Tasmania and the Pennines in Britain, which show considerable monthly and seasonal variation in lapse rates (Table 1).

Mountains with more continental climates also typically display lapse rates close to the moist adiabatic lapse rate ( $0.4\text{--}0.6^{\circ}\text{C } 100 \text{ m}^{-1}$ ), as in the European Alps and central China (Table 1). In the Rocky Mountains at  $52^{\circ}\text{N}$ , representing a continental climate at a similar latitude to Macquarie Island, annual mean lapse rates are only around  $0.4^{\circ}\text{C } 100 \text{ m}^{-1}$  due in part to the moderating influence of frequent temperature inversions, but with little increase in summer (Diaz and Bradley 1997).

Since cool moist conditions generally produce shallower lapse rates (e.g. Ashcroft and Gollan 2013), it is surprising that Macquarie Island's uniformly cool moist climate supports steep mean lapse rates. Steep mean lapse rates ( $0.98^{\circ}\text{C } 100 \text{ m}^{-1}$ ) have been reported from the subantarctic, on a glacier on the lee side of South Georgia in the summer months (Smith 1960). In contrast, mean lapse rates at Marion Island, with a subantarctic climate comparable to Macquarie Island, are around  $0.4\text{--}0.5^{\circ}\text{C } 100 \text{ m}^{-1}$  (Hedding 2006). Lapse rates for the internal temperature of *Azorella selago* cushion plants on Marion Island varied between four altitudinal transects ( $0.31\text{--}0.61^{\circ}\text{C } 100 \text{ m}^{-1}$  in winter,  $0.51\text{--}0.72^{\circ}\text{C } 100 \text{ m}^{-1}$  in summer) with no consistent

difference between western (windward) and eastern (lee) slopes (Nyakatya & McGeoch 2007). Heard Island has similar lapse rates to Macquarie Island, but differs seasonally, with steeper rates in winter (Table 1).

Solar radiation has daily and annual cycles, with steeper lapse rates associated with greater insolation in daylight periods and in summer (Pepin *et al.* 1999). These associations fit our observations of diurnal and annual variability in lapse rates and suggest that terrestrial lapse rates on Macquarie Island may not be representative of free air lapse rates over the Southern Ocean. On the western slope, a greater influence of the prevailing winds and orographic lifting may over-ride local convection. The influence of solar radiation on air temperature may be accentuated in our study by direct heating of the temperature loggers due to a lack of radiation screening. However, we removed outliers from the temperature dataset.

Seasonal patterns of steeper lapse rates in summer and gentler lapse rates in winter observed in the present study for the eastern slope are consistent with previous work on Macquarie Island (Tweedie 2000), in central Europe (Rolland 2003), in the maritime mid-latitude Cascade Mountains (Minder *et al.* 2010) and subtropical Taiwan (Chiu *et al.* 2014). However, mean free air lapse rates at Heard Island, measured by radiosonde, are steepest in September-October ( $0.79^{\circ}\text{C } 100 \text{ m}^{-1}$ ) and lowest in January-February ( $0.62^{\circ}\text{C } 100 \text{ m}^{-1}$ ) (Allison & Keage 1986).

The outlying mean lapse rate for December 2014 fits the seasonal pattern of a summer maximum but is notably higher than any other summer months, yet there are no anomalies in the meteorological variables to explain this result. Our analysis provides some indication of seasonal trends in lapse rates, but we note that data collected over a longer period than 12–18 months would be more robust in relation to interannual variation. Apart from the discrepancy between December 2014 and December 2015, other months displayed similar or less interannual variation than the variation between contiguous months.

Our observations of seasonal variation in  $E_{LR}$  ( $0.864^{\circ}\text{C } 100 \text{ m}^{-1}$ , or 0.52 after removing outlier) is much higher than previously reported ( $0.3^{\circ}\text{C } 100 \text{ m}^{-1}$ ) for the eastern slope of the island 2 km north of our transect (Tweedie 2000). However seasonal variation on the western slope in this study ( $0.25^{\circ}\text{C } 100 \text{ m}^{-1}$ ) is close to that reported by Tweedie (2000) for the eastern slope. The seasonal variation in lapse rates on Macquarie Island is low compared to more continental mountains, where temperature inversions tend to influence winter lapse rates (Rolland 2003,

Blandford *et al.* 2008, Minder *et al.* 2010). Positive lapse rates associated with temperature inversions were rare on Macquarie Island, where they are relatively more frequent for  $E_{LR}$  than  $W_{LR}$ .

The less distinct seasonal trend for  $W_{LR}$  may be due to the strong influence of orographic lift related to the westerly airflow over-riding any effects of solar radiation on air temperature. However,  $W_{LR}$  varies independently of wind speed. Furthermore, Peterson and Scott (1988) suggest that local patterns of wind flow on Macquarie Island, such as windward rotors, respond to topography.

The diurnal increase in lapse rates in summer occurs earlier on the east-facing slope (see Fig. 8), suggesting that surface heating from solar radiation shifts near-ground temperatures above the free air lapse rate. This supposition is supported by the differential between simultaneous lapse rates on each slope, which is strongly related to time of day, time of year and air temperature (and is mostly driven by fluctuations in  $E_{LR}$ ) and by previous observations from Macquarie Island's eastern slope (Tweedie 2000). Differences in cloud cover between the two slopes may also be influential, with potentially greater cloud cover on the western slope. However, Wang *et al.* (2016) modelled higher rainfall on the downwind (eastern) side of Macquarie Island, suggesting more cloud cover on the eastern slope.

Tweedie (2000) found strong correlations between meteorological data from an altitudinal transect on the eastern slope of Macquarie Island and the data from the BoM station. Therefore, the BoM data are a useful proxy for synoptic weather patterns since weather variables such as wind direction, air temperature and MSLP are largely driven by synoptic conditions. We found limited explanation for changes in lapse rates based on meteorological data (from both the BOM station near sea level and the boundary layer to 400 m altitude), suggesting that synoptic conditions have little influence on lapse rates at Macquarie Island, which may be better explained by physiographic factors.

Sea level air temperature and relative humidity are related to lapse rates since they reflect atmospheric processes of convection and latent heat flux. Atmospheric pressure relates to vertical movement of air masses, which influence lapse rates at a synoptic time scale (Blandford *et al.* 2008). Surprisingly, given our expectation that MSLP would represent the passage of circumpolar cyclones and associated fronts (i.e. synoptic scale processes), there was



not a strong relationship between MSLP and lapse rates (unpublished data). As with our data, Blandford *et al.* (2008) found that lapse rates related less to humidity than air temperature.

The relation between atmospheric stability and lapse rates is consistent with mountain wave behaviour since airmasses with vertical stability or weak winds (low Froude Number) are blocked by the topography of the island and result in shallow lapse rates while strong winds with large wavelengths (high Froude Number) promote orographic lifting on the windward slope and turbulences with potential reverse flow upslope on the lee slope (Lin and Wang 1996; Bao and Tan 2012).

Snow cover can influence near-surface air temperature (Pepin and Norris 2005) and consequently variable snow cover might affect lapse rates. A lack of data for snow cover on Macquarie Island precludes consideration of this factor.

### Cloud cover

The strong relationship between cloud level and atmospheric pressure indicates that synoptic scale processes are the dominant determinant of cloud base level in the atmospheric boundary layer at Macquarie Island. Observations of cloud cover from webcam images show the higher peaks of Macquarie Island (above around 300 m a.s.l.) experience cloud cover around 50% of the time, by one of two mechanisms. Discrete cloud confined to peaks or plateau (cap or crest clouds, respectively) are indicative of orographic clouds formed by cooling of upslope winds. Macquarie Island provides exceptionally good conditions for orographic cloud formation, presenting a steep barrier up to 400 m a.s.l. mostly perpendicular to the strong prevailing winds which drive uplift of moist air. Less frequently the cloud base extends to sea level, representing low-level stratus cloud (fog), which is associated with relatively warm moist northerly airflows and occurs on around 70 days per year (Streten 1988).

The lowest cloud base levels were associated with more northwesterly (rather than westerly) winds with slightly lower wind speed and higher air temperature than under more elevated cloud. These associations are consistent with low stratus cloud formed by the cooling of relatively warm pre-frontal northwesterly or northerly airmasses driven by a blocking anticyclone system (Streten 1988). The relatively high air pressure and temperature associated with low cloud is consistent with this phenomenon but, surprisingly given the

directional component to these weather systems, wind direction is not strongly related to cloud base level.

Intermediate cloud base levels may represent either orographic or synoptic (e.g. stratus or stratocumulus) cloud. On Heard Island, at a similar latitude to Macquarie Island (53°S), oxygen isotope ratios from snow indicate that orographic processes dominate precipitation (Allison and Keage 1986). On Macquarie Island, high-resolution climate models suggest orographic forcing results in higher precipitation on the lee than the windward side of the island under both drizzle and frontal conditions (Wang *et al.* 2016).

Our observations concur with previous studies using other methods to describe cloud base levels on Macquarie Island. Cloud base height estimated from recorded air temperature, dew point and lapse rate has mean monthly values of around 220-340 m a.s.l. (Tweedie 2000). Median cloud base level at 0900 hours at Macquarie Island station is 300 m a.s.l. (Bergstrom *et al.* 2015). The height range of 260–500 m a.s.l. contains the highest frequency of cloud cover determined from Macquarie Island sonde data (Huang *et al.* 2012). Similarly, typical cloud base levels are around 300 m a.s.l. on other Southern Ocean islands: Heard Island (Thost and Allison 2006) and King George Island (Bitanja 1995).

On subantarctic Marion Island, Nyakatya and McGeoch (2007) hypothesise that less seasonal variation in substrate temperatures on the western side and at higher elevations is due to more frequent cloud cover than occurs at lower elevations and on the eastern side of the island. Macquarie Island also has a higher frequency of cloud at higher elevations, yet we found no support in our observed annual range of mean monthly air temperature for an associated lower seasonal variation in air temperature.

In Britain, Pepin *et al.* (1999) observed steeper lapse rates with more elevated cloud base level, attributing this effect to higher solar radiation and lower humidity. However, apart from the lower segment of the western slope, our results do not support the suggestion of Tweedie (2000), based on eastern slope data, that lapse rates generally increase with higher cloud base level. Indeed, our eastern slope lapse rates were consistent across all categories of cloud cover. The constant high humidity regardless of cloud cover which is characteristic of Macquarie Island's climate may explain this lack of relationship between cloud base level and lapse rates.

## Conclusions

To the best of our knowledge, this work is the most detailed study of environmental lapse rates in a hyper-oceanic climate and the first to compare annual environmental lapse rates on different aspects of a subantarctic island. Our use of webcam imagery to determine cloud base level and our attempt to determine cloud base level from lapse rates we also believe to be novel and relevant to other regions. The weak correlation between sonde-derived lapse rates and those recorded at 1 m above the surface of the island suggests that free air lapse rates are not a useful proxy for terrestrial lapse rates for ecological applications.

Our observations of lapse rates on the eastern slope of Macquarie Island are consistent with diurnal and annual variation in solar radiation. However, lapse rates on the western slope do not show a similar pattern and appear to be largely decoupled from both daily and annual solar radiation cycles. The main differences between the slopes are greater wind exposure and later daily direct sun on the western slope. Diurnal and seasonal patterns in lapse rates are relevant to vegetation microclimates and climate change scenarios, including altitudinal migration of vegetation communities in response to atmospheric warming.

Despite a modest elevation range, compared to other Subantarctic islands and to continental massifs, Macquarie Island's location in an oceanic context with almost constant vigorous movement of humid air drives frequent development of orographic cloud. Combined with a similar frequency of low cloud and precipitation related to synoptic processes, the highlands of Macquarie Island experience cloud cover around half the time, with no seasonal or diurnal pattern.

The year-round dominance of westerly airflows and limited seasonal variation in air temperature and humidity explain the general lack of seasonal patterns in cloud cover or lapse rates in this study. Environmental lapse rates on Macquarie Island are generally not closely related to cloud coverage. Both environmental lapse rates and cloud cover, along with wind exposure, provide an explanation of the altitudinal zonation of plant species and communities on Macquarie Island.

## **Chapter Four: Patterns of vegetation and landscape change before and after rabbit eradication on subantarctic Macquarie Island**

This chapter examines how climate and topography shape the vegetation of Macquarie Island, in combination with a history of grazing by rabbits.

Interpretation of landscape photography was used to examine vegetation change on Macquarie Island over two consecutive time periods spanning 33 years. This method was compared with changes in vegetation observed from vegetation plot data and from satellite remote sensing. Spatial analysis of vegetation change from repeat photography allowed investigation of environmental factors related to these changes.

Previous chapters informed the selection and interpretation of certain environmental variables (i.e. wind exposure, elevation).

This chapter has not previously been published.

## Abstract

Eradication of invasive European rabbits from subantarctic Macquarie Island was achieved in 2011. The extensive impacts of introduced rabbits on the vegetation of Macquarie Island are well-documented but few studies have investigated the ecosystem recovery process following the eradication. This study uses repeat landscape photography covering a 34 year period to examine differences in vegetation characteristics at three times with different rabbit populations: moderate, high and none. The hypothesis was that changes in vegetation would vary in their magnitude and direction in different environmental situations. Vegetation change recorded from repeat photographs and plant species cover data from long-term monitoring sites were used to obtain spatial data. Spectral vegetation indices derived from satellite imagery provided a wider geographic picture of change covering the transition from high rabbit numbers to no rabbits. Vegetation change trajectories varied between sites. No change was observed in some sites over periods of 29 or 34 years. Vegetation dominated by tussock grass and megaherbs was severely impacted by rabbits with a consequent shift to short grassland and herbfield communities. An increase in tussock grass and megaherbs from 2009 to 2014 signalled recovery of these elements of the vegetation. In some cases where no such recovery was evident, these species may be slow to recover or have been fixed in an alternative steady state by long-term grazing pressure. In high elevation feldmark vegetation, where rabbit impacts were minor, we observed no patterns consistent with climate change over 34 years.

## Introduction

Macquarie Island is a small (128 km<sup>2</sup>) very isolated landmass in the Southern Ocean roughly halfway between New Zealand and Antarctica (54.50°S 158.94°E). A steep-sided plateau above 200 m.a.s.l. comprises most of the island, with a maximum elevation of 420 m.a.s.l. Valleys and lakes are typically associated with faults while tectonic uplift has created a near-flat coastal terrace on the west coast (Adamson *et al.* 1988). The climate is characterised by a small diurnal and seasonal temperature range (3.1°C and 6.6°C annual mean minimum and maximum air temperature at sea level), strong predominantly westerly and northwesterly winds (mean 35 km/hr), frequent but typically light rainfall (annual mean 1033 mm) and frequent cloud cover (Australian Bureau of Meteorology; Jovanovic *et al.* 2012; see also Chapters 2 and 3).

The tundra vegetation of Macquarie Island is dominated by grasses, graminoids and forbs, including the megaherb form characteristic of subantarctic tundra (Little *et al.* 2016), with no woody plants among the 42 native vascular plant species (Selkirk *et al.* 1990). The island is a Nature Reserve and World Heritage Area managed for conservation and research (Carmichael 2007). A major management intervention was undertaken during 2010–2014, following years of planning, to eradicate invasive rabbits, rats and mice (Springer 2016).

The vegetation and landscape of Macquarie Island has been altered by European rabbits (*Oryctolagus cuniculus*) since their introduction in the late 1800s (Costin & Moore 1960; Copson & Whinam 2001; Scott & Kirkpatrick 2008, 2012). The first detailed studies of Macquarie Island vegetation examined an ecosystem which had been subject to rabbits for at least 75 years and had no previous history of native mammalian herbivores, meaning the natural vegetation structure and patterns on the island can only be inferred from remnant vegetation on sites inaccessible to rabbits (Copson & Whinam 1998).

Environmental change coinciding with rabbit introduction was abrupt and unprecedented in the palaeo-ecological record (Saunders *et al.* 2014). Subsequent changes in vegetation structure and species composition have reflected fluctuations in rabbit numbers and selective grazing of certain plant species (Bergstrom *et al.* 2009; Copson & Whinam 1998; Scott & Kirkpatrick 2012; Whinam *et al.* 2014a). For example, the largest plants on Macquarie Island, the megaherbs *Stilbocarpa polaris* and *Pleurophyllum hookeri* and the tall tussock grass *P. foliosa*, were disadvantaged by rabbits (Whinam *et al.* 2014a). Some recovery of disturbed

vegetation has occurred since rabbit eradication in 2011 (Shaw *et al.* 2011), including some unexpected species responses (Williams *et al.* 2016).

Following rabbit eradication, the extant disturbance processes are localized and include impacts of native fauna (regular trampling of vegetation by marine fauna in near coastal environments; soil disturbance by burrowing seabirds) and mass movement processes (such as landslides and debris flows) which occur frequently but irregularly due to substantial accumulation of peat on steep slopes with high soil moisture (Dykes & Selkirk-Bell 2010; Selkirk *et al.* 1990). Soil disturbance by frost action (Selkirk *et al.* 1988) and erosion by wind and water (Adamson *et al.* 1988) may also affect vegetation.

Aside from broadscale disturbance caused by rabbits, and localized natural disturbances, the other major driver of vegetation change is climate change. Although some climate change response has been observed in the vegetation (Scott & Kirkpatrick 2012), the impacts of climate change on Southern Hemisphere maritime tundra vegetation are not well understood. Altered precipitation patterns, higher rainfall, shifting wind regimes and increased air temperature have been observed at Macquarie Island since the mid 1900s (Adams 2009; Hande *et al.* 2012; Jovanovic *et al.* 2012; Pendlebury & Barnes-Keoghan 2007). Air temperature has cooled slightly and increased in variability since 1980 following warming of around 1°C during the earlier part of the century (Turney *et al.* 2017). Substantial and spatially variable range changes of vascular plants have occurred on Marion Island, which is similar in latitude and flora to Macquarie Island but has experienced warming and reduced rainfall since 1980 (le Roux and McGeoch 2008a). Climate change is therefore expected to be a confounding factor in determining historical rabbit impacts and post-eradication vegetation response as well as the major driver of future vegetation dynamics.

Previous multi-decadal studies have observed vegetation change related to rabbit impacts at long-term monitoring plots (Scott & Kirkpatrick 2008, 2012; Whinam *et al.* 2014a). However, long-term data are lacking for much of the island. Extensive archives of landscape photography covering many areas of Macquarie Island provide a potential source for change detection to complement the more localized monitoring plots.

Repeat photography (rephotography) of the same scene over time is widely used for assessing landscape changes such as erosion, vegetation succession and glacial retreat (Webb *et al.* 2010). Limited numbers of repeat photographs (often time series of only two images),

variation in timing, and small and spatially biased sets of locations can be problems for analysing and interpreting post hoc rephotography (Kull 2005; Pickard 2002). These problems can be avoided by photographing different sites at similar times and selecting photo-points in order to sample a wide range of landscape features, or features of interest for change monitoring.

Satellite imagery and aerial photography can provide quantifiable data with extensive coverage, making them preferable to on-ground photography in many situations (Kull 2005). However, on-ground photography may have greater temporal coverage and can display detail that is not present in coarser-scale imagery. On Macquarie island, there is no satellite imagery available before the late 1980s and very infrequent imagery up to around 2005. Vertical aerial photography is limited to three series, the earliest, in 1976, covering less than half the island in monochrome. Frequent cloud cover (Chapter 3) makes complete aerial coverage of the island very rare. Satellite image change detection has been used to examine spatial extent of rabbit damage between 2000 and 2005 on part of Macquarie Island (Bergstrom *et al.* 2009).

On Macquarie Island, on-ground photography provides an archive of landscape change with greater frequency over a longer period than is available from either aerial photography or satellite imagery. Linking ground photography with satellite imagery and spatial data characterising the landscape can provide mappable results, unlike traditional rephotography or photo-monitoring which is site specific and not readily extrapolated spatially.

We use a large dataset of repeat photographs covering a variety of vegetation types and landscapes on Macquarie Island to identify different types of vegetation and landscape change over two periods spanning 34 years. Vegetation surveys over a comparable period provide species-level data. We expected that vegetation change influenced by rabbit grazing, removal of rabbits and climate change would vary spatially due to environmental differences such as site history, microclimate, soils and topographic position. Since feldmark vegetation has suffered minimal rabbit impact (Whinam *et al.* 2014b) we expect to see a climate change response in this environment given the observed change in Macquarie Island's climate over past decades. At lower elevations previous studies have shown a decline in megaherbs and tussock grass related to increased rabbit population density (e.g. Scott & Kirkpatrick 2012; Whinam *et al.* 2014a) so we expect these grazing-sensitive species to increase post-eradication with a concomitant decrease in grazing-tolerant short grassland.



Here we test the following hypotheses: impact of rabbits is spatially variable; vegetation recovery trajectories following rabbit eradication are site-specific; megaherbs and tall tussock grass will replace lower elevation communities of shorter stature; high elevation feldmark vegetation (which has suffered minimal rabbit impact) will display a response to climate change between 1980 and 2014.

## Methods

### *Photo interpretation*

Photo-points were established in 1980 by JJS. Photographs have been retaken from these points several times by the same photographer, always in the summer months. Previous studies have noted a time lag of several years for signs of vegetation recovery following peaks of rabbit populations (Copson & Whinam 1998; Scott & Kirkpatrick 2012). Consequently, we selected three time steps covering the full temporal extent of the photo series: 1980 (three years after the major rabbit population peak), 2009 (three years after secondary rabbit population peak), 2014 (three years after rabbit eradication). These times represent periods of moderate-high, moderate and zero rabbit populations (Table 1).

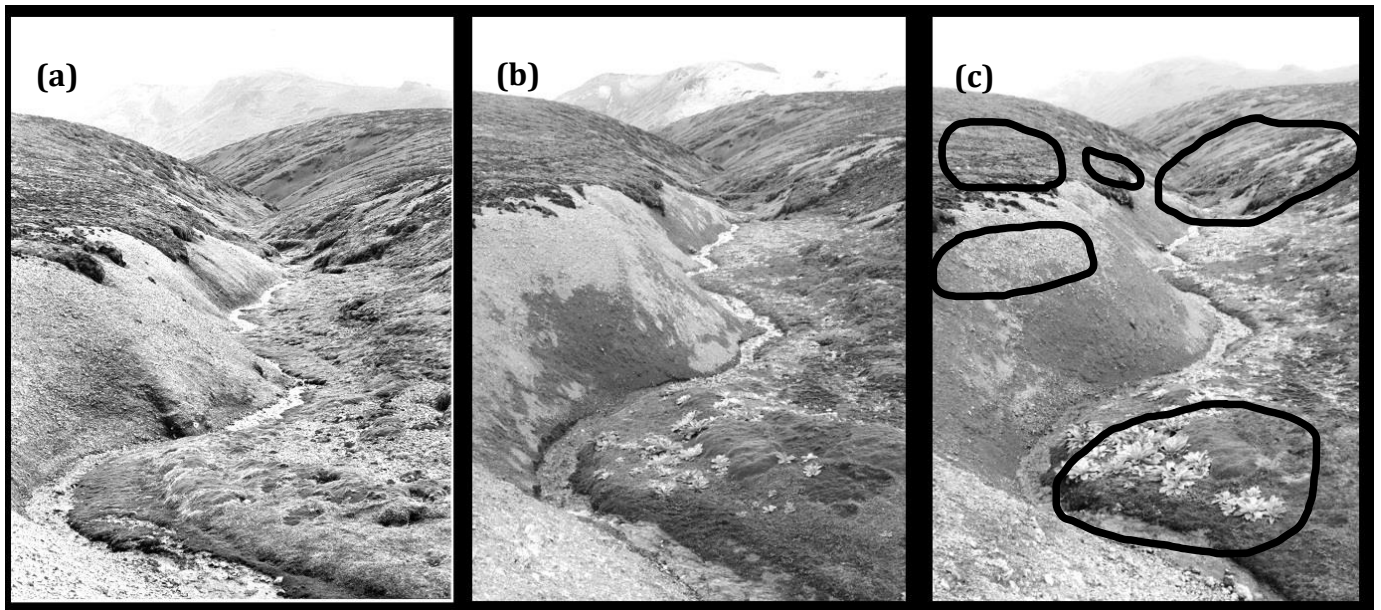
In most cases a panorama comprising several images was taken at each photo-point, providing extensive coverage of the landscape. For the 1980 photographs, black and white prints from 35 mm film were digitized using a scanner. The 2009 and 2014 photographs were captured in colour using a digital camera. All photographs were then printed in greyscale, providing comparable images for analysis (Fig. 1).

To avoid issues with attempting to quantify variables or randomize sampling of oblique photographs we subjectively selected one or more polygons (zones of variable size and shape with a uniform pattern of change within a particular landscape type) on each photograph and scored variables using three classes: increase, decrease, no change. Increase and decrease are visually detectable expansion or contraction of features such as plant species, life-forms or vegetation communities which can be readily identified from photographs. We also noted if the location was affected by erosion/mass movement or a walking track and these observations were removed prior to analysis to avoid confounding changes due to grazing or climate. Polygon sizes ranged from approximately 25—500 m<sup>2</sup>.

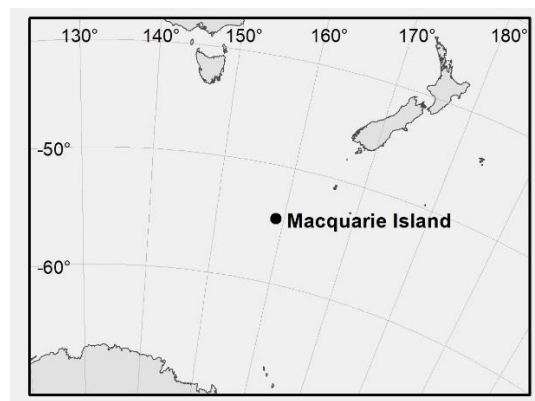
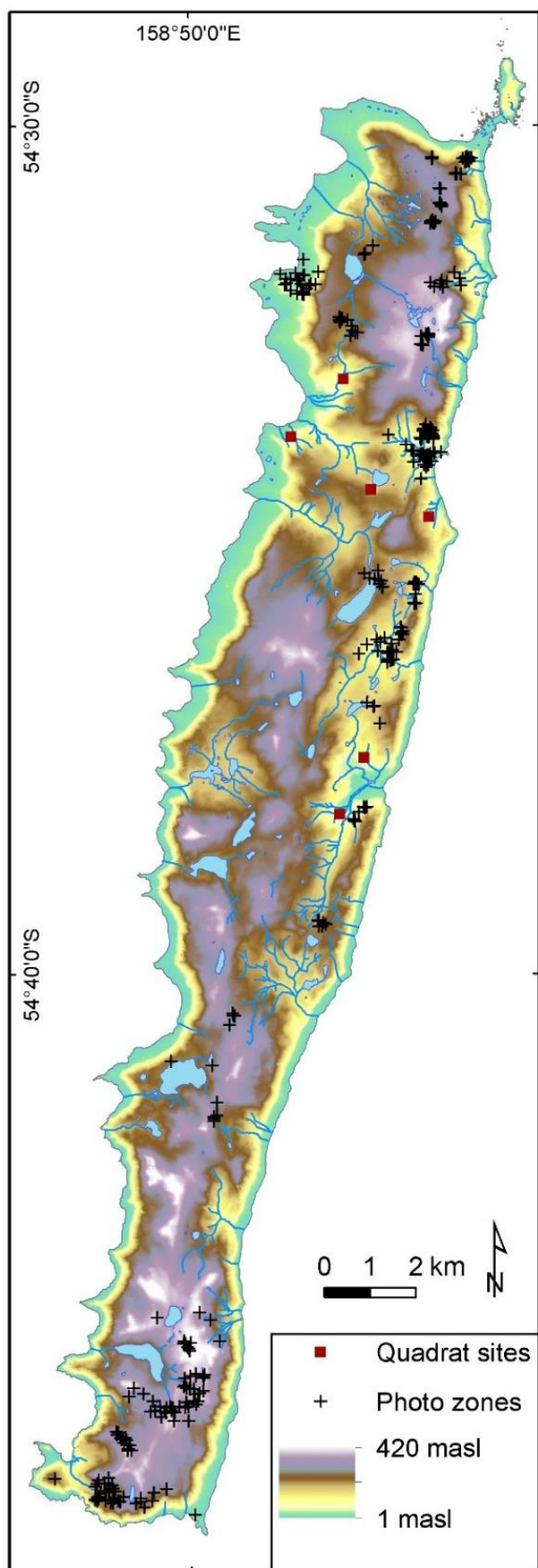
Land cover type was determined from the earliest photograph using the following categories (cf. Van der Putten *et al.* 2012): bare ground (no vegetation), feldmark (sparse vegetation dominated by moss or *Azorella macquariensis*); tussock grassland (dominated by the tall tussock grass *P. foliosa*); short grassland (dominated by a mix of *Agrostis magellanica*, *Festuca contracta*, *Deschampsia chapmanii*, *Luzula crinita* and *Uncinia* spp.); *Acaena* herbfield (dominated by either or both *Acaena magellanica* and *A. minor*.); and *Pleurophyllum* herbfield (dominated by *P. hookeri*).

**Table 1.** Rabbit population estimates for Macquarie Island for the years relevant to photograph series (from Terauds *et al.* 2014).

Photo year	Rabbit population	Rabbit population (preceding three years)
1980	~200,000 (moderate-high)	200,000–355,000 (high)
2009	~125,000 (moderate)	120,000–220,000 (moderate-high)
2014	0	0–50,000 (none to low)



**Fig. 1.** An example of a rephotography series at Whisky Creek in the south of Macquarie Island: (a) 1980; (b) 2009; (c) 2014. Polygons used for change observations shown on (c).



**Fig. 2.** Location of photograph observations (i.e. polygons) and grassland/herbfield vegetation monitoring quadrats on Macquarie Island.

Individual species frequently occur in different combinations across different communities, so instead of land cover types we used a different set of variables for change observations, focused where possible on species or structural elements of the vegetation. For example, short grass can occur in feldmark or tussock grass communities and tussock grass can occur in short grassland communities. Given the purpose of observing broad-scale vegetation change and the limits of species identification possible from photographs we grouped ‘short grass’ (the dominant species of short grassland) and ‘*Acaena* species’ (patches of *Acaena magellanica* and/or *A. minor*). The megaherbs *P. foliosa*, *P. hookeri* and *S. polaris* and the cushion plant *A. macquariensis* were all recorded individually.

For each polygon, any apparent vegetation change (or absence of change) that could be detected between a time-series pair of photographs was recorded using the three change classes. This process was repeated for both periods: 1980–2009 (hereafter P1) and 2009–2014 (hereafter P2).

### Geolocation

To enable spatial analysis of the photographic observations, we used ArcGIS 10.2 to locate a point for each polygon. We used a georectified satellite image overlaid with topographic contour lines and the photo-point locations from GPS data (i.e. the position where the photographer was standing) to identify a point in the landscape representative of each polygon in the photograph, based on topography and features visible in both the photograph and satellite image. To aid this visual assessment we often created viewsheds, to show which parts of the landscape were visible from the photo-point. Polygons which could not be confidently geolocated were excluded from further analysis. In total, 355 polygons from 109 photographs were geolocated (Fig. 2).

### Environmental variables

Spatial layers representing environmental factors which might influence vegetation distribution and dynamics were used to characterize the environment in each polygon (Table 2). ArcGIS 10.2 was used to create all variables, except for wetness index (SAGA GIS; Bricher 2012) and wind exposure (WindNinja software; Forthofer 2007). Correlations between all environmental variables were examined to determine which variables might be redundant. Elevation and TPI1000 (Topographic Position Index with a 1000 m radius neighbourhood)

were the only pair of variables with a Pearson correlation coefficient exceeding a nominal threshold of 0.8 and on this basis TPI1000 was excluded from the statistical analysis.

Topographic Position Index describes ridges, valleys and midslopes at a specified spatial scale (Guisan *et al.* 1999).

### *Photo interpretation data analysis*

A chi-square test with Monte Carlo simulation was used to examine the proportions of the three change classes in each vegetation type and period. Topographic variation in vegetation change was tested using four classes for each of elevation (0–100, 101–200, 201–300 m), slope angle (0–5, 6–10, 11–20, >20°) and aspect (north, east, south, west) tabulated against the three changes classes for each combination of vegetation category and period. Data analysis was performed in R v.3.4.1 (R Core Team 2014).

**Table 2.** Spatial variables used as explanatory variables in random forest models of vegetation change.

Variable	Ecological relevance	Data preparation
Elevation	Air temperature, soil temperature, cloud cover, wind	5 m DEM derived from NASA PACRIM Mission 2
Slope angle	Drainage	Derived from DEM in ArcGIS
Northness	Aspect (sun, wind)	Derived from DEM in ArcGIS
Eastness	Aspect (sun, wind)	Derived from DEM in ArcGIS
Wetness index	Drainage/ waterlogging (also typically a surrogate for soil depth and organic matter)	Derived from DEM in SAGA (see Bricher 2012)
Six month total solar radiation	Relative solar radiation during main growing season	Derived from DEM in ArcGIS (not considering cloud) (Fu & Rich 1999)
Wind exposure	Wind damage and desiccation	Analysis at 100 m grid cell scale (from DEM) using WindNinja software (Forthofer 2007), fitted to 5m surface using a spline in ArcGIS
Topographic Position Index (TPI180m, TPI500m)	Drainage, wind exposure	Derived from DEM using tools from Jenness <i>et al.</i> (2013) with neighbourhood size of 180 m radius and 500 m radius
North-south (latitude)	Regional differences in environment	Calculated distance from a horizontal line at the northernmost tip of Macquarie Island in ArcGIS
Distance from coast	Saltspray, aerosol nutrients	Distance from Macquarie Island coastline outline in ArcGIS

To test the relationship between each vegetation change variable, we trialled both logistic regression and random forest models. Based on the area under the curve (AUC) of the receiver



operating characteristic curve, both methods had similar predictive accuracy. We chose the *cforest* package for R, since this implementation of random forest is not biased by independent variables with different measurement scales and provides a conditional importance measure to estimate the importance of each predictor while controlling for collinearity, unlike logistic regression and most random forest models where collinearity can preclude interpretation of genuine variable importance (Strobl *et al.* 2008).

For each of the two time periods, random forest models were fitted for each vegetation change variable (change versus no change) with all environmental variables. Model performance was assessed by error rates (comparing bootstrapped samples to actual observations) and AUC. To deal with uneven numbers of observations in each class (change/no change) we randomly sampled observations from the more frequent class to match the number of observations in the smaller class so that the dataset was balanced. This was repeated ten times.

We used the conditional variable importance (mean value from ten replicates of the random forest model) to determine which environmental variables were important predictors of each type of vegetation change.

### *Vegetation plot data*

To compare observed vegetation change from rephotography with quantitative data on plant species change over a comparable period we used a long-term dataset of vascular plant species cover comprising six sites (Fig. 2) each with five 20 x 20 m quadrats located in short grassland and herbfield vegetation. While these sites are not directly comparable to the photo-point observations they do provide a sample of similar habitats over a similar timeframe. Site details and survey methods are described in Whinam *et al.* (2014a). Since projected foliage cover was recorded using broad percentage cover classes we converted these classes to a numeric value representing the midpoint of each class so that a mean value could be determined for percentage cover for each species across all 30 quadrats. For each species we fitted lowess lines to mean percentage cover value over time using data from 15 surveys, 1981 to 2015. Missing data for two sites which were not surveyed in 2013 were interpolated as the mean of the 2011 and 2015 values for each plot.

*Remote sensing*

We used Spectral Vegetation Indices (SVIs) calculated from high resolution WorldView-2 satellite images to investigate the potential for vegetation change detection and monitoring using remote sensing. Given the limited availability of high resolution imagery covering Macquarie Island, we selected images from December 2009 and January 2013 to approximate P2 of our rephotography dataset. These two images provided a mostly cloud-free coverage at 1.84 m pixel resolution of the northern half of Macquarie Island four years apart. After masking out areas of cloud, shadows and lakes, the satellite image time series covered 22% of the land area.

Image pre-processing involved orthorectification and atmospheric correction to generate surface reflectance values (using ENVI software), and georeferencing to align the two images (in ArcGIS). For each image we calculated SVIs using inbuilt formulae in ENVI, utilizing various combinations of the blue, green, red and near-infrared (NIR) spectral bands (Harris Geospatial 2018). Many SVIs are highly correlated and produce very similar results. Some SVIs have limited applicability to the tundra vegetation of Macquarie Island. Three SVIs with a mix of characteristics and spatial patterns were chosen for further analysis: Normalized Difference Vegetation Index (NDVI), Modified Triangular Vegetation Index – Improved (MTVI2) and Sum Green Index (SGI). NDVI is the ratio of red to near-infrared values, which characterizes the main reflectance and absorption of green foliage and has been widely used for remote sensing of vegetation. MTVI2 uses red, NIR and green spectral bands to represent vegetation leaf area index and bare soil. SGI is simply the total reflectance of green wavelengths.

To investigate the relationship between change in SVIs between 2009 and 2013 and change in vegetation observed from rephotography over a slightly longer but overlapping period we calculated the difference between 2009 and 2013 values at the pixel level for each SVI, resulting in a difference image where 0 is no change over time. In ArcGIS, we calculated the mean difference value for each SVI within a 5 m radius of each polygon centroid, to reflect a typical size polygon and to reduce errors associated with position uncertainties for polygons. Multiple logistic regression was used to test combinations of SVIs as predictors for rephotography binary vegetation variables (change/no change) for the 227 rephotography polygons which had SVI difference values (that is, excluding polygons which did not have coverage in both satellite images). A model selection process informed by AIC and calculated

variable importance was used to select the simplest of the best models in order to identify which SVIs were most effective for predicting each type of vegetation change. AUC was calculated to measure the performance of each selected model.

We tested for variations in SVI change with terrain characteristics using the same elevation, slope angle and aspect classes as in the rephotography analysis. Each of the three SVIs was reclassified into five classes (middle class = no change) and spatially cross-tabulated with the three terrain layers in ArcGIS. We used the chi-square statistic to test for a relationship between the SVI and terrain classes.

## Results

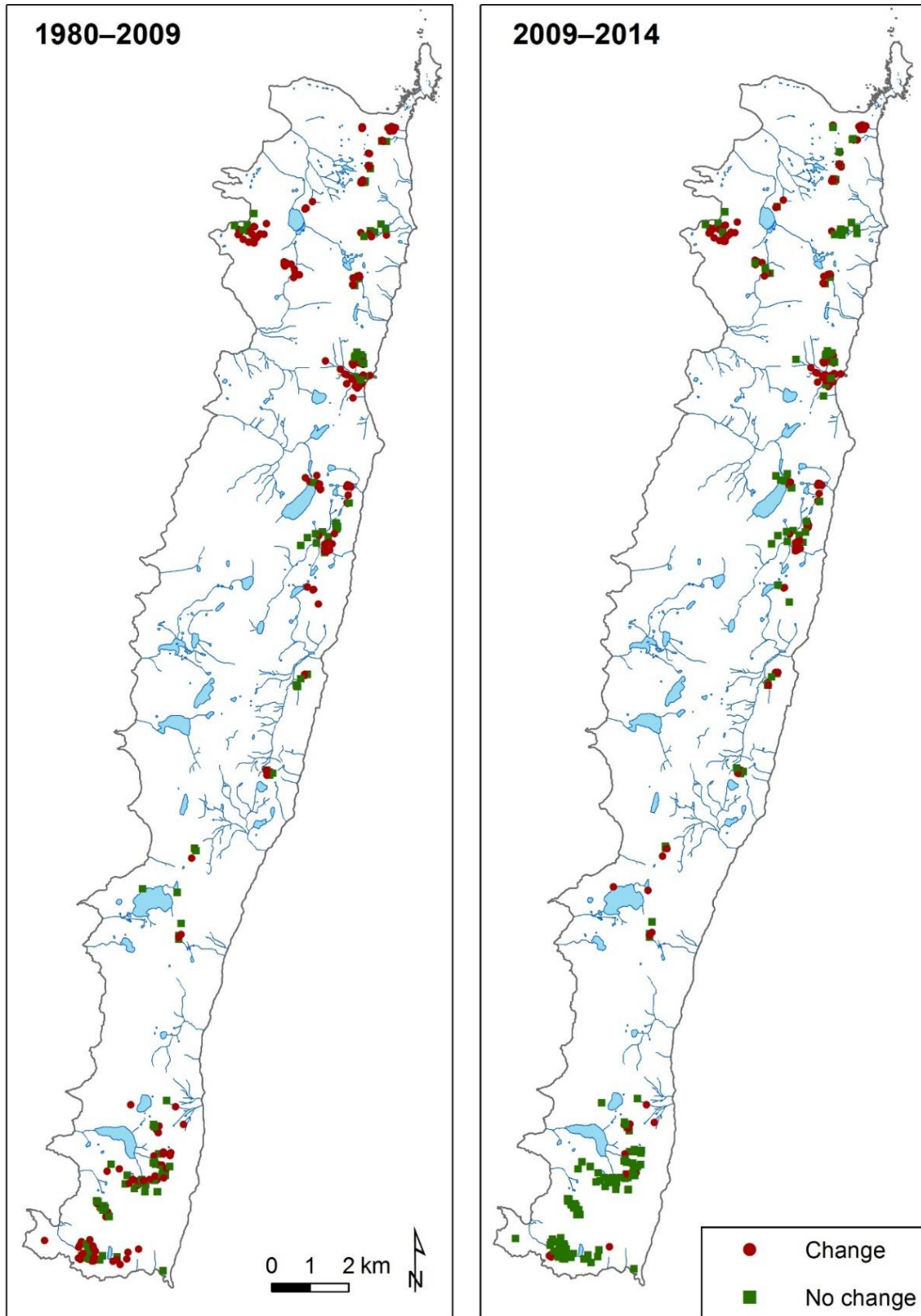
### *Rephotography — contingency table analysis*

Vegetation change was observed in all parts of the island covered by the rephotography series (Fig. 3). The far southern end of the island shows the most difference between the two periods, with most polygons containing vegetation change in P1 but not in P2.

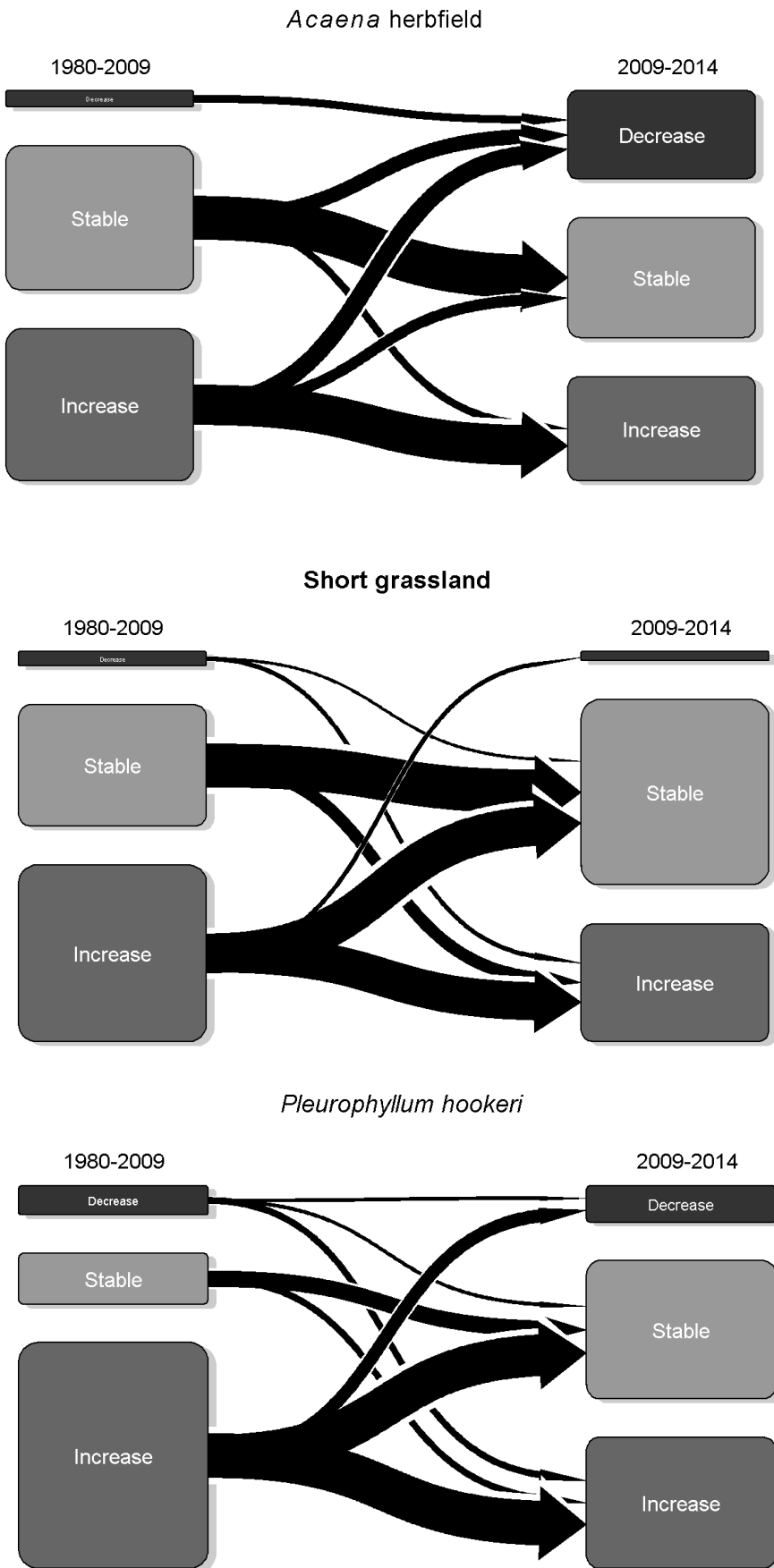
Most vegetation classes showed distinct trends in the direction of change in both time periods, except for *Acaena* which had similar proportions of each change category (Table 3, Fig. 4a). Short grass largely increased in P1 and was mostly stable (no change) in P2, with few observations of decrease in either period (Fig. 4b). *Pleurophyllum foliosa* declined in the first period and increased in the second. *Pleurophyllum* increased at most sites in both time periods, though there was a greater proportion of stable *P. hookeri* in P2 (Fig. 4c). *Azorella macquariensis* displayed a mixture of responses, with similar proportions of increases and decrease but a much higher proportion of stable observations in P2. In P2, bare ground was mostly stable and showed very little increase compared to P1.

In P2, tussock grass increased in most polygons where it was present while short grass was stable or increased (Table 3). Short grass species were more stable in short grassland than in tussock grassland. *Stilbocarpa polaris* was observed to decline in all 11 polygons where it was observed in P1 and only showed recovery in one case in P2; the small number of observations precluded statistical analysis for this species.





**Fig. 3.** Map of vegetation change observed from photographs over two periods, showing location of polygons in which some change was observed and polygons which appeared stable (no change).



**Fig. 4.** Transition plots for proportion of decrease, stable (no change) and increase for selected vegetation types/species for each period. Box sizes and arrow width are proportional to the number of observations in each class and transition.

**Table 3.** Observed change in land cover type within two periods. Where sufficient observations were available, the total number of observations in each of three categories (decrease, stable, increase) was compared to a null distribution using the chi-square test (with Monte Carlo simulation to account for zero and low cell counts). Total number of observations varies between time periods and categories due to limits of photo interpretability. P1: 1980–2009; P2: 2009–2014. Dashes indicate insufficient data for analysis.

Vegetation class	Period	Decrease	Stable	Increase	$\chi^2$	p value
Short grass	P1	9	46	79	54.9	<0.001
	P2	9	105	66	77.7	<0.001
<i>Pleurophyllum</i>	P1	2	5	27	32.9	<0.001
	P2	4	20	31	20.1	<0.001
<i>Acaena</i> spp.	P1	0	13	15	-	-
	P2	13	18	15	0.83	0.687
Tussock grass	P1	60	0	0	-	-
	P2	0	0	51	-	-
<i>Stilbocarpa</i>	P1	11	0	0	-	-
	P2	0	0	1	-	-
<i>Azorella</i>	P1	10	1	14	10.6	0.005
	P2	10	17	6	5.64	0.060
Bare ground	P1	70	7	63	51.1	<0.001
	P2	60	77	2	66.7	<0.001

Elevation was associated with differences in change trajectories in many cases but aspect and slope rarely were (Table 4). *Pleurophyllum hookeri* was largely stable at lower elevations (< 100 m.a.s.l.) and on south-facing slopes and tended to increase elsewhere. Post-2009, short grass showed similar proportions of increase and stability below 200 m.a.s.l. with stability dominating at higher elevations (Fig. 5). In both periods, *Acaena* spp. generally increased below 100 m.a.s.l. and was stable at higher elevations. No decrease in *Acaena* spp. was observed at any sites in P1 and increases were associated with north- and east-facing sites. At elevations below 100 metres, bare ground tended to increase in P1 and decrease in P2, while higher elevations were associated with decreases in P1 and stability in P2. North-facing slopes showed the greatest decrease in bare ground, while south-facing slopes were most stable in P2.

#### Rephotography — random forest models

Table 5 shows the most important variables for explaining change in features from random forest models. *Poa foliosa* followed a trajectory of overall decline in the first period and

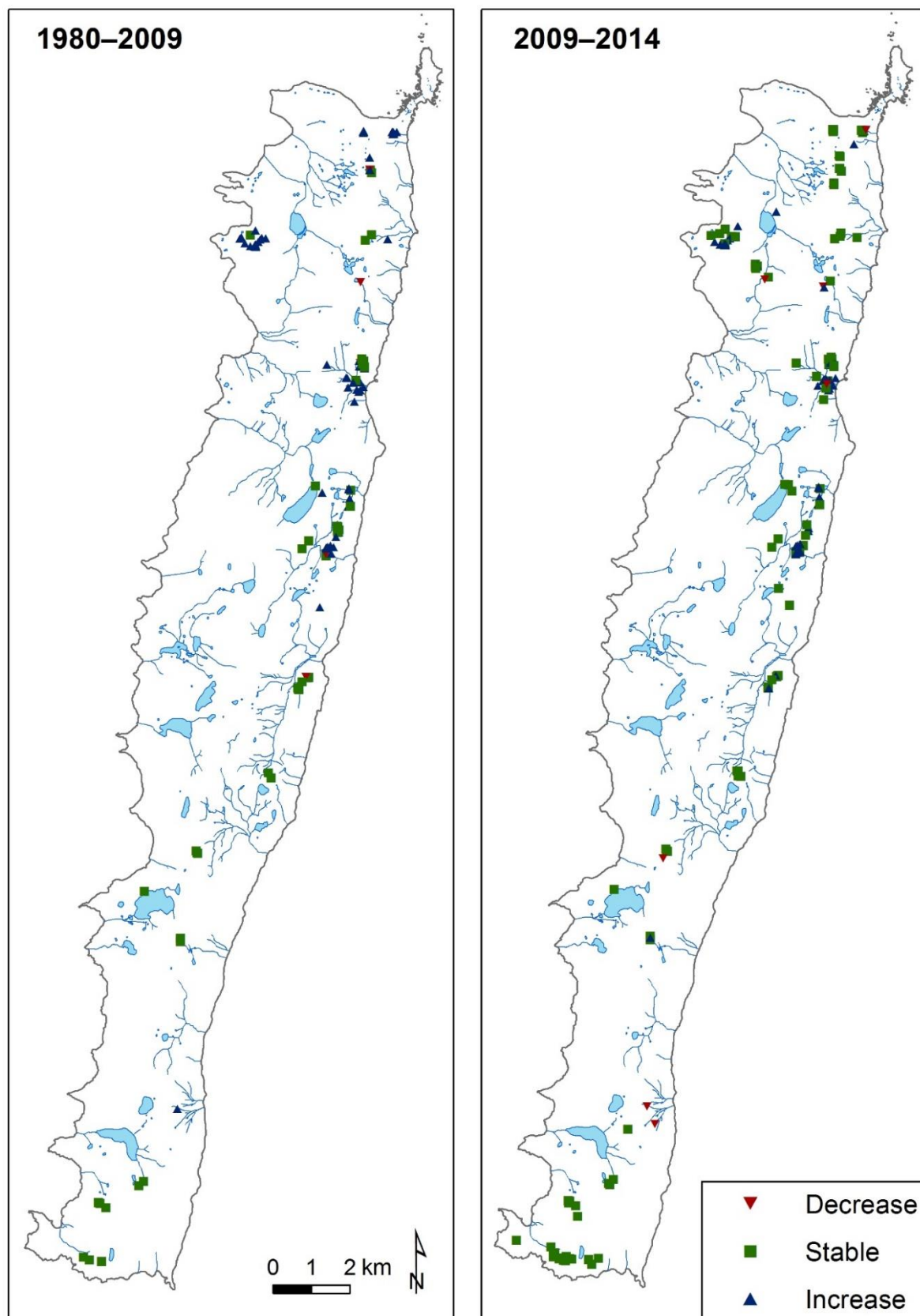
recovery in the later period. The most important variables explaining decline were wind exposure and wetness index, with decreases in tussock grass associated with sheltered well-drained sites. Tussock increase post-2009 was associated mostly with sheltered south- and west-facing slopes. However, the random forest models had limited ability to distinguish decrease and increase from stable in each period.

*Pleurophyllum hookeri* increase post-2009 was associated with steeper upper slopes above 250 m elevation. Short grassland increase in both periods generally occurred near the coast below 150 m.a.s.l. in the northern half of the island. Elevation was the main determinant of changes in bare ground, with increases in bare ground occurring at low elevations, particularly on upper slopes, and decreases at mid elevations in P1. In P2, however, bare ground decreased mostly at lower elevations in the northern half of the island. Random forest models were unable to successfully classify change in *Azorella macquariensis* based on the explanatory variables.

Sites which displayed no change in P1 were generally in the interior of the island, yet at lower elevations. Post-2009, distance from the coast was again associated with sites of no change but they were strongly biased toward high elevations in the far south.

#### *Vegetation plot data*

Most vascular plant species showed a decrease in cover during the years 1981 to 2008 and an increase between 2011 and 2015 (Fig. 6). Trends are evident in the grass species *A. magellanica* and *D. cespitosa* which both decreased during the first period and increased following rabbit eradication. The native tussock grass *P. foliosa* generally declined while the exotic *P. annua* showed the opposite trend. Common co-dominants of short grassland, *Acaena magellanica* and *Luzula crinita*, showed considerable inter-annual variation, but generally increased. The megaherbs *S. polaris* and *P. hookeri* remained at low cover levels.



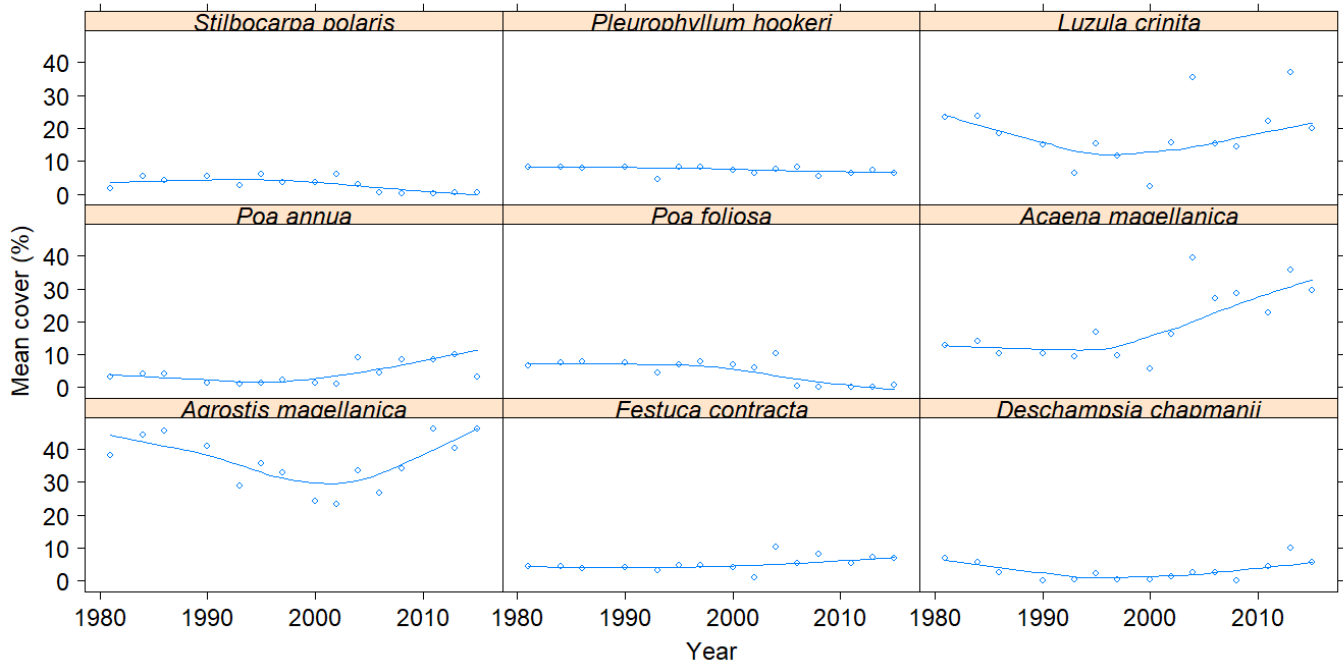
**Fig. 5.** Map of short grassland change observed from photographs over two periods.

**Table 4.** Chi-square test results comparing the three vegetation change classes with four classes each for elevation, aspect and slope angle. Insufficient observations precluded analysis of tussock grass and *S. polaris*. P1: 1980–2009; P2: 2009–2014. Elevation classes: 0–100, 101–200, 201–300, >300 m. Aspect classes: north, east, south, west. Slope classes: 0–5, 6–10, 11–20, >20°. *p* values in bold are <0.01, in italic <0.05.

Vegetation class	Period	Elevation		Aspect		Slope	
		$\chi^2$	<i>p</i> value	$\chi^2$	<i>p</i> value	$\chi^2$	<i>p</i> value
Short grass	P1	12.39	0.060	4.75	0.610	12.00	0.061
	P2	23.64	<b>0.002</b>	8.30	0.219	2.70	0.866
<i>Pleurophyllum</i>	P1	20.05	<b>0.002</b>	15.07	<i>0.012</i>	4.44	0.658
	P2	11.90	0.062	7.23	0.301	7.49	0.274
<i>Acaena</i> spp.	P1	6.34	<i>0.031</i>	8.07	<i>0.036</i>	1.03	0.846
	P2	13.11	<i>0.023</i>	7.79	0.283	10.09	0.134
<i>Azorella</i>	P1	1.94	1.000	8.476	0.180	7.54	0.076
	P2	4.21	0.389	10.68	0.099	3.177	0.530
Bare ground	P1	21.98	<b>0.002</b>	6.39	0.388	16.37	<i>0.012</i>
	P2	50.53	<b>&lt;0.001</b>	12.53	<i>0.030</i>	7.42	0.270

**Table 5.** Classification error rates for random forest models and most important variables for each model, based on conditional variable importance measure (mean of ten models in each case). Only change categories with sufficient observations to perform random forest models are shown. P1: 1980–2009; P2: 2009–2014.

Change (inc. = increase, dec. = decrease)	Period	False negative rate	Overall misclassification	Most important variables (in decreasing importance)
<i>P. foliosa</i> dec.	P1	0.42	0.49	Wind exposure, Wetness index
<i>P. foliosa</i> inc.	P2	0.57	0.44	Wind exposure, Eastness, Northness
<i>P. hookeri</i> inc.	P2	0.226	0.218	TPI500m, Slope, Elevation
Short grass inc.	P1	0.127	0.167	Elevation, North-south, Dist. Coast
Short grass inc.	P2	0.136	0.287	Elevation, North-south, Dist. Coast
Bare ground inc.	P1	0.071	0.222	Elevation
Bare ground inc.	P1	0.206	0.170	TPI180m, Elevation
Bare ground dec.	P2	0.071	0.148	Elevation, North-south
Constant	P1	0.135	0.270	North-south, Dist. Coast, Elevation
Constant	P2	0.160	0.137	North-south, Dist. Coast



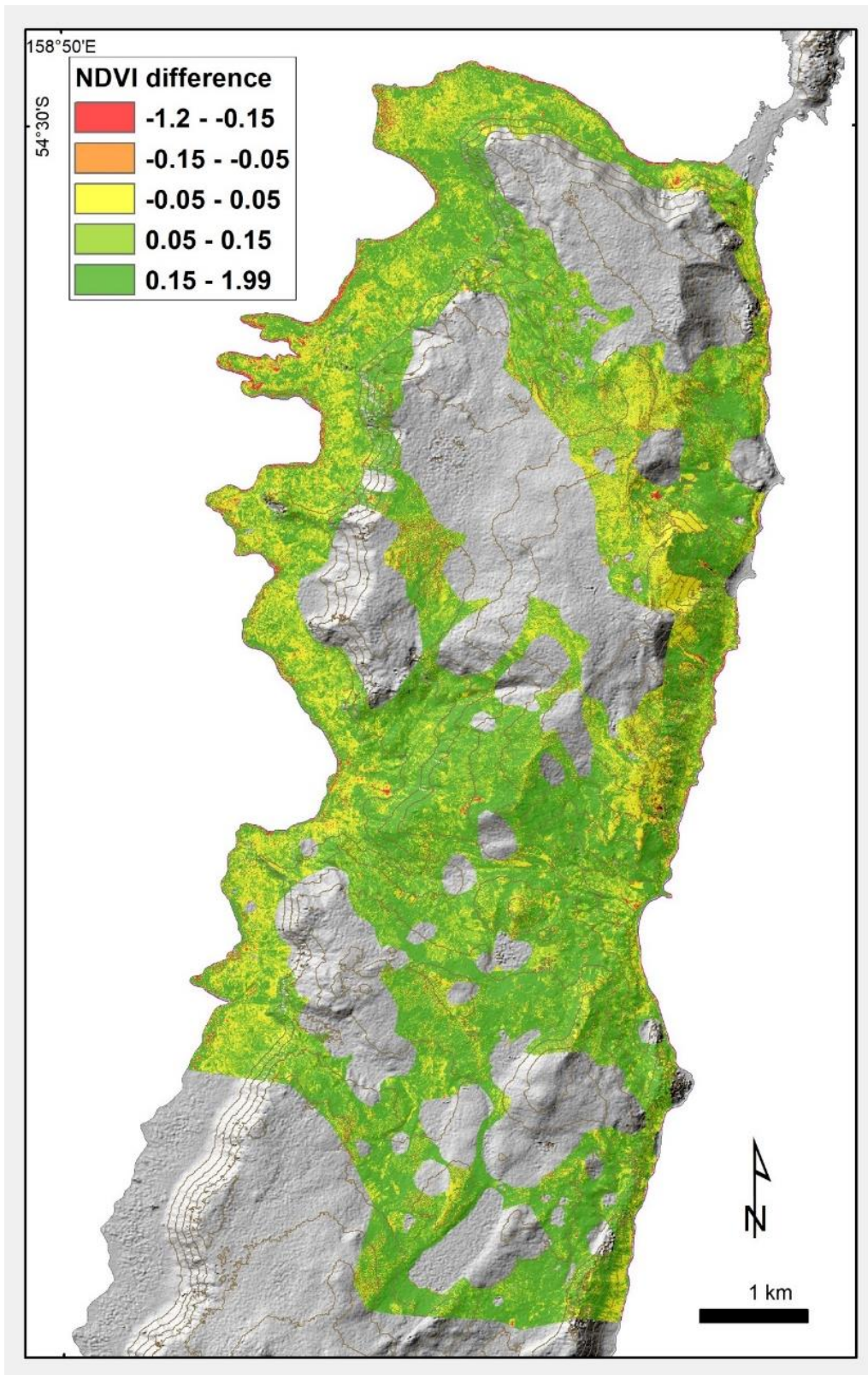
**Fig. 6.** Change in estimated per cent cover averaged across 30 quadrats in short grassland and herbfield vegetation 1981–2015 with lowess lines fitted.

### Remote sensing

Vegetation change classes for 2009–2014 were poorly differentiated by SVI change values, with logistic regression models often performing close to a null model ( $AUC = 0.5$ ) and not exceeding an  $AUC$  of 0.7. Multiple logistic regression models improved discrimination up to  $AUC = 0.79$  (*Acaena* spp. increase with two SVI predictors). Sample sizes for many vegetation change categories were too small to analyze but we expect these would be no more related to SVIs than the common types we tested.

Spectral vegetation index change classes varied spatially, with only two cases where SVI change was independent of a terrain class (Table 6). All SVIs showed less frequent change with increasing elevation. NDVI rarely decreased over the 2009–2013 period. NDVI change was independent of aspect and increased NDVI was mostly associated with steep slopes (Fig. 7). MTVI2 was mostly stable over the period. MTVI2 changes were independent of slope angle. MTVI2 increase was more frequent on north- and east-facing aspects. Unlike the other indices, SGI is negatively correlated with vegetation cover. SGI rarely increased, indicating an overall increase in vegetation reflectance consistent with the other SVIs. SGI decreases were mostly associated with steeper slopes and had little variation with aspect.





**Fig. 7.** Change in Normalized Difference Vegetation Index (NDVI) between 2009 and 2013. Negative difference values indicate a decrease in NDVI over time. Gaps in the mapped NDVI surface are where clouds and lakes have been excluded. 50 m contours lines shown.



**Table 6.** Five 2009–2013 change classes for each WorldView-2 spectral vegetation index compared with four classes each for elevation, aspect and slope. Elevation classes: 0–100, 101–200, 201–300, >300 m. Aspect classes: north, east, south, west. Slope classes: 0–5, 6–10, 11–20, >20°. NDVI = Normalized Difference Vegetation Index, MTVI2 = Modified Triangular Vegetation Index (Improved), SGI = Sum Green Index.

	Elevation		Aspect		Slope	
	$\chi^2$	<i>p</i> value	$\chi^2$	<i>p</i> value	$\chi^2$	<i>p</i> value
NDVI	170.61	<0.0001	5.906	0.921	31.23	0.002
MTVI2	228.12	<0.0001	55.29	<0.0001	17.139	0.144
SGI	51.882	<0.0001	27.378	0.007	88.905	<0.0001

## Discussion

Rabbit impacts on Macquarie Island vegetation effectively ceased when aerial baiting concluded in July 2011, with only thirteen rabbits killed in the subsequent four months (Parks and Wildlife Service 2014). The five years of P2 (2009–2014) therefore captures the first 2.5 years of ecosystem recovery.

While some vegetation recovery was evident almost immediately following rabbit eradication (Shaw *et al.* 2011) and the present study has observed widespread vegetation change over the five years of P2, it is likely that change will be slower in some instances and therefore may not be evident 2.5 years after rabbit eradication. Slow change may explain the general increase in the proportion of stable vegetation across most classes in P2, compared to the much longer time-frame of P1. In all of the areas covered by the photograph series there were very local differences in responses of different polygons, rather than consistent changes in various vegetation types, suggesting the importance of local, as well as regional, drivers of change (Fig. 3).

### Lowland communities

*Acaena* herbfield is a coloniser of disturbed ground and, like short grassland, appears to have been a seral community promoted and maintained by rabbit grazing (Copson & Whinam 1998; Whinam *et al.* 2014a). Both vegetation types frequently display long-term stability despite changes in rabbit pressure, over either or both time periods.

*Acaena* is a component of short grassland which can become dominant, forming *Acaena* herbfield when grass species decline due to disturbance (Copson 1984). In the present study,

most increases in *Acaena* herbfield occurred at sheltered low elevation sites where rabbit grazing was likely to be most intensive. *Acaena* herbfield was frequently stable over one or both of the time periods examined, indicating that, at least in certain situations, it is not a transient early successional phase and appears to maintain stability by competitive exclusion of other plant species. Copson & Whinam (1998) suggest that seral communities such as these become established after prolonged moderate to heavy rabbit grazing depletes other species and their propagules. Walton (1976) notes that *Acaena magellanica* is highly successful throughout the subantarctic in terms of longevity and the development of extensive pure stands on various soil types. *Acaena* species are sometimes also prominent in the disturbed and nutrient-enriched soils of burrowing petrel colonies (Bergstrom *et al.* 2002).

Short grass and *Acaena* mostly increased at lower elevations and remained stable at higher elevations during P1 in the rephotography dataset. In contrast, *P. hookeri* decreased at lower elevations and increased at higher elevations. Short grass species and *Acaena* generally benefited from rabbit grazing while *P. hookeri* was disadvantaged by rabbits (Copson 1984; Whinam *et al.* 2014a), suggesting a possible elevational trend in rabbit grazing pressure with more impact at lower elevations (Copson *et al.* 1981; Terauds *et al.* 2014). However, decreases in *P. hookeri* were rarely observed in the photograph series despite the known impact of rabbits on this species (Copson & Whinam 1998; Jenkin & Ashton 1979).

The increase in bare ground at lower elevations during P1 is consistent with rabbit impact, particularly on steep slopes, followed by a reversal of the trend in P2 which appears to indicate the first phase of vegetation recovery, namely an increase in vegetation cover without notable shifts in plant species composition. Less severe rabbit impact at higher elevations (Copson *et al.* 1981) may explain the different trends in bare ground with elevation.

While the landscape photograph series reveals changes in the extent of the short grassland community, the vegetation plot data show that within this community the native grasses *Agrostis magellanica* and *D. chapmanii* have increased since rabbit eradication. Among the native grass species, *Agrostis magellanica* was considered to benefit most from rabbit grazing, which probably expanded its range and abundance (Whinam *et al.* 2014a). However, this species was frequently grazed by rabbits (Copson & Whinam 1998) and is now showing an increase in cover consistent with release of grazing pressure (Shaw *et al.* 2011), along with other short grassland/herbfield species such as *Deschampsia chapmanii*. Some smaller native

herbs which favour soil disturbance or a more open sward with less competition (e.g. *Cardamine corymbosa*, *Ranunculus crassipes*) have declined in frequency within short grassland since rabbit eradication (DPIPWE, unpublished data) in a reversal of the trend observed by Bergstrom *et al.* (2009) when the rabbit population was increasing. However, there is insufficient data to determine trends in many smaller species with consistently low foliage cover.

Rephotography shows that many locations currently dominated by *Agrostis* have been occupied by megaherbs or *P. foliosa* in the past and some presently support low densities of these species. Post-rabbit invasion of short grassland by *P. foliosa* plants (often in sites which were *P. foliosa* dominated tussock grassland in 1980) indicates an apparent succession process from short grassland to tussock grassland and a reversal of the preceding increase in short grass species concurrent with *P. foliosa* decline.

Qualitative modelling of the Macquarie Island ecosystem response to eradication of rabbits, rats and mice predicts a positive response in tussock grassland and herbfield and no change in short grassland (Raymond *et al.* 2011). Our observations showed both increases and no change in extent of short grassland sites to 2014, but we expect a future increase in tussock grassland and herbfield, as predicted by the modelling, will have a direct negative effect on the extent of short grassland.

If the trend of increasing abundance of *P. foliosa* and megaherbs since rabbit eradication continues, it will lead to a shift from short grassland to communities dominated by a combination of *P. foliosa*, *P. hookeri* and *S. polaris*. Recovery of *P. foliosa* - *S. polaris* climax vegetation on coastal slopes following severe grazing takes around 15 years, although the dominant species become established in less time (Scott & Kirkpatrick 2008). However, in many short grassland sites there is no *P. foliosa* present, possibly due to lack of dispersal, since competition from short grass species does not appear to exclude *P. foliosa*, based on our observations of successful *P. foliosa* establishment in dense short grassland in both rephotography and quadrat sites. Where megaherbs were heavily impacted by rabbits and locally eliminated (Copson & Whinam 1998) a state shift in vegetation type has occurred (Shaw *et al.* 2011) and it remains unclear how long it will take for re-establishment of the previously dominant species.

Expansion and reinvasion by palatable megaherb and grass species has followed rabbit eradication on other subantarctic islands but with varying results on each island. While the response of native plants was rapid on Enderby Island (Torr 2002) it was often slow on two islands in the Kerguelen Archipelago where exotic plant species increased substantially in the years following eradication (Chapuis *et al.* 2004). Concurrently, *Acaena magellanica*, which formed monospecific stands under rabbit grazing, declined in abundance (Robin *et al.* 2011).

Trends in *P. foliosa* cover from quadrat surveys in short grassland are consistent with the photographic record of decline and subsequent increase. However, the quadrat dataset shows very gradual change, perhaps because it does not include sites which were initially dense tussock grassland, which in the rephotography series displayed dramatic declines (while not quantified, the decline is consistent across all sites and the magnitude is visually apparent). This may reflect propagule availability for *P. foliosa* and grazing history, in that sites where this species dominated in 1980 have greater capacity to revert to this vegetation type compared to those areas where grazing eliminated *P. foliosa* prior to 1980. The longevity and viability of native plant seed banks on Macquarie Island is not known (Shaw 2005) so the role of soil seed banks in recovery following grazing is uncertain. *Poa foliosa* seed is wind dispersed and dominates seed rain in tussock grassland, though seedling survival is low and vegetative reproduction is more important for recruitment (Bergstrom *et al.* 1997; Shaw 2005).

*Stilbocarpa polaris* shows slower recovery than *P. foliosa*, consistent with previous observations (Kirkpatrick & Scott 2002; Scott & Kirkpatrick 2008), making it difficult to predict how widespread this dominant species may be in the future. *Stilbocarpa*, like the other megaherbs, has substantial reproductive capacity (Shaw 2005). Seed dispersal can occur over considerable distances on Macquarie island (Shaw 2005) which suggests that once mature plants become locally established, recruitment and expansion may proceed rapidly.

Changes in the tussock communities of steep coastal slopes are consistent with our rephotography observations. *Poa foliosa* and *S. polaris* cover in 2009 was less than 25% of the 1980 extent, though the trend was not linear due to a peak in the mid 1990s apparently related to decreased grazing pressure (Scott & Kirkpatrick 2012). Island-wide time-series photographs of the coastal slope tussock grasslands showed a severe increase in grazing damage between 2005 and 2007 (Carmichael 2008).

Given the recent appearance of megaherbs and *P. foliosa* in some locations, these species may have yet to disperse to the full extent of their potential niches. While there is little doubt short grassland will be replaced by taller vegetation across much of the island, it remains unclear where short grassland and *Acaena* herbfield will survive, if at all, as megaherb and *P. foliosa* tussock grassland recovery progresses. Short grassland and *Acaena* herbfield intergrade with the lower elevation boundary of feldmark (Selkirk *et al.* 1990), which suggests they may persist at this ecotone. However, Taylor (1955) observed that the transition from *P. foliosa* tussock to feldmark was either an abrupt boundary or a *P. hookeri*-dominated ecotone. Regardless of the fate of the possibly rabbit-induced short grassland community, the vascular flora of this association is comprised of generalist species which occur in other vegetation types and so will remain widespread on the island with lower abundance even if major shifts in vegetation communities occur. Furthermore, the concept of climax communities may be an oversimplification, with undisturbed dense tall vegetation possibly becoming more open and increasing in species richness by endogenous processes over time (Kirkpatrick & Scott 2002).

Increasing *P. hookeri* was frequent in the rephotography dataset during P2 and associated with steep upper slopes, while quadrat data shows an increase in *P. hookeri* at flat low-elevation sites (the only sites where *P. hookeri* was present in quadrats). Therefore, *P. hookeri* increase was observed at the geographic extremes of the species' distribution while continuing declines occurred in intermediate habitats, perhaps due to competition from other species.

*Pleurophyllum hookeri* has been observed to vary in morphology and ecology between environments on Macquarie Island, where it occupies a range of ecological niches (Jenkin & Ashton 1979) and therefore the species may respond to environmental change differently depending on the ecological context including habitat type and interspecific interactions.

Climate change has had an effect on the abundance of plant species on Macquarie Island over the time period of our study, as evidenced by a gradual increase in several species on the coastal slopes irrespective of grazing pressure (Scott & Kirkpatrick 2012). These increasing species include several dominant species of short grassland (*Agrostis magellanica*, *Luzula crinita*, *Festuca contracta*), plus herbs associated with wet ground. If similar patterns have occurred elsewhere on the island they are likely to have gone undetected given the lack of accurate historical distribution data and the confounding influence of rabbits.

It is therefore likely that the trajectory of ecosystem recovery from grazing impacts is superimposed on a background of species responses to ongoing climate change, which might alter our predictions based on responses to grazing removal. Idiosyncratic responses to climate change among plant species could lead to no-analogue plant communities as has already occurred on subantarctic Marion Island (le Roux and McGeoch 2008a).

### Feldmark

The cushion plant *A. macquariensis*, which dominates the highland feldmark ecosystem, displays a mix of responses with no geographic pattern and no apparent relation to rabbits. Rabbit populations were low at high elevations and rabbits sometimes damaged cushion plants by digging (Copson 1984). There was minor damage to *Azorella* plants from rabbit grazing, but this did not appear to lead to death or decline of cushion plants even during a time of moderate rabbit population (Whinam *et al.* 2014b). We therefore assume that rabbit impacts are negligible in feldmark, although it is possible that even minor or infrequent impacts of rabbit grazing or digging could influence the observed responses given the small spatial scale of observed changes and the slow growth rates of feldmark vegetation. These issues of spatial scale and slow response time also limit the certainty of any inferences about climate change responses in this ecosystem.

*Azorella* dieback (Bergstrom *et al.* 2015; Whinam *et al.* 2014b) was observed at seven of the ten polygons in which *A. macquariensis* declined during 2009–2014, but this does not explain change prior to 2009 since the first instances of dieback were observed in December 2008 (Bergstrom *et al.* 2015). The extent of bare ground at higher elevations, where feldmark predominates, and of *A. macquariensis* in P2 rarely exhibited change, suggesting that feldmark vegetation is relatively stable over time-frames of at least five years.

Given the limited impact of rabbits on feldmark and the observed changes in Macquarie Island climate we would expect to see some climate change response in *A. macquariensis* over the 34 year period of this study. Regardless of the confounding influence of *Azorella* dieback (which may be a climate change response; Bergstrom *et al.* 2015) there is no directional trajectory or geographic pattern of *A. macquariensis* change to suggest a response to climate change. In Tasmanian feldmark, multi-decadal increase in vegetation cover observed from aerial photography was as low as 0.01% per decade in the more maritime mountains (Annandale &

Kirkpatrick 2017), therefore the magnitude of change in feldmark may be too small to detect with our qualitative rephotography method.

### *Remote sensing*

SVI change values were not useful for predicting vegetation changes, with no clear discrimination between change classes using any of the tested SVIs singly or in combination. Even changes in bare ground observed from rephotography were not related to SVIs, perhaps due to bare ground changes typically being small shifts in the margins of vegetation patches, meaning they were not consistent across a polygon (therefore potentially misaligned with satellite pixels) and possibly too small to detect. In contrast, vegetation changes occurred at a larger scale, consistent with a polygon of at least one pixel in size.

Previous subantarctic vegetation analysis using spectral data has been successful in determining vegetation cover but poor at discriminating vegetation type (Bricher 2012; Murray *et al.* 2010; Robin *et al.* 2011; Santin-Janin *et al.* 2009). Apart from the occurrence of landslips and sand blows, and their subsequent revegetation, vegetation dynamics on Macquarie Island do not involve substantial changes in absolute vegetation cover. Even under heavy rabbit grazing pressure, vegetation cover in short grassland and herbfield was close to 100% and has increased in height but not total cover since rabbit eradication (Whinam *et al.* 2014a).

Less frequent change in SVIs at higher elevations from 2009–2013 is consistent with our rephotography observations of greater vegetation stability at higher elevations in both periods. Change in SVIs was most frequent at low elevations, where increased vegetation reflectance was greatest. Rephotography data showed increases in short grassland, *P. foliosa* and *Acaena* species at low elevations in the same period, so these may all contribute to the increasing vegetation cover or density.

The greatest increases in SVIs occurred on low elevation steep slopes. These coastal slopes, which ascend from the coastal terrace or shoreline to the plateau, were previously highlighted as the area of greatest vegetation loss during a major phase of rabbit population increase. Comparison of 2000 and 2005 satellite imagery of the northern part of Macquarie Island showed considerable spectral change including a decrease in NDVI on coastal slopes and some other areas which were related to field observations of tall tussock grassland loss due to rabbit

grazing (Bergstrom *et al.* 2009). That study covered a period when the rabbit population increased around four-fold (Terauds *et al.* 2014). The 2009–2013 NDVI increase showed a reversal of this previous vegetation degradation, including extensive areas of *P. foliosa* re-establishment on coastal slopes (personal obs.).

The 2009 satellite imagery captures a period of extensive rabbit impacts, while the 2013 image represents nearly two full summer growing seasons without rabbits. The rephotography from a year later shows *P. foliosa* plants as scattered immature individuals amongst short grassland and herbfield. Therefore, we expect an even stronger spectral signal in the future as *P. foliosa* cover increases. Mapping accuracy for tussock grassland could be improved using a combined texture and spectral analysis, which improved detection of *Poa cookii* tussock grassland on Heard Island (Murray *et al.* 2010).

### *Remote sensing methodological issues*

The SVI analysis demonstrates some of the problems with remote sensing of vegetation in the subantarctic. High resolution imagery for Macquarie Island with low cloud cover is rarely available. Cloud-free areas common to both WorldView-2 images used here covered less than 25% of the extent of Macquarie Island. Shadows resulting from the steep terrain further limited the surface area with useful spectral reflectance. Seasonal cycles in NDVI were clearly evident from high temporal frequency imagery for the subantarctic Kerguelen Islands (Santin-Janin *et al.* 2009). Given the distinct seasonal growth cycles of flora on Macquarie Island we would expect considerable intra-annual variation in SVIs. However, based on our observations of change over five years from rephotography, it is unlikely the one month difference in timing between the 26 December 2009 and 26 January 2013 satellite images (both during peak growing season) would be significant compared to the magnitude of change over the four years.

Vegetation classification from satellite imagery is not effective where the spectral signature is highly variable within a vegetation type, or similar across different vegetation types (Xie *et al.* 2008). This appears to be the case with our data, where spectral signals are variable and not distinct between vegetation types and change classes.

Modern satellite imagery has high spectral and spatial resolution allowing quantitative analysis of change from a time series of images, but accurate georeferencing and atmospheric



corrections are critical to reduce errors. In contrast, time series analysis using on-ground rephotography involves more subjective and less quantitative data but it can detect changes in certain plant species (e.g. the megaherb *P. hookeri*) and vegetation formations (e.g. differentiating grassland from herbfield) which have not been possible with satellite imagery. Possible biases in rephotography datasets relate to the detectability of change, with some plant species, such as tussock grass, being more prominent and readily observed than others. When comparing satellite imagery with on-ground photographs there are several potential sources of error, imprecision and uncertainty. These include geolocation accuracy, temporal mismatch, choice of thresholds or classes and lack of quantitative data from photographs (e.g. a broad range of magnitudes of change can occur within the increase or decrease class in our data).

Both methods have utility for environmental monitoring in the subantarctic terrestrial environment. A rephotography study could be improved by more accurately determining photograph locations in the field using handheld GPS to geolocate features in the scene, in addition to the photographer's location. Change detection analysis using SVIs could be used to identify areas with a high magnitude of vegetation change in order to inform or stratify the location of new rephotography sites. Satellite image analysis could be improved with appropriately scaled and stratified vegetation quadrats for ground-truthing and calibration of the spectral data (Bricher *et al.* 2013). The most promising applications of satellite monitoring on Macquarie Island are for detecting change in the extent of tussock grassland, but the necessary very high resolution images with minimal cloud cover are rare.

### Conclusions

Rephotography observations agree with previous studies documenting the impact of rabbits on Macquarie Island's vegetation following the rabbit population peak around 2006, in which susceptible vegetation such as tussock grassland was severely reduced in abundance. This is the first broad-scale study of ecosystem recovery following the eradication of rabbits from Macquarie Island. Comparison of vegetation in 2009, near the peak of rabbit impact, with the same sites in 2014, nearly three years after the removal of rabbits, shows indications of the early stages of ecosystem recovery. However, in some cases little or no change was observed, due to either slower rates of recovery or to a state shift in vegetation and subsequent resistance to change (e.g. 'biological inertia', Von Holle 2003).

Apart from the generally higher magnitude of rabbit damage and subsequent vegetation recovery at lower elevations, it is difficult to determine spatial patterns in vegetation change, which may be influenced by other factors such as site history (e.g. rabbit grazing intensity). Where no change was observed in rephotography between 2009 and 2014 it is unclear whether change is too slow to detect over this period, too small to detect using this method or if the vegetation is presently in a stable state. Vegetation plot data up to 2017 (M. Visoiu, unpublished data) shows that, at least in the case of megaherbs, a positive response to rabbit removal is occurring gradually and may have been at an undetectable level in 2014 photographs.

While the observed recovery of vegetation from rabbit impacts is proceeding it was not possible to detect any potential subtle climate change response in the lowland vegetation. In fieldmark where rabbit impacts were minimal no clear trends were evident from rephotography, although this method is unable to detect fine-scale change such as changes in abundance of the smaller plant species where overall vegetation extent is constant.

In the post-rabbit era, apart from localized disturbances caused by mass movement or marine animals, Macquarie Island vegetation should be more stable, as it was prior to rabbit introduction (Saunders *et al.* 2014). Indeed, given the lack of dispersal limitation and the short generation times of the flora, the vegetation should achieve a dynamic equilibrium driven by climate with little time lag. Effects of ongoing climate change on the vegetation are difficult to predict but will probably involve a gradual shift in the extent and distribution of vegetation communities and plant species which will be readily observable (particularly at ecotones) in the absence of major confounding factors such as invasive species impacts.

## **Chapter Five: Using species distribution models to predict floristic assemblages in subantarctic herbaceous vegetation following grazing release**

This chapter examines how the post-grazing distribution of plant species on Macquarie Island is changing and makes predictions about the future spatial organization of vegetation communities, as these communities reflect the distributions of dominant flora species.

This chapter investigates the application of species distribution models for predicting present and near-future vegetation community distributions. The novel approach distinguishes core range from non-core range for plant species which typically are dominant constituents of the vegetation within the core part of their range.

Chapters Two and Three informed the selection and interpretation of certain environmental variables (i.e. wind exposure, elevation). Observations of spatial and temporal variation in vegetation in Chapter Four informed the application and interpretation of species distribution models in this chapter and their implications for vegetation community prediction.

This chapter has not previously been published.

## Abstract

Subantarctic Macquarie Island is presently undergoing ecological recovery following the eradication of feral mammals. Plant species distributions are changing and grazing-induced communities are being replaced by the megaherb and tussock grass communities characteristic of lowland subantarctic habitats.

Vegetation classification and mapping is a key tool for understanding and monitoring ecosystem change but is plagued by theoretical and practical problems. Mapping vegetation using traditional remote sensing interpretation can discriminate only three vegetation structural types on Macquarie Island, much fewer than the described floristic communities. Where sufficient species location data are available, mapping species using species distribution models (SDMs) can reduce the uncertainty and assumptions involved in delineating communities. Most SDM projects use presence only or presence/absence data. Here an additional category is used, which is easily determined during field data collection or from existing floristic plot data to represent the core range of a species. On Macquarie Island we test this simple repeatable approach to see how it characterizes potential vegetation communities compared to interpretation from binary presence/absence maps.

A typical SDM approach using only presence records would not be very informative in the subantarctic where many dominant plant species are widespread generalists. Using three classes (absent, not-dominant, dominant) for SDMs allows better inferences about vegetation communities. This shows that widespread species with extensively overlapping ranges have core ranges which are spatially more partitioned. The resulting map of Macquarie Island vegetation in the initial stages of ecosystem recovery provides a basis for future environmental monitoring. This method is more informative than presence/absence modelling of species distributions.

The present distribution of plant species assemblages on Macquarie Island reflects both environmental gradients and grazing history. Large, potentially dominant plant species such as the megaherbs *Stilbocarpa polaris* and *Pleurophyllum hookeri* and the tussock

grass *Poa foliosa* presently occupy only part of their modelled niche, particularly *S. polaris*. This is likely due to historic effects of rabbit grazing on these species; if so the ranges and populations of these species are expected to expand with consequent shifts in vegetation communities.

## Introduction

Species niche or distribution models have been widely used in diverse contexts to estimate the potential niches of species (Elith & Leathwick 2009; Franklin 2009). Numerous methodological approaches have been employed to develop species models depending on the purpose of the modelling, the available data and the background of the researcher (Austin 2007; Elith & Leathwick 2009). Similar methods have been applied to the mapping of plant species communities or vegetation types (Ferrier & Guisan 2006).

Species distribution models (SDMs) involve creating a statistical model to explain the distribution (presence/absence or probability of occurrence) of a species (the response variable) based on a select set of predictor variables, which are typically abiotic factors such as climatic and topographic parameters (Elith & Leathwick 2009; Franklin 2009). Such models provide an estimation of the potential niche of the species, which can be useful for purposes such as predicting the future range of invasive species and endangered species (Franklin 2013; Rovzar *et al.* 2016). However, in most cases these models neglect the interspecific interactions, temporal factors (such as successional processes) and stochastic factors (including disturbance and dispersal) which determine the realized niche of a species (Austin 2002; Elith & Leathwick 2009; Mod *et al.* 2016). In many applications, understanding the realized niche is as important or more so than the potential niche. Consequently, a number of methods have been developed to incorporate dynamic, stochastic and biotic factors into species models (Anderson 2016; Cassini 2011; Franklin 2010; Heikkinen *et al.* 2007; Mod *et al.* 2014).

Species modelling necessarily involves translating complex ecological processes into a simplified model based on limited data and therefore involves assumptions and uncertainty. In untangling complex ecological webs we risk making inferences about causality, particularly where biotic and abiotic factors which are important are not included in the model, or interact in ways which change the response surface (Kissling *et al.* 2012; Mod *et al.* 2014; Wisz *et al.* 2013). Despite their limitations, SDMs can be useful for understanding the distribution of individual species and ecological communities, for conservation planning and for predicting change in species distributions driven by environmental change (Franklin 1995, 2009, 2013).

It has been demonstrated that individual plant species have differential responses along environmental gradients and therefore vegetation is a continuum comprising varying abundances of different species rather than discrete communities (Austin 2002). Nevertheless, recognizable plant communities do occur as a reflection of the underlying landscape and climatic patterns, their boundaries being correspondingly abrupt or diffuse (Austin & Smith 1989; Woodward & Williams 1987). Mapping the distribution of species therefore offers the potential to map vegetation communities, given some knowledge of the interactions between particular species, with both species and vegetation maps providing key information for understanding ecosystems and ecological change.

Plant species have individualistic responses to environmental gradients with a relative performance advantage at some position on these gradients (Austin & Smith 1989; Brown 1984). Consequently, we might expect co-occurring species to differ in their relative abundance and dominance in the landscape. Where several potentially dominant plant species co-occur they can either form a community with co-dominant species or one of the species outcompetes the others, becoming dominant. These patterns of relative abundance may change over time with disturbance and succession (Johnson & Mayeux 1992) or vary spatially with localized habitat variation leading to a mosaic pattern of dominance (Leathwick & Mitchell 1992).

The tundra vegetation of Macquarie Island comprises bryophytes, forbs, graminoids and pteridophytes (Selkirk *et al.* 1990). No woody plants are present and invasive plant species are widespread in very low densities apart from localized patches of *Poa annua* associated with soil disturbance (Williams *et al.* 2018). Factors determining the distribution of plant species and communities on the island include soil depth, waterlogging and wind exposure (Selkirk 2012; Taylor 1955). Given the hyper-oceanic climate with no extreme temperatures and constant high humidity (Currey 1974), bioclimatic factors which frequently limit species distributions in other climates, such as thermal tolerances and water stress, are less likely to be relevant on Macquarie Island. Organic peat soils tend to mask the effects of underlying geology, soils are low in nutrients but do not have serious deficiencies and saltspray and aerosol nutrients are significant near the coast but decline with elevation (Jenkin 1975).

There is no evidence of vertebrate folivores in Macquarie Island's history (although two extinct bird species were likely omnivores which may have eaten some foliage) until the introduction of the European rabbit (*Oryctolagus cuniculus*) in the 1800s, with consequent severe damage to soils and vegetation (Copson & Whinam 1998; Jenkin 1975). Due to preferential grazing by rabbits of *P. foliosa* and *Stilbocarpa polaris*, these large dominant species were widely replaced by short grassland or herbfield (Copson & Whinam 1998; Costin & Moore 1960). Since the eradication of rabbits, black rats (*Rattus rattus*) and mice (*Mus musculus*) in 2011, there are no vertebrate herbivores other than the introduced common redpoll (*Acanthis flammea*), a granivorous bird.

Most Macquarie Island vascular plant species are widely distributed on the island and elsewhere in the subantarctic (Copson 1984; Taylor 1955; Selkirk *et al.* 1990). While some species are largely confined to specific habitats such as bogs or the coastal spray zone, the most prominent species in terms of biomass are generalists with broader niches (Taylor 1955).

In common with other subantarctic islands, Macquarie Island vegetation can be broadly classified along an elevation gradient into lowland vegetation on organic soils, with highland

vegetation on mineral soils and a narrow rocky coastal zone at the extremes (Smith & French 1988). In the lowland environment, a number of vegetation communities have been identified by different researchers (Bricher 2012). In addition to soil type, climate and disturbance, a variety of drivers may be responsible for determining the distribution of plant species and communities. For example, on subantarctic Marion Island, these include wind exposure, nutrient inputs and hydrology (Smith & French 1988; Smith & Steenkamp 1990).

On Macquarie Island, the frequent co-occurrence of species which dominate different communities suggests that rather than climatic limits to species distributions, the relative dominance of particular species (and consequent vegetation community) is determined by either local site characteristics (e.g. hydrology, soil) or interspecific competition. Interactions between factors may be important. For example, climate and soils may mediate competition such that certain species will be dominant in particular parts of the landscape (Taylor 1955).

This co-occurrence of species also means that vegetation communities often intergrade rather than being well defined. The difficulty of defining community boundaries and mapping species from remote sensing are two key reasons why the only detailed vegetation map of Macquarie Island uses simple classes based on vegetation structure (Selkirk & Adamson 1995). Co-occurring widely distributed species make it difficult to accurately map much of the landscape in classes defined by a single or two dominant species (Bricher 2012).

Species distribution modelling typically determines climatic limits for a species or probabilities of occurrence but does not indicate the optimum habitat or consider interspecific competition. Topographic, soil and climatic variables used as predictors do not capture more dynamic aspects of the environment. Spectral reflectance data from remote sensing instruments such as satellite imagery can indicate various properties of soils and vegetation. Variation in features such as land cover and primary productivity measured by satellite-derived indices can be useful for species distribution modelling (Rose *et al.* 2014). While remotely sensed data can improve the accuracy of SDMs there is a risk of biasing models toward the realized rather than the fundamental niche if spectral variables are



detecting the actual plant species present rather than underlying environmental variables which influence habitat suitability (Bradley *et al.* 2012).

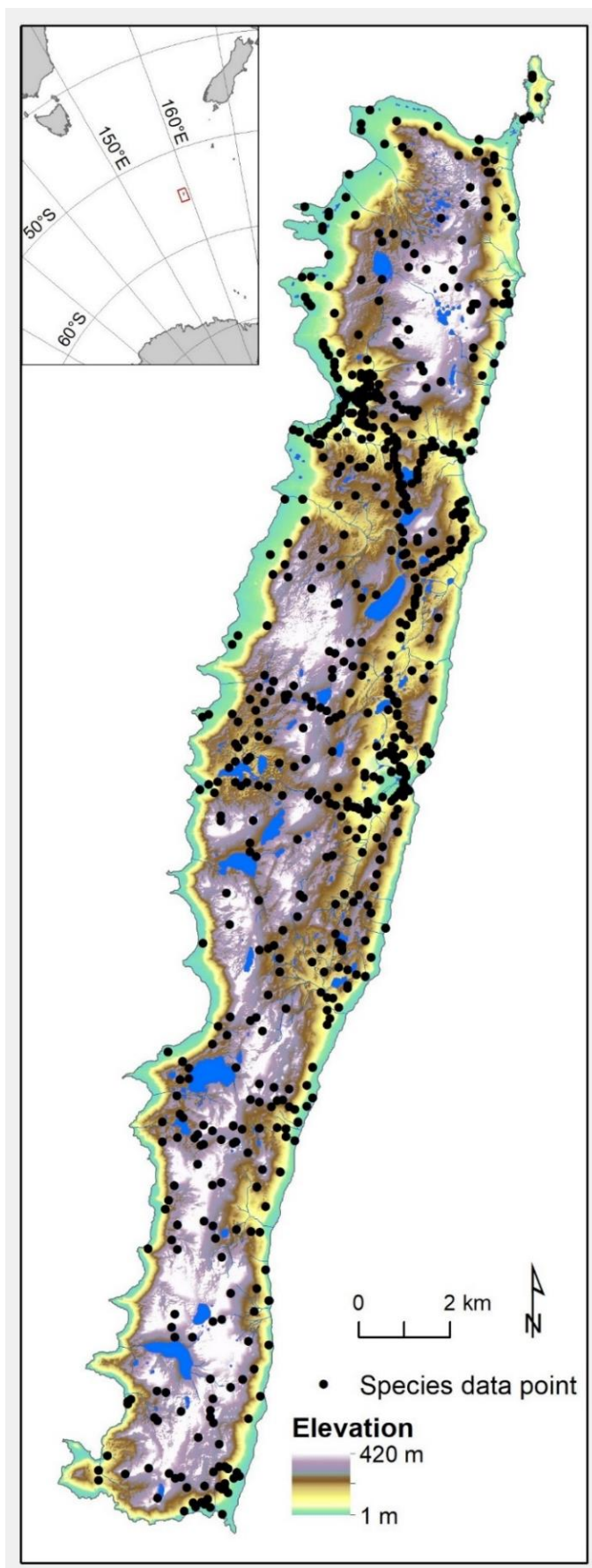
Most SDM projects use presence only or presence/absence data. We use an additional category that is easily determined during field data collection or from existing floristic plot data to represent the core range of a species. We define the core range as the environmental envelope in which a plant species is potentially a dominant species in terms of ground cover, with a minimum of 25% projected foliage cover. Biomass or leaf area index are more accurate means of determining dominance but projected foliage cover is easier to measure and is closely correlated to these other measures in herbaceous tundra vegetation (Chen *et al.* 2009). On Macquarie Island we test this approach to see how it characterises potential vegetation communities compared to interpretation from binary presence/absence maps.

This study aims to compare inferences about vegetation communities from SDMs, by determining the extent of assemblages of co-occurring species, using both the entire range for a species and the core range. We expect that the widespread dominant vascular species will each have very similar environmental envelopes with distributions limited by extremes of climatic and edaphic conditions (total range) but will be more differentiated in their core ranges. Secondly, we test whether including satellite-derived spectral data improves the predictive performance of SDMs compared to models using only terrain variables. Thirdly, we consider the environmental determinants of species distributions by interpreting the importance values of predictor variables.

## Methods

### *Site description*

Macquarie Island (54.50°S, 158.94°E) emerged from the Southern Ocean less than one million years ago and is the only subaerial portion of the extensive submarine Macquarie Ridge (Adamson *et al.* 1996). The 128 km<sup>2</sup> island comprises mostly igneous rocks such as basalts.



**Fig. 1.** Location of species observation points on Macquarie Island used for species distribution modelling. Inset shows location of Macquarie island (red outline) in the Southern Ocean.

Escarpment slopes rise steeply from the ocean on the east coast and from a flat coastal terrace in the west, reaching an undulating plateau mostly over 200 m.a.s.l. which comprises the majority of the landmass, with peaks reaching 420 m.a.s.l. (Fig. 1).

Macquarie Island is subject to constant geostrophic winds and frequent cold fronts, in a region with the highest annually averaged sea level wind speeds on Earth (Hande *et al.* 2012). The hyper-oceanic climate is characterized by very low diurnal and annual temperature ranges (January mean monthly temperature range, 5.3–8.8°C; July, 1.6–4.9°C), high relative humidity (mean 86%) and rain or drizzle almost every day. Annual mean rainfall (1033 mm for 1980–2010) has increased by around 20% since 1948 (Jovanovic 2012). Low cloud (fog) is frequent at higher elevations (Chapter 3).

### *Species Data*

Data for nine vascular plant species, representing most of the dominant species of non-coastal vegetation on Macquarie Island, were compiled from various sources.

Quantitative vegetation cover data from plot-based studies (Bricher *et al.* 2013; DPIPWE, unpublished data, 2017; Jenny Scott, unpublished data 2014) was reclassified into three classes for each of the target species: absent, present, dominant. A species was considered dominant if projected foliage cover exceeded 25%. Plots varied in size from 1 x 1 m (in which case several nearby plots were averaged as a single point) to 2.5 x 3.5 m. The 410 observations from Bricher *et al.* (2013) were sampled using a geostratified design to capture environmental gradients on Macquarie Island.

These data were supplemented with observations collected opportunistically during 2015–2017, using a handheld GPS to record location and noting the presence/absence/dominance of target species within a 5 m radius of the observer. In total 770 points were compiled, spanning the years 2009–2017 (Fig. 1).

### *Environmental data*

We used 14 terrain and topoclimatic predictor layers derived from a 5 m resolution digital elevation model for Macquarie Island (Table 1). Correlations between pairs of

predictors did not exceed 0.8 (Pearson correlation coefficient) so we consider each predictor to have unique information to potentially contribute to the models. The most frequent and strongest winds on Macquarie Island are from the northwesterly and westerly sectors while southwesterly winds appear to be the most limiting to plant growth (Fitzgerald & Kirkpatrick 2017; see Chapter 2). We therefore modelled local wind speed across Macquarie Island based on the 95th percentile wind speed for each of three wind directions (225/270/315°) using WindNinja software (Forthofer 2007). These wind speed models do not incorporate turbulence so may have reduced accuracy at high wind speeds in complex or steep terrain, as is typical of Macquarie Island.

**Table 1.** Topographic layers used as predictors for the species distribution models, with some examples of how they might influence the distribution of plant species either positively or negatively.

Variable	Ecological relevance	Source data
Elevation	Air temperature, soil temperature, cloud cover, wind, humidity	5m DEM
Slope	Drainage	5m DEM
Northness	Aspect (sun, wind)	5m DEM
Eastness	Aspect (sun, wind)	5m DEM
Wetness index	Drainage/ waterlogging (also typically a surrogate for soil depth and organic matter)	5m DEM (calculated in SAGA GIS)
Solar radiation	Relative solar radiation	5m DEM (calculated in ArcGIS as total for 6 month growing season)
Wind exposure (NW, W, SW)	Wind damage and desiccation	5m DEM (Analysis at 100 m grid cell scale using WindNinja software (Forthofer 2007), fitted to 5m surface using a spline in ArcGIS)
Topographic Position Index (TPI180, TPI500)	Site preference, drainage, soil depth	5m DEM (using tools from Jenness <i>et al.</i> 2013)
North-south (latitude)	Regional differences in environment	Macquarie Island coastline polygon
Distance from coast	Saltspray, aerosol nutrients	Macquarie Island coastline polygon
Across island gradient	Potential gradient in precipitation or aerosols from windward to leeward side of island	Represents distance from the west coast by determining distance from a baseline west of Macquarie Island and parallel to the main axis of the island

To investigate whether species models could be improved by the addition of spectral reflectance data we also performed the modelling with a set of eight spectral layers in addition to the terrain layers (Table 2). Spectral layers were obtained from a cloud-free 2016 Sentinel-2 image of Macquarie Island. Pre-processing involved atmospheric correction using the European Space Agency's Sen2Cor algorithm, followed by orthorectification and georeferencing in ArcGIS. We used each of the three visible wavelengths and the near infrared band as individual layers plus four spectral vegetation indices (SVIs) derived from these bands (Table 2) using ENVI software (Harris Geospatial 2018).

**Table 2.** Satellite-derived predictors used for the species distribution models: four spectral reflectance bands (10 m pixel size) from Sentinel-2 satellite and three vegetation indices derived from these.

Spectral band or indice	Description
Blue	Blue reflectance band (443 nm central wavelength)
Green	Green reflectance band (560 nm central wavelength)
Red	Red reflectance band (665 nm central wavelength)
Near Infrared (NIR)	Near Infrared band B8 (842 nm central wavelength)
Normalized Difference Vegetation Index (NDVI)	Ratio of NIR to red reflectance. Represents greenness and therefore live vegetation density.
Optimized Soil Adjusted Vegetation Index (OSAVI)	Similar to NDVI but with a parameter to minimize soil effects. Useful for areas of sparse vegetation where there is a strong soil signal.
Improved Modified Triangular Vegetation Index (MTVI2)	Derived from green, red and NIR bands. Good predictor of Leaf Area Index.

### Random forest modelling

Modelling was performed using the *biomod2* package for R (Thuiller *et al.* 2009). Exploratory analyses with various models showed consistently good results from random forest models (RFMs) with our data. Random forest is a machine-learning algorithm for classification or regression which develops models based on a training set of data and validates these models using an evaluation data set (Breiman 2001; Liaw & Wiener 2002). We employed random sampling of the dataset to select 65% of records for training and set aside 35% for evaluation for each decision tree in each RFM. Trial

runs of RFMs with a subset of species showed that the default parameters of  $ntree = 500$  (trees per RFM) and  $mtry = 4$  (number of variables randomly selected for each decision tree split) were effective at minimizing out-of-bag (OOB) error rates. Unlike some other SDMs, random forest models are not adversely affected by spatial autocorrelation of species (Marmion *et al.* 2009) so we did not investigate spatial autocorrelation in our data.

To compare model performance between models with spectral predictors and those with only terrain predictors we calculated the mean and standard deviation for the AUC of 100 RFMs for each set of predictors, using a subset of only those species observations from 2016 to avoid temporal disparity with the satellite derived data. SDMs for most species were improved with the inclusion of spectral data. While spectral reflectances vary over time we assume that broad patterns in reflectances will be reasonably consistent and potentially indicate features such as vegetation cover and structure that change little over the study period. A lack of multiple cloud-free satellite images from a particular sensor at difference times precluded investigation of temporal variability in reflectance. Since there is no need to reduce the number of independent variables or remove poorly-predictive variables in RFMs we retained the spectral variables for the final models.

Modelling involved running 100 RFMs and selecting the best model based on the highest AUC score. The three-class species dataset was split into two datasets: presence/absence (PA) where present includes dominant; and dominant/not-dominant (DN), which comprises all presence records but not absences (i.e. not-dominant is defined as present with <25% cover). For each species two RFM models were produced: PA, which models the total range (presence) of the species; and DN, which models the dominant or core range as a subset of the total range. The resulting RFM regression layers for each species were converted to binary layers using a threshold determined by the true skill statistic (Hanssen and Kuipers discriminant) (Allouche *et al.* 2006). These two layers were overlaid to produce a final layer with three classes: absent/non-core range/core range.

To determine which predictor variables were related to the distribution of each species we calculated the mean and standard deviation of the variable importance value from the 100 RFMs and plotted response plots for all variables for each species.

### *Species assemblages*

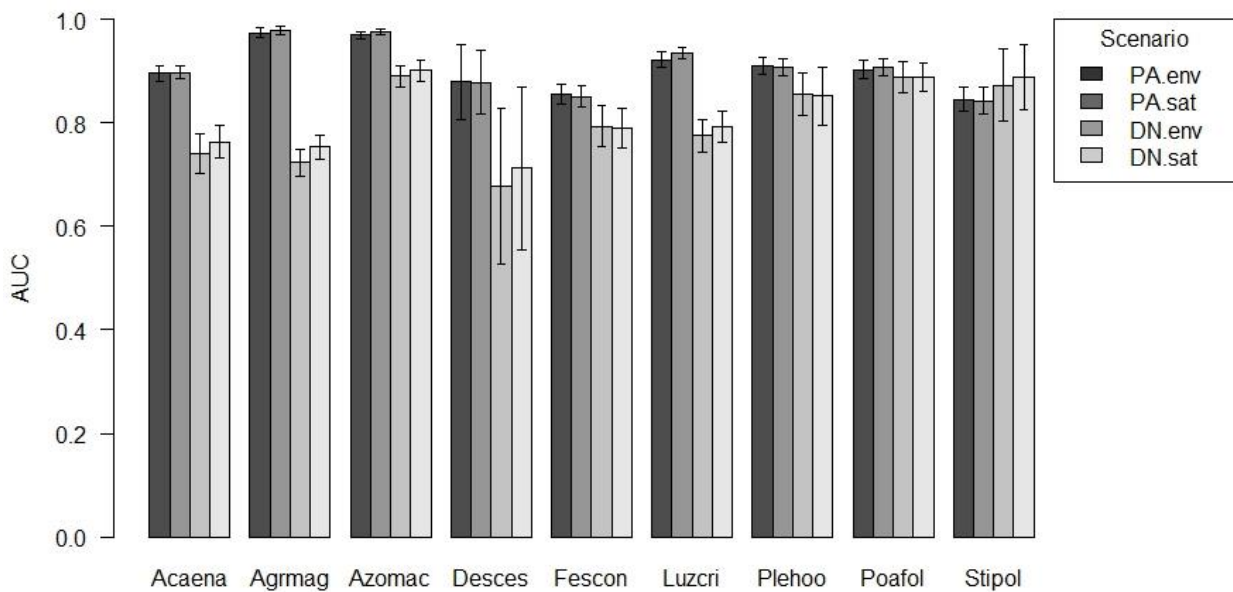
To predict the potential climax vegetation from the species projections we employed a ruleset (Table 3) based on observations of plant community assemblages on Macquarie Island and largely following the classification of Selkirk *et al.* (1990). Essentially the tallest plants with largest leaf area were expected to dominate smaller plants. An assemblage comprising megaherbs and tussock grass could have a single dominant or two co-dominant species. The short grass species and *Acaena* can occur as three or more co-dominant species. We applied this ruleset to both modelled core range and total range (i.e. core plus non-core range) models to see how they differ.

### **Results**

Model performance was acceptable with AUC values exceeding 0.8 for the best models in almost all cases (Table 4). Including spectral layers in the random forest models made little difference to the performance of models for most species (Fig 2, Table 4). The core range models had lower mean AUC values than the total range models for all species except for *Stilbocarpa polaris*.

The combined three-class range models for each species are shown in Fig. 3. The short graminoid species *Agrostis magellanica*, *Festuca contracta* and *Luzula crinita* have ranges covering almost the entire island but their core ranges are limited to low to mid elevations, particularly in the east (Fig. 3). *Poa foliosa* is mostly confined to the coastal terraces and slopes, while *S. polaris* and *P. hookeri* have ranges covering a wide range of elevation but mostly in the northern half of the island. The core range of *Azorella macquariensis* covers the entire high elevation plateau habitat. *Deschampsia cespitosa* has the smallest and most fragmented range of the species considered here.





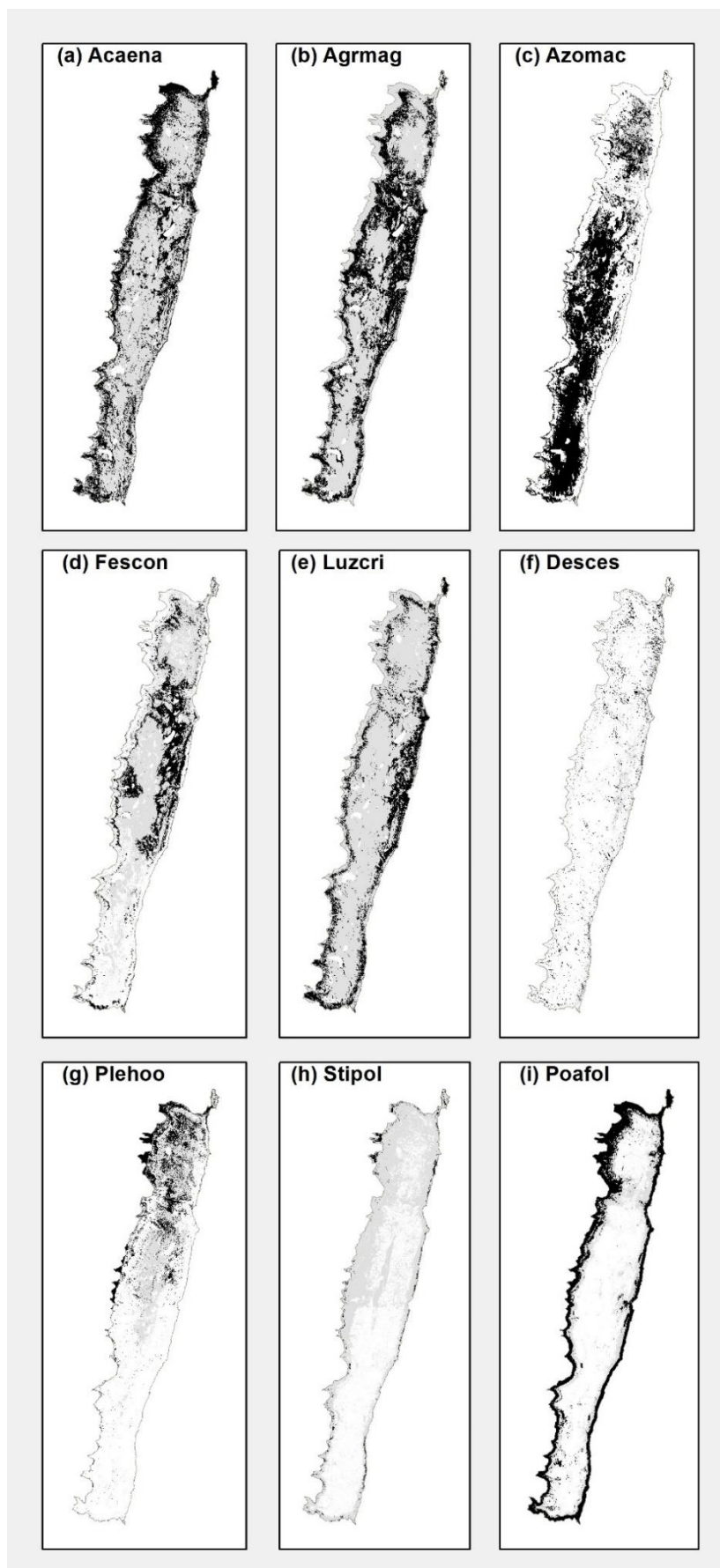
**Fig. 2.** Model performance of 100 random forest models was assessed using the area under the curve of a receiver operating characteristic plot (AUC) for two datasets, with and without satellite reflectance variables. Bars are mean AUC of 100 models, error bars are one standard deviation. PA = presence/absence model, DN = dominant/not-dominant model, env = terrain predictors only, sat = terrain plus satellite predictors. See Fig. 3 for key to species names.

Variable importance for the core range models for each species is shown in Fig. 4.

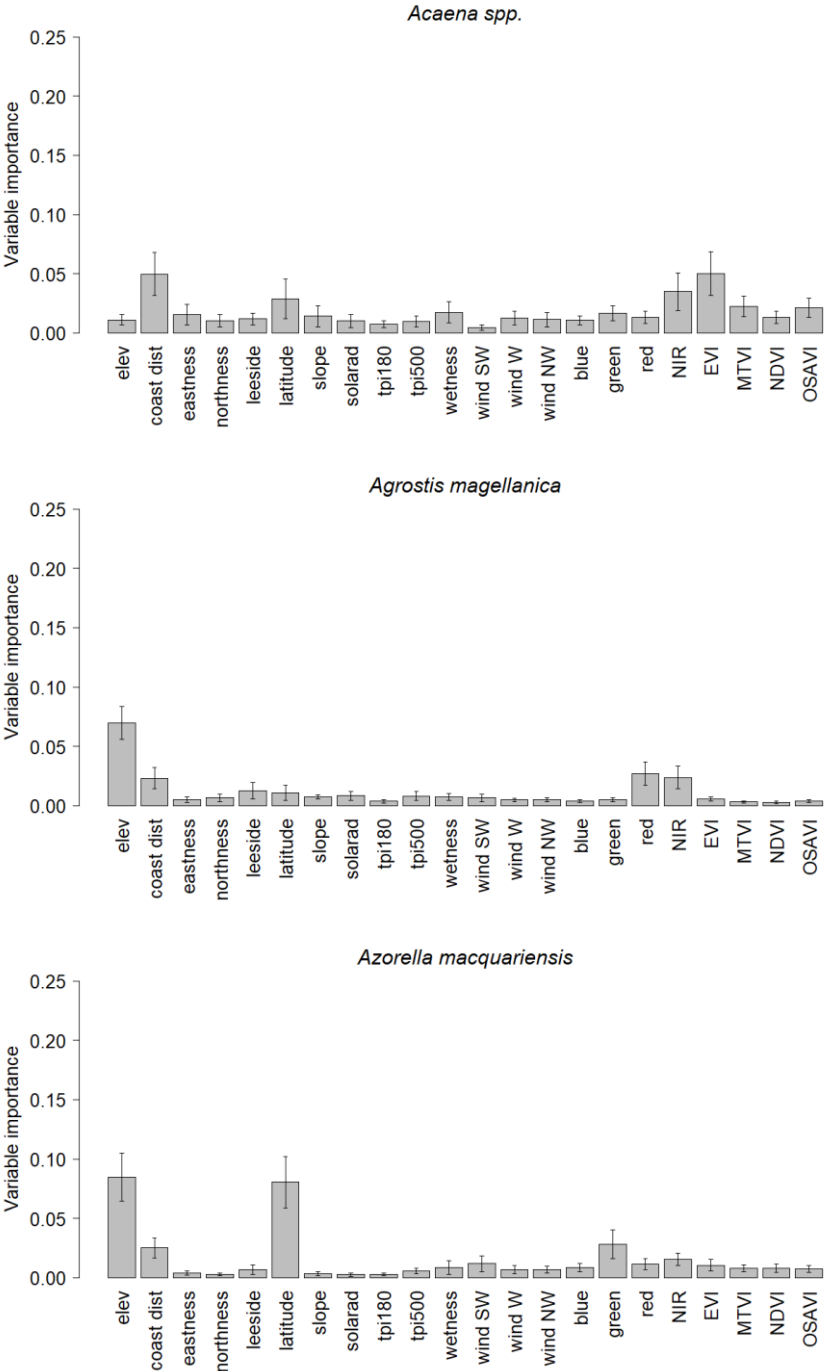
Elevation and distance from the coast are important for several species including *A. magellanica*, *A. macquariensis*, *F. contracta*, *P. foliosa* and *S. polaris*. Distance from the coast is important for *Acaena* spp. but elevation is not, while *L. crinita* is opposite.

*Pleurophyllum hookeri* shows a strong response to latitude, with a distribution biased to the north, while *A. macquariensis* has the opposite pattern. The short grasses *D. cespitosa* and *F. contracta* are biased toward the east (lee) side of the island. Exposure to northwesterly winds and topographic position had some influence on the core range of *S. polaris*. Wind exposure and topographic position were not important for any of the other models.





**Fig. 3.** Modelled core range (black) and non-core (total) range (pale grey) for nine dominant Macquarie Island plant taxa, classified from random forest models: (a) *Acaena* spp., (b) *Agrostis magellanica*, (c) *Azorella macquariensis*, (d) *Festuca contracta*, (e) *Luzula crinita*, (f) *Deschampsia cespitosa*, (g) *Pleurophyllum hookeri*, (h) *Stilbocarpa polaris*, (i) *Poa foliosa*.



**Fig. 4.** Variable importance for species core range models. Mean variable importance with standard deviation from 100 random forest models is shown. Predictor variable abbreviations are explained in Tables 1 and 2.

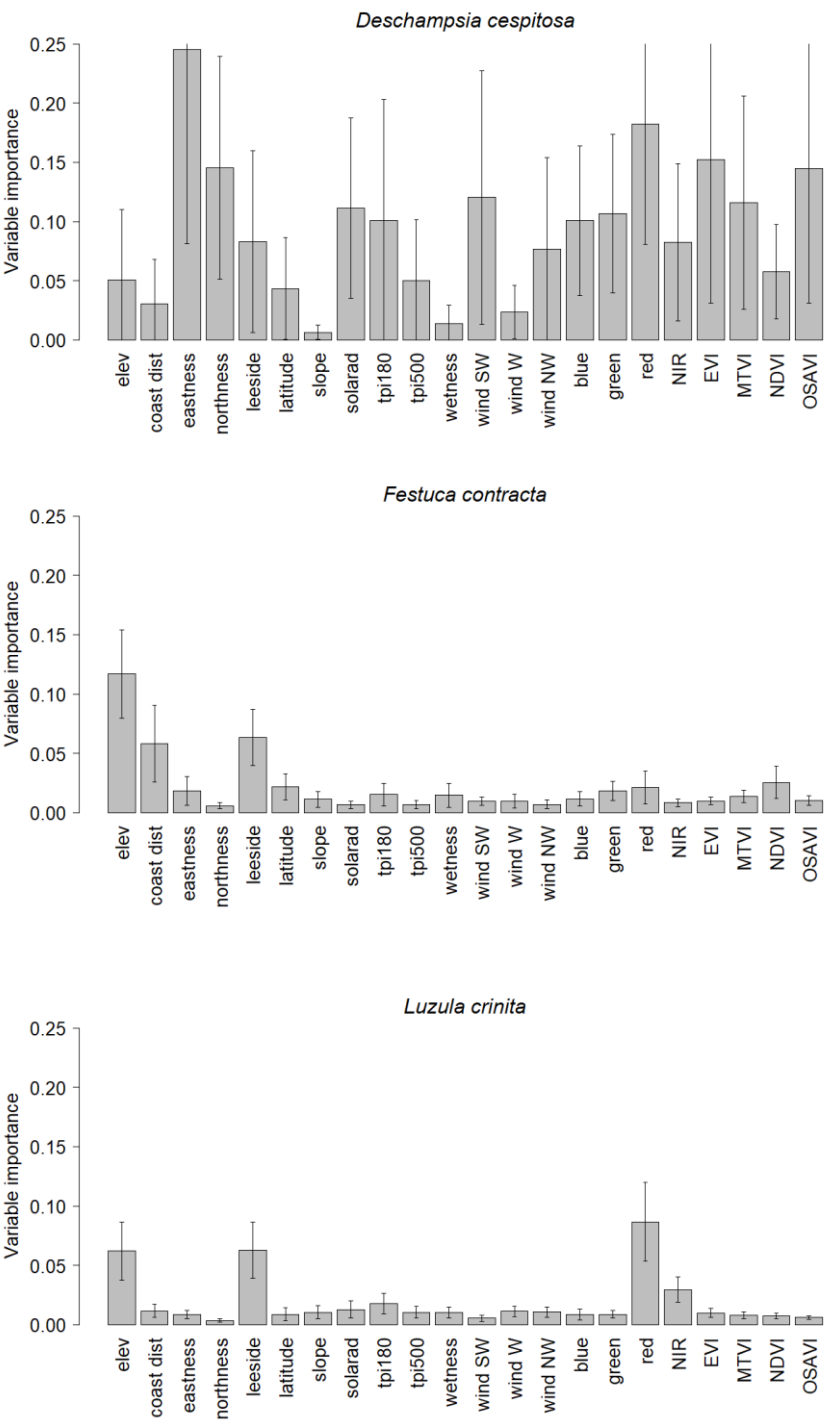
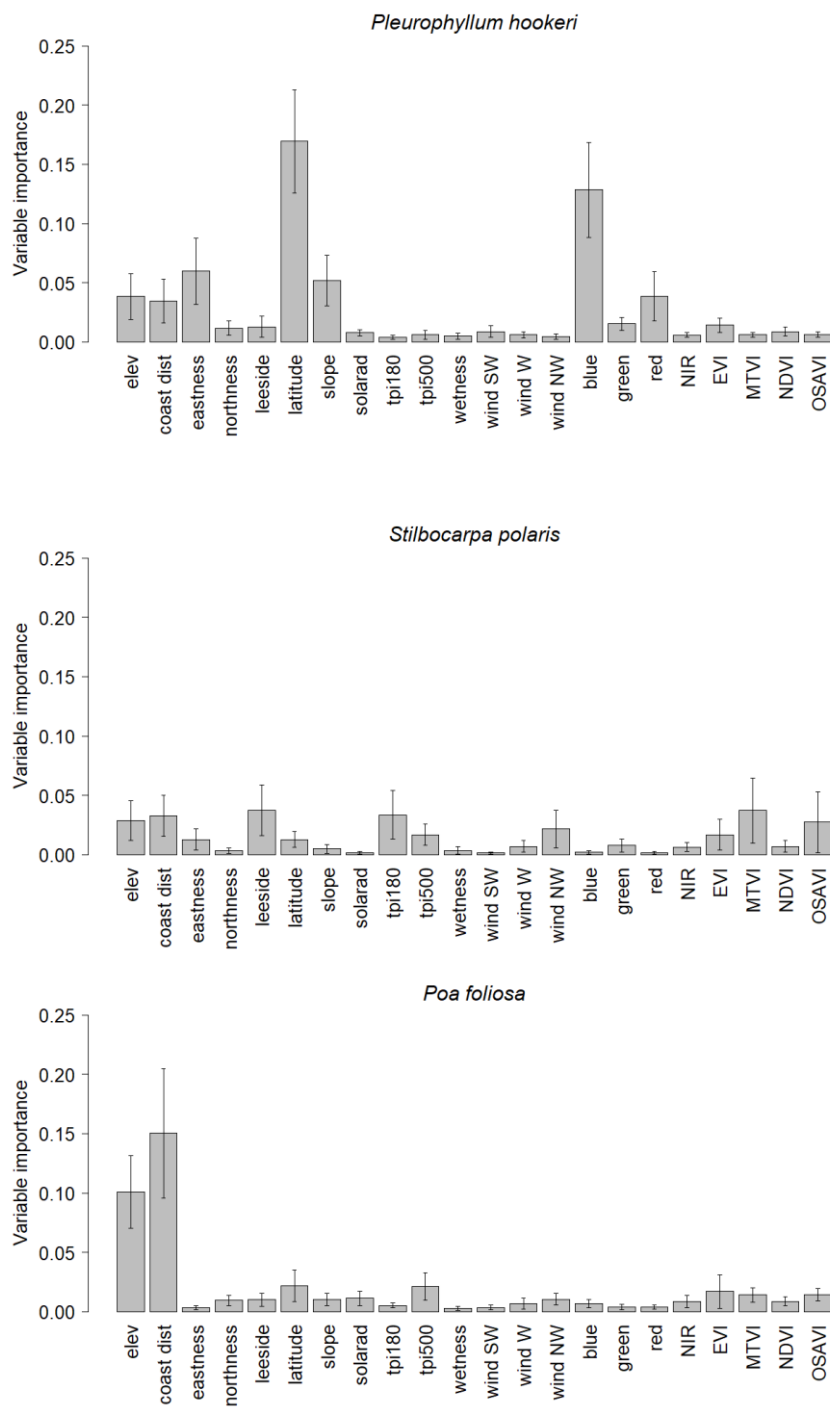


Fig. 4. (cont.)



**Fig. 4.** (cont.)

Some spectral indices feature in most models but the particular variables differ between species in their importance. In some cases, the original satellite bands were more important than vegetation indices. Low levels of green reflectance, indicating sparse vegetation, were indicative of *A. macquariensis*. The blue band was important for modelling the core range of *P. hookeri*, apparently by discriminating the distinctive bluish foliage of this species, but was not important for the total range.

**Table 3.** Ruleset for determining floristic assemblage from modelled species ranges and core ranges. The process is iterative starting with the first category, if the species range rule is not met it proceeds down the table.

Species range	Floristic assemblage
Core range of <i>P. foliosa</i> and <i>S. polaris</i>	<i>P. foliosa</i> – <i>S. polaris</i> tall herbfield
Core range of <i>P. foliosa</i> (Range of <i>S. polaris</i> )*	<i>P. foliosa</i> tussock grassland ( <i>S. polaris</i> tall herbfield)*
Core range of four or more of <i>Acaena</i> spp., <i>A. macquariensis</i> , <i>A. magellanica</i> , <i>F. contracta</i> , <i>L. crinita</i> , <i>P. hookeri</i>	Short grassland and herbfield complex
Core range of <i>P. hookeri</i>	<i>P. hookeri</i> herbfield
Core range of three or more of <i>Acaena</i> spp., <i>A. magellanica</i> , <i>D. cespitosa</i> , <i>F. contracta</i> , <i>L. crinita</i>	Short grassland
Core range of <i>Acaena</i> spp.	<i>Acaena</i> herbfield
Total range of <i>A. macquariensis</i>	Feldmark
None of the above	Unclassified

\* *S. polaris* herbfield only included in alternative analysis based on total ranges

**Table 4.** Best models for each scenario, based on highest area under the curve of a receiver operating characteristic plot (AUC) value from 100 models. PA = presence/absence model, DN = dominant/not-dominant model, env = terrain predictors only, sat = terrain plus satellite predictors.

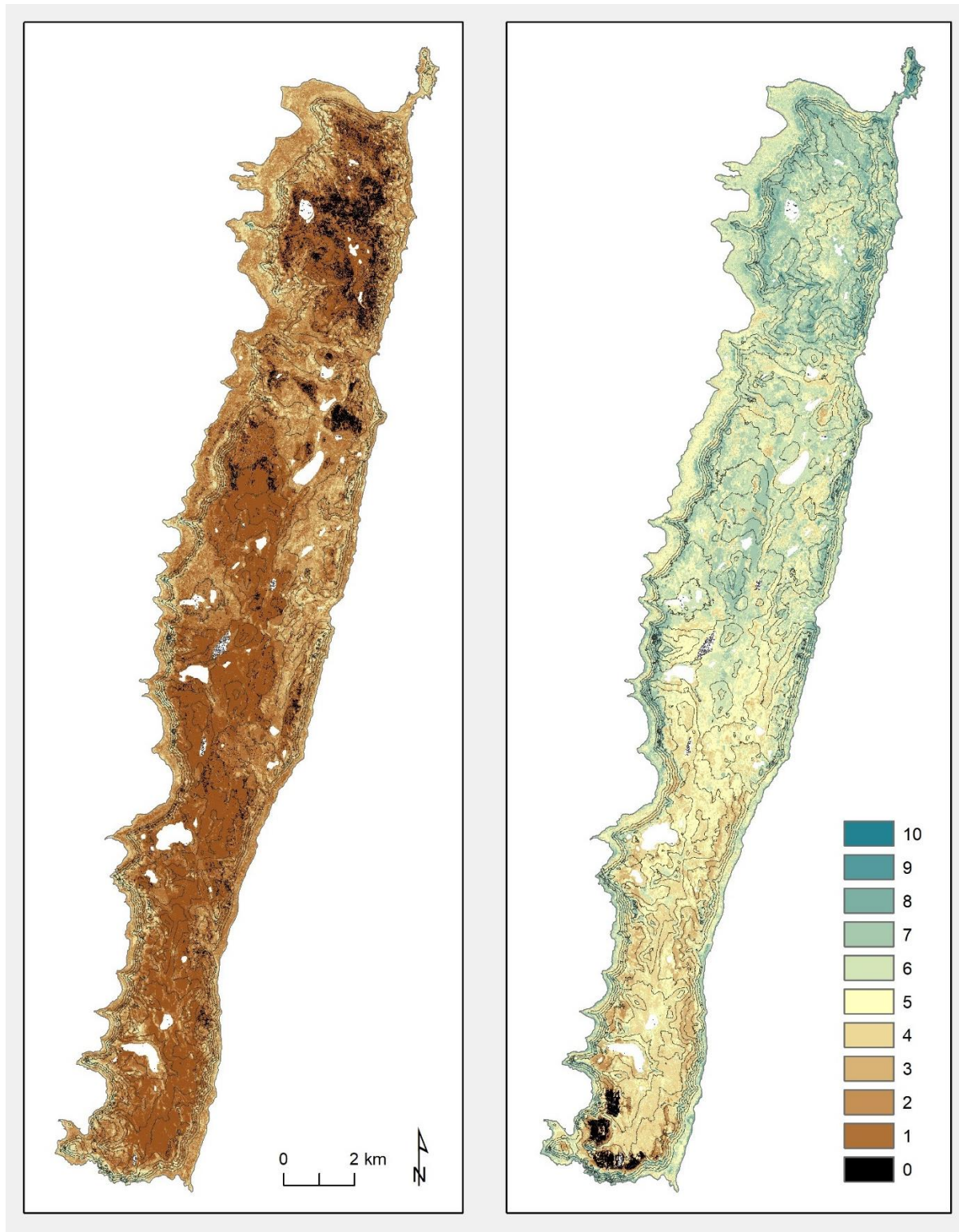
	PA sat	DN sat	PA env	DN env
<i>Acaena</i> spp.	0.924	0.830	0.926	0.819
<i>A. magellanica</i>	0.991	0.846	0.994	0.779
<i>A. macquariensis</i>	0.986	0.952	0.985	0.934
<i>D. cespitosa</i>	0.976	0.959	0.978	0.984
<i>F. contracta</i>	0.903	0.867	0.898	0.882
<i>L. crinita</i>	0.960	0.845	0.958	0.859
<i>P. hookeri</i>	0.941	0.945	0.944	0.944
<i>P. foliosa</i>	0.951	0.954	0.940	0.955
<i>S. polaris</i>	0.888	0.988	0.902	0.989

Core range as a proportion of total range varied greatly, from 4% for *S. polaris* to 81% for *A. macquariensis* (Table 5). Most of the ten dominant species considered here potentially co-occur across large parts of Macquarie Island (Fig 5a). However, the extent of overlapping core ranges is much lower, ranging from eight of the ten species in some coastal situations and declining with elevation (Fig 5b). The core ranges of some species coincide strongly, for example *S. polaris* is almost always associated with *P. foliosa* (Table 6).

**Table 5.** Modelled habitat area of key Macquarie Island plant species

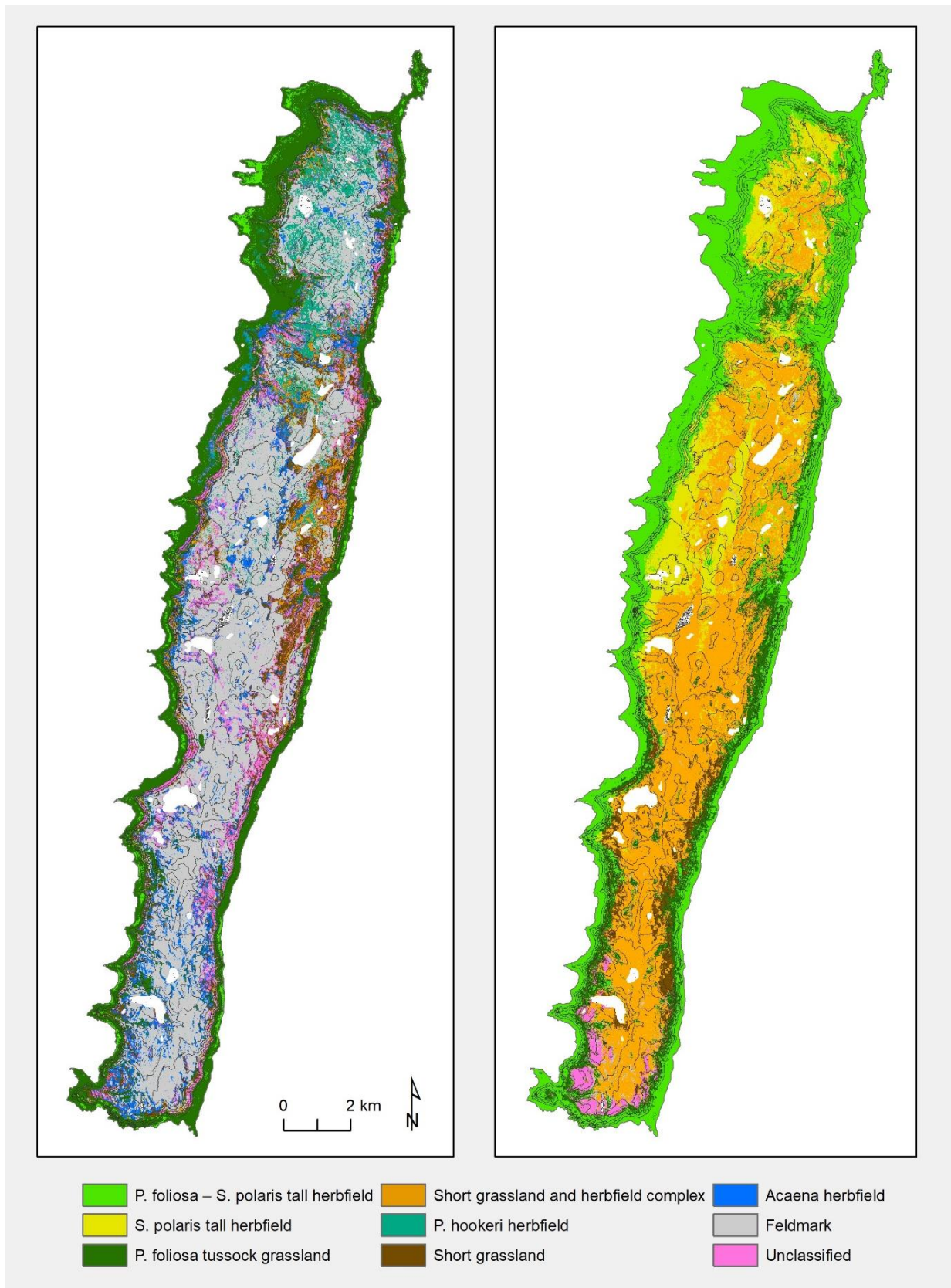
	Non-core range (ha)	Core range (ha)	Total range (ha)	Core range as % of total range
<i>Acaena</i> spp.	7515	4120	11635	35.4
<i>A. magellanica</i>	7446	4498	11944	37.7
<i>A. macquariensis</i>	1314	5516	6830	80.8
<i>D. cespitosa</i>	998	512	1510	33.9
<i>F. contracta</i>	5798	2199	7997	27.5
<i>L. crinita</i>	9457	2532	11989	21.1
<i>P. hookeri</i>	2764	1590	4354	36.5
<i>P. foliosa</i>	2398	2997	5395	55.6
<i>S. polaris</i>	5640	229	5869	3.9

Combining range maps into a species assemblage classification produced an original map with eight classes but since *S. polaris* herbfield was predicted to cover under two hectares it was removed from the ruleset, leaving seven vegetation assemblages plus an unclassified category (Fig 6a, Table 7). Applying the assemblage ruleset to total range maps instead of core ranges resulted in a very different spatial pattern with the taller vegetation (three assemblages including *Stilbocarpa* herbfield which was retained in this analysis) and short grassland/herbfield complex covering most of the island with dramatic reductions in feldmark, *P. hookeri* herbfield and *Acaena* herbfield (Fig 6b, Table 7). A simple structural vegetation map can be produced by grouping the floristic assemblages into the equivalent structural mapping units used by Selkirk & Adamson (1998) and subsequently in TASVEG 3.0 (DPIPWE 2013) (Fig 7).



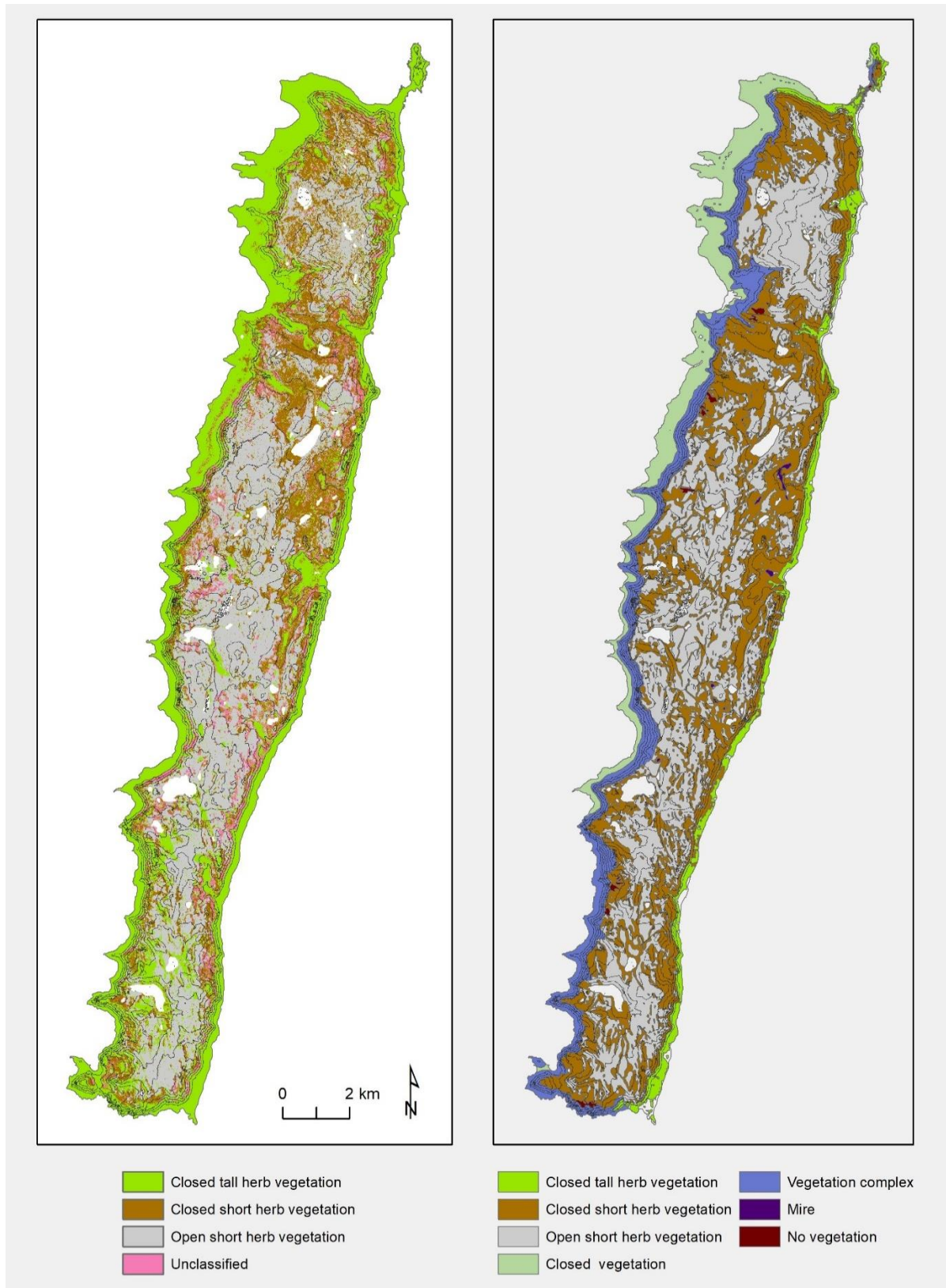
**Fig. 5.** Spatial coincidence of the nine modelled species: (a) core range models, (b) total range models. Colouring indicates how many of the nine species have overlapping core or total range at any point on Macquarie Island.





**Fig. 6.** Species assemblages: (a) based on core ranges of key species; (b) based on total ranges of key species.





**Fig. 7.** Structural vegetation types (a) this study, derived by reclassifying the floristic assemblages in Fig 6a *sensu* Selkirk & Adamson (1998); (b) Macquarie Island vegetation *circa* 1997 (Harris *et al.* 1999) based on Selkirk & Adamson (1998), published as TASVEG 3.0 (DPIPWE 2013).

**Table 6.** Co-occurrence of species pairs by core range overlap. Values are per cent of the core range of the species in the column.

	<i>Acaena</i>	<i>Agrmag</i>	<i>Azomac</i>	<i>Desces</i>	<i>Fescon</i>	<i>Luccri</i>	<i>Plehoo</i>	<i>Poafol</i>	<i>Stipol</i>
<i>Acaena</i> spp.	100.0	47.0	16.9	75.8	31.4	63.6	45.2	63.5	69.0
<i>A. magellanica</i>	51.3	100.0	18.5	52.5	63.8	75.2	33.0	30.1	10.9
<i>A. macquariensis</i>	22.6	22.7	100.0	12.3	40.2	11.7	18.4	17.8	8.7
<i>D. cespitosa</i>	9.4	6.0	1.1	100.0	3.0	10.6	4.5	7.6	16.2
<i>F. contracta</i>	16.7	31.2	16.0	13.1	100.0	26.3	25.7	11.1	3.9
<i>L. crinita</i>	39.1	42.3	5.4	52.3	30.3	100.0	14.7	34.3	27.9
<i>P. hookeri</i>	17.4	11.6	5.3	14.1	18.6	9.2	100.0	23.1	39.7
<i>P. foliosa</i>	46.2	20.1	9.7	44.7	15.1	40.6	43.5	100.0	99.6
<i>S. polaris</i>	3.8	0.6	0.4	7.2	0.4	2.5	5.7	7.6	100.0

**Table 7.** Total area (ha) classified in each floristic assemblage using either modelled core ranges or total ranges.

Floristic assemblage	Species core ranges	Species total ranges
<i>P. foliosa</i> – <i>S. polaris</i> tall herbfield	228	4189
<i>S. polaris</i> tall herbfield	NA	1679
<i>P. foliosa</i> tussock grassland	2769	1170
Short grassland and herbfield complex	474	4448
<i>P. hookeri</i> herbfield	741	1
Short grassland	818	357
<i>Acaena</i> herbfield	1042	1
Feldmark	5062	76
Unclassified	972	184

## Discussion

Modelling the distribution of selected plant species on Macquarie Island provides a framework for making inferences about the present and future spatial distribution of plant species assemblages (and consequent structural vegetation types) as well environmental correlates of species distributions which can indicate the relative importance of different environmental drivers for biodiversity in the terrestrial subantarctic.

### *Plant species assemblages*

Austin and Smith (1989) suggest that communities will have fewer dominant species (as a proportion of total biomass) at three points on an environmental gradient: under optimal conditions near the middle of the gradient where competitive processes favour the most competitive species and at either end, where few species can tolerate the harsh environment. Conversely, species richness peaks at the two intermediate points in environmental space, representing more diverse communities where resources and competition are less limiting.

On Macquarie Island, environmental extremes indirectly related to elevation are the sea spray zone and the feldmark zone. Megaherb or tussock grass communities with one or two dominant species accounting for most of the biomass occur in the most productive and least stressed sites. Therefore, under the concept of trimodal dominance along a gradient, where several dominant species can coexist in intermediate locations between high stress and high productivity, we can identify short grassland and herbfield complexes. At the altitudinal extreme, feldmark is dominated by one or two species (*Azorella macquariensis* and or the moss *Ditrichum strictum*) based on our threshold of 25% cover, though in some cases no species meet this definition of dominant due to low total cover of vegetation (Selkirk 2012). As abiotic conditions (wind exposure, air temperature, substrate instability) ameliorate at lower elevations, vegetation cover and species richness increase (le Roux & McGeoch 2008b).

This study assumes that generalist species with wide distribution on Macquarie Island have a narrower niche (core range) in which they can achieve ecological dominance due to physiological differences (Austin & Smith 1989). Furthermore, this core range may be further narrowed by other factors such as interspecific competition and grazing history. Although the models have not been ground-truthed, the vegetation assemblages based on species core ranges, as opposed to total ranges, much more closely resemble the published mapping and descriptions of spatial distribution of vegetation on Macquarie Island.

Because the ruleset gives precedence to the taller growing species, in cases where these species have more than 25% cover they will be assumed to dominate over co-occurring short plants which also have more than 25% cover and therefore the models are predictive of near-future vegetation in some situations where the vegetation is in transition from a grazing-modified community. Also, some areas of potential but unoccupied core range will be identified

as core range based on similar habitats where a species is presently dominant, so the modelled assemblages are a prediction of potential climax vegetation based on niches defined by present species distributions. Since present species distributions may be influenced by grazing history it is possible that release from grazing may alter the environmental envelope occupied by some plant species.

Vegetation structural classes on Macquarie Island are closely associated with topographic features (Selkirk & Adamson 1995). Given the close correspondence between vegetation structure and species composition both the structural and floristic approaches to vegetation mapping are likely to reflect the underlying topography. Our combined models of key Macquarie Island flora species show a mosaic of potential species assemblages which appears to reflect the topographic complexity of the island. On Macquarie Island, topography may represent bioclimatic, hydrological, nutrient or soil depth gradients. These factors are inter-related, with warmer low elevation sites supporting vegetation with high primary productivity which decomposes to form water-holding peats while higher elevations have low productivity and vegetation cover due to a harsh climate and loss of soil and nutrients by erosion (Smith & French 1988; Tweedie 2000).

Applying the assemblage ruleset to the total range of all species assumes that the tallest species will potentially be dominant across their entire range. This outcome could happen where a species has an abrupt range boundary due to interspecific competition or a sharp environmental discontinuity, but in cases where shallow environmental gradients are the controlling factors there will be a gradual tail in the species abundance curve representing the non-core range (Brown 1984). For example, *P. hookeri* plants in mires are smaller than those on adjacent better drained soils and constrained to microtopographic rises (Rich 1996), which suggests this species is close to its physiological limits when soil saturation is high.

*Pleurophyllum* herbfield was extensive on the plateau in the northern third of Macquarie Island in the 1980s, but may have been more widespread previously (Selkirk *et al.* 1990). Our model clearly shows a comparable distribution of *Pleurophyllum* herbfield. There were few presence records for *P. hookeri* and *S. polaris* in the southern third of Macquarie Island. Copson (1984) mapped these species as less abundant in the southern parts of the island. The southern region lacks certain species despite the presence of suitable habitat, including the mat-forming fern

*Blechnum penna-marina*, the herb *Hydrocotyle novae-zeelandiae*, and the filmy fern *Hymenophyllum falklandicum* (Copson 1984). There are no obvious direct environmental gradients or geological discontinuities associated with latitude, nor barriers to dispersal, on Macquarie Island to explain this latitudinal biogeographic differentiation.

The core ranges of the short graminoids *D. cespitosa*, *F. contracta* and *L. crinita* are centred on the sheltered subcoastal valleys and slopes in the central eastern part of Macquarie Island. The more widespread *A. magellanica* and *Acaena* species are also prominent in this part of the landscape, resulting in an abundance of short grassland assemblage in these areas. It is possible that these sheltered valleys provided optimum rabbit habitat and therefore the meadow-like vegetation reflects a long and persistent history of grazing, in which case tall closed vegetation such as tussock grassland or fernbrake will be the eventual climax.

Similarly, *Acaena* herbfield is possibly a grazing-induced disclimax. This assemblage is not widely recognized as distinct from other short closed vegetation on Macquarie Island vegetation but has been mentioned by some authors (e.g. Selkirk *et al.* 1990; Wace 1960) and is described on other subantarctic islands (Van der Putten *et al.* 2012; Wace 1960; Walton 1976). On Grande Terre in the Kerguelen Islands, extensive *Acaena magellanica* herbfields are attributed to rabbits (Lebouvier & Frenot 2007). Without grazing perhaps this community may be replaced by taller vegetation, or by a more diverse assemblage of short grasses and herbs.

The short grassland and herbfield complex assemblage aims to capture vegetation that is not an entirely graminoid-dominated meadow (short grassland) but rather has a mix of graminoids and prominent herbs such as *P. hookeri*. While both these species rich assemblages probably represent a grazing-induced disclimax in many places, the gradient theory of Austin & Smith (1989) suggests they may have a natural niche in the transition between highly productive and highly stressed environments. Two such ecotones might occur on Macquarie Island: permanently wet soils between the well-drained tussock grass/tall herbfield and waterlogged mires, and immediately below the feldmark zone where lowland vegetation decreases in stature and productivity as climatic and edaphic conditions become less favourable.

In the latter example, this topographic partitioning of vegetation types is consistent with the stress gradient hypothesis, where interaction between plant species is increasingly positive (facilitative) as abiotic stress increases, as demonstrated in a similar environment, by

vegetation patterns along an altitudinal gradient on subantarctic Marion Island (le Roux & McGeoch 2008b). *Azorella* grows slowly and does not tolerate shade and therefore is excluded by competition except where harsh conditions preclude taller growing plants (Bergstrom *et al.* 1997). *Azorella* is used here to define feldmark communities which are typically co-dominated by mosses, notably *Ditrichum strictum* and *Racomitrium crispulum*, which are frequently more abundant than vascular plants (Selkirk 2012). The ecotone between feldmark and taller vegetation therefore would be a zone in which species from the two adjacent communities coexist and neither competition or facilitation are strong factors.

Our broadscale modelling of floristic assemblages does not explicitly consider some localized factors which influence vegetation structure and composition. Tussock grassland dominated by *Poa cookii* occurs in the immediate proximity of penguin rookeries and burrowing petrel colonies due to high nutrient levels but may have had a broader habitat which has been reduced by selective rabbit grazing (Copson 1984). In our analysis, and previous floristic classifications, this is subsumed in *P. foliosa* tussock grassland, but could perhaps be identified by spectral differences, or inferred from mapped penguin rookeries. Coastal vegetation is structurally and floristically distinct (Selkirk *et al.* 1990; Taylor 1955) but being confined to a narrow linear strip it is not conducive to mapping at the island scale, since it varies from absent to several metres in width and can occur in a mosaic with other vegetation in areas of complex rock formations.

Some areas were undefined by the assemblage ruleset, suggesting that these areas either do not fit into the community classification or the species models are underestimating the core ranges. The main gap in our analysis is the exclusion of mire species such as *Montia fontana*, *Juncus scheuchzerioides* and *Isolepis aucklandica* due to insufficient data. Mires occur on the coastal terrace and inland valleys where the watertable is constantly high. *Pleurophyllum* can occur in mires (Rich 1996) and there is probably a continuum from bryophyte-dominated mires to increasing graminoids and small herbs and eventually the wetter *Pleurophyllum* herbfields, making mires somewhat complex to define floristically. However, the unclassified areas do not correspond to the most extensive mires and therefore the mire community appears to have been mostly classified as other assemblages. Extensive coastal terrace mires were wrongly classified as *S. polaris* and *P. foliosa* in this study and Bricher (2012) noted the same problem with a similar spatial modelling project which neglected mire species.

Many unclassified areas occur as narrow bands bordering feldmark and these appear to be a real ecotonal assemblage representing the transition from lowland vegetation to feldmark with a mix of species and less than total vegetation cover (Selkirk *et al.* 1990). Selkirk and Adamson (1998) note that the western and southern coastal slopes comprise a complex mix of vegetation types, scree and cliffs which was not possible to map as distinct vegetation types. However, unclassified areas were more common on the eastern slopes in our analysis, suggesting the ranges of potential dominant species at these coastal slope sites has been underestimated leaving gaps in their projected core range and consequently in the assemblage map.

### *Predictors*

Direct environmental gradient variables (e.g. air temperature) tend to more reliably represent the underlying ecological influence on species distributions than indirect gradients (e.g. elevation) (Elith & Leathwick 2009). However, in practice indirect gradients are widely used because they are often more readily quantifiable and available as spatial datasets (Mod *et al.* 2016).

Given the correlation between elevation and several direct gradients it is difficult to interpret which environmental factors or combination of factors are involved in species responses to the elevation gradient. Relative humidity and windspeed increase with elevation on Macquarie Island, while soil temperature and air temperature decrease (Tweedie 2000; Chapter 3). Soil freeze-thaw cycles are an important environmental factor at higher elevations and frequency of fog increases with elevation (Chapter 3) so these may be key proximal factors related to the elevation gradient. Wind exposure is frequently cited as an important climatic influence on vegetation in the subantarctic, particularly in determining the distribution of feldmark, yet wind variables were not important for core or total range models in our analysis.

None of the satellite-derived predictors were useful for multiple SDMs but most were important for some species, suggesting that it is worthwhile including a variety of spectral predictors if they are available when developing SDMs. Although we tested the relationship between satellite-derived variables and species observation from the same year, in using these variables as predictors for the full floristic dataset we make an assumption that broad trends in



satellite variables will be fairly constant over time, reflecting broad patterns of vegetation cover.

Environmental factors that were not included in the RFMs include attributes of geology and soils. Ultramafic rocks occur in some locations and are associated with lower vegetation cover than topographically comparable surrounding areas, but the dominant species do not change (Adamson *et al.* 1993). In terms of plant nutrients, this is the most atypical bedrock which might be expected to influence plant species distribution, so we surmise that geology has no influence on species distributions. Only two classes of soils are present: wet peats and dry tundra soils (Taylor 1955). The boundary between these organic and mineral soils is perhaps the most important environmental discontinuity determining the limits of plant species and communities. While there is no soil map for Macquarie Island, the distribution of tundra soils on higher more exposed parts of the landscape should be indirectly captured in our SDMs with terrain variables such as topographic position index and those spectral variables that indicate vegetation density.

Enrichment from animal manure can have a substantial localized impact on vegetation in the immediate vicinity of penguin colonies, seabird nesting sites and seal haul-outs (Bergstrom *et al.* 2002; Erskine *et al.* 1998). Beyond these zones of nutrient enrichment, animal-derived nitrogen is carried as aerosols across the island. Analysis of plant nutrient content on subantarctic Marion Island showed distinct spatial patterns related to distance from the coast and to aspect, particularly from windward to leeward (Rossouw 2014). Some indirect environmental gradients used in our models would therefore reflect similar nutrient gradients on Macquarie Island.

### *Grazing legacy effects and climate change*

SDMs assume that the ranges of species reflect current environmental conditions (Elith & Leathwick 2009) but this is often invalid. Macquarie Island vegetation is still in a transition phase due to release of grazing pressure. Species that are slow to expand their range, or increase in abundance, will therefore be underestimated. *Stilbocarpa* has a very low proportion of its range modelled as core range yet it is the second tallest growing species on the island and was abundant during periods of low rabbit population. Pure stands of tall *Stilbocarpa* herbfield



can occur on Macquarie Island (Bergstrom *et al.* 1997). Our modelling shows that if *S. polaris* was potentially dominant across its total range it would form extensive tall herbfields.

Most of the *S. polaris* observations used for the modelling were of low abundance (<25% cover) yet these may be early colonisers of sites where this species is potentially dominant. Likewise *P. foliosa* is increasing in range and abundance in many areas (see Chapter 4) and so our data probably reflect a transition from grazed vegetation to another state. Consequently, the *P. foliosa* and *S. polaris* dominated assemblages are likely to be under-mapped. The climax vegetation of the lower slopes includes pure and mixed stands of *P. foliosa* and *S. polaris* with isolated patches of *Polystichum vestitum* fernbrake (Scott 1985; Selkirk *et al.* 1990). We separated these into five assemblages based on the modelled occurrence of individual species to see whether there is a landscape pattern but it may be more realistic to consider them all as a variation within a tall herbfield and tussock grassland mosaic, perhaps with the fernbrake as a distinct assemblage. Since all these taller species are undergoing range expansion it will be necessary to reconsider the distribution and floristic character of this tall closed vegetation during the next decade.

Vegetative reproduction is frequent among the megaherb species on Macquarie Island (Bergstrom *et al.* 1997; Tweedie 2000), suggesting that while seed transport is effective for medium to long distance dispersal, vegetative reproduction may be more important in expansion of founder populations and eventual dominance of a site.

*Polystichum* fernbrake is a vegetation community dominated by the fern *P. vestitum*, which has been reduced to relictual patches by rabbit grazing (Bergstrom *et al.* 2009; Whinam *et al.* 2014a) and has disappeared from the west coast (Copson 1984). Due to a lack of data we were unable to model the habitat of *P. vestitum*. It grows on lower slopes and in valleys below about 120 m.a.s.l., apparently limited by wind, waterlogging and shallow soils (Taylor 1955). With a maximum height of under one metre, it is unclear how *Polystichum* fernbrake will coexist with the taller *P. foliosa* and *S. polaris*. *Polystichum* occurs most frequently in mixed communities with *P. foliosa*, *S. polaris* and *P. hookeri* (Selkirk *et al.* 1990). On Campbell Island, *P. vestitum* often defines gullies in grassland (Meurk *et al.* 1994) and this habitat is characteristic of the relictual populations on Macquarie Island. More data on the distribution of *Polystichum* is needed to resolve its potential extent.

Recovery of vegetation is likely to proceed for many more years. For example, after more than ten years of low rabbit numbers following the introduction of the myxoma virus in 1979/1980 changes in floristic composition were still occurring (Copson & Whinam 1998). High altitude populations of plants will recover even more slowly from rabbit impacts due to a short growing period, slow growth rates and low rates of reproduction (Tweedie 2000).

Species are expected to migrate upslope to track their climatic envelope as global air temperatures increase. Range shifts to higher elevations and latitudes have been observed in many taxa and locations (Chen *et al.* 2011; Parmesan 2006; Scheffers *et al.* 2016), including subantarctic plants (le Roux & McGeoch 2008a). On Macquarie Island the increasing wind speed may limit upward migration because higher elevations generally offer less shelter. Range shifts could also be influenced by changing interactions between plants species with climatic warming (Brooker *et al.* 2007). For example, the facilitative relationship between *Azorella* and *Agrostis* in exposed sites might shift to competition (le Roux & McGeoch 2008b). Most Macquarie Island plant species also occur in warmer climates so it is unlikely that they will be intolerant of warming. However, species that are less competitive in a warmer climate may decline in extent or abundance.

The current hiatus in warming at Macquarie Island and the removal of grazing impacts provides an ideal opportunity to establish baseline data to study species responses to future climate change by establishing altitudinal transects with different degrees of wind exposure. Such a research framework could also address theoretical questions around species and vegetation responses to environmental gradients.

Bricher (2012) suggests that mapping individual plant species is probably more useful for change detection on Macquarie Island than mapping vegetation because it avoids the definitional uncertainties associated with vegetation community classification. Our approach includes species level mapping and modelling but also provides a model of floristic associations, both of which are informative for detecting and understanding change.

This study provides a basis for more detailed floristic vegetation mapping in the future, which could be refined by systematic ground-truthing and the inclusion of species representative of mires and *Poa cookii* tussock grassland.

### *Conclusion*

We demonstrate a simple variation of the typical binary presence/absence SDMs by adding a third class representing the core range of a species. This approach is useful on Macquarie Island where most of the dominant plant species co-occur across a wide range of environments yet the vegetation varies considerably in the abundance of particular species and, consequently, in structure. This method is repeatable and data-driven. Models could be improved with more data points from more extensive fieldwork, although the major gaps in coverage are inaccessible terrain.

The present distribution of plant species assemblages on Macquarie Island reflects both environmental gradients and grazing history. We expect that plant species distributions on Macquarie Island are still shifting as species approach their climatic limits following the release of grazing pressure. Data points capturing recent expansion in species distributions would allow these models to be updated with a closer projection of the future vegetation.

## Chapter Six: General discussion

### Introduction

Studies of the environment of subantarctic islands can provide useful information for the conservation management of the globally unusual subantarctic terrestrial ecosystems. Moreover, these relatively simple and well-delineated ecosystem are ideal case studies for research into plant community dynamics and impacts of invasive species and climate change on natural systems, with relevance to ecology and environmental management well beyond the subantarctic.

This thesis addresses the question of how topography, climate and release from grazing pressure influences the distribution of plants and vegetation communities on subantarctic Macquarie Island. Research questions were: (i) How does the topography and climate shape vegetation communities on Macquarie Island? (ii) How will plant species occupy the landscape following release from grazing pressure?

This thesis comprises four research chapters, each presented in the format of an academic paper, preceded by an Introduction chapter which includes a literature review relevant to the topic. This final chapter presents a synthesis of the results of the four research chapters in the context of the literature reviewed in the Introduction.

### Climate of Macquarie Island and its influence on vegetation

Abiotic drivers of plant species distribution include temperature, moisture availability, solar radiation and wind exposure. These bioclimatic drivers are modified by landscape factors such as slope, aspect, elevation and soil depth at scales relevant to plant communities and individual plants. Therefore, to understand climatic influence on vegetation at the landscape scale it is necessary to consider both the regional climate and local variation due to topographic and edaphic factors which result in the microclimate experienced by the flora. This thesis investigated three climatic parameters on Macquarie Island in order to inform spatial modelling of plant species and communities in Chapter 5. Wind exposure was examined in Chapter 2, while air temperature and cloud cover were the focus of Chapter 3.

### *Wind exposure*

Persistent strong winds are a distinctive feature of Macquarie Island's climate and have been regarded as an important climatic influence on the vegetation of the island (Taylor 1955; Jenkin 1972; Tweedie 2000). Wind speed near ground level, where wind interacts with vegetation, can vary greatly depending on topographic exposure. Where wind is a determining factor in the distribution, growth form and abundance of plant species and, consequently, vegetation communities, this effect is expected to reflect the spatial variation in wind exposure in the landscape.

In Chapter 2 we inferred the directional influence of wind on plants in maritime alpine and subantarctic environments by observing directionality in the growth form of both woody and herbaceous plants. Interestingly, this showed that the strongest and most frequent winds, as measured by meteorological stations, were not consistent with the directional growth or damage response of the flora.

In Macquarie Island feldmark habitats, reanalysis of photo-monitoring sites showed that winds from the west and southwest shaped the vegetation, whereas the dominant winds are from the west and northwest. The southwesterly bias in wind damage implies that the relatively infrequent and weak southwesterly winds have a disproportionate effect on the vegetation. Similarly, in Tasmanian feldmark there was a disproportionate frequency of wind influence on plants from the south and southwest. While wind distortion in trees has been used as an indicator of prevailing wind direction in montane environments (Noguchi 1979; Wooldridge *et al.* 1996) our research suggests that feldmark vegetation may not be a reliable indicator of dominant wind direction. More research is warranted to investigate processes and patterns of wind influence on feldmark plants.

Most of the literature on wind influence on native vegetation is from trees and krummholz shrubs in treeline environments in the Northern Hemisphere (e.g. Foster 1988; Holtmeier & Broll 2010; Wooldridge *et al.* 1996) where snow cover persists during winter and the summer growing season is short. Subantarctic and Australian alpine environments, with a more maritime climate and differences in vegetation physiognomy, have been subject to very limited study in regard to wind. This thesis provides a significant contribution to the study of wind

influence on vegetation in non-woody plants and in maritime high altitude and high latitude environments.

### *Altitudinal trends in air temperature and cloud cover*

The distributions of plant species are frequently controlled by physiological responses to temperature which determine growth rates, growing season length and damage due to extreme temperatures (Bradie & Leung 2016; Woodward & Williams 1987). Air and soil temperature influence plant growth and, often, phenology. Seasonal and diurnal patterns in air temperature in the subantarctic are notable for their extreme oceanicity, which is comparable with few other environments on Earth (Currey 1974). Plants adapted to the subantarctic environment may therefore have little tolerance to changes in air temperature (Tweedie 2000).

Using temperature loggers to record air temperature along altitudinal gradients on Macquarie Island we found that average air temperature lapse rates are relatively steep in comparison with reported averages from other regions, possibly due to the lack of positive lapse rates (temperature inversions) which reduce the average steepness in continental climates (Chapter 3). Seasonal and diurnal patterns observed in more continental climates were not evident except for an increase in the steepness and variability of diurnal lapse rates during summer on the eastern slope, which appears to be driven by high levels of solar radiation.

Few studies have previously examined air temperature lapse rates in the subantarctic region or in highly maritime climates. No studies, to our knowledge, have examined the relationship between lapse rates and the observed presence of low cloud at ground level. This was investigated because there are potential causal mechanisms for each of these factors to influence the other. Furthermore, low cloud base levels are a frequent phenomenon on Macquarie Island (Streten 1988) and may therefore be an important aspect of the bioclimatology which is not captured by standard meteorological observations.

While our results show little relationship between lapse rates and cloud base level the observations of cloud base level provide an improved understanding of each of these processes on Macquarie Island, including their diurnal and seasonal patterns. Given the prevailing influence of synoptic, rather than topographic, factors on lapse rates at Macquarie Island and the climatic similarities of the other non-glaciated subantarctic islands it might be expected

that lapse rates from Macquarie Island would be representative of the subantarctic region. However, lapse rates from this study and some others on Macquarie Island (Davies and Melbourne 1999; Taylor 1955; Jenkin 1972) are around twice the average values reported from Marion Island (Hedding 2008) which suggests there is no such generality of lapse rates.

### *Ecological implications of low cloud*

The high frequency of fog observed in this study supports earlier assertions about the likely ecological significance of occult precipitation on Macquarie Island (Jenkin 1972; Tweedie 2000), particularly at high elevations where fog is most common and mineral soils provide limited water holding capacity (Taylor 1955). Wind speed and vegetation structure are key determinants of fog interception, which accounts for much more fog moisture input than gravitation of fog droplets (Katata 2014). Thus, Macquarie Island's windy and humid climate is highly conducive to occult precipitation (i.e. fog deposition).

Fog capture is proportional to the drag force of vegetation and wind speed (Grace 1977). On Macquarie island, the vegetation with the greatest height and vertical leaf area, and therefore fog interception capacity, is dominated by tussock grasses and the megaherb *Stilbocarpa polaris*. These formerly extensive vegetation communities have been widely replaced by short grassland due to grazing by rabbits (Whinam *et al.* 2014a) with a possible reduction in water yields (Kirkpatrick 2009). Tussock grasses on Subantarctic islands are also likely to derive plant nutrient ions by interception of sea-derived mist with consequent increases in plant productivity (Meurk *et al.* 1994).

Several studies have investigated the role of fog precipitation in snow tussock (*Chionochloa* spp.) grasslands of the Otago uplands in New Zealand. The structure and the large horizontal leaf area index of tussock grasses makes them efficient collectors of fog, at least during the annual six month snow-free period (Ingraham & Mark 2000). Estimates of occult precipitation vary between studies and catchments, adding 0—22% of the recorded rainfall amount (Fahey *et al.* 2011; Ingraham & Mark 2000). Tussock grasses (*Poa foliosa*, *P. hamiltonii*) and tussock grassland communities on Macquarie Island have a similar physiognomy. Given the high frequency of fog, particularly on the plateau, and the relatively infrequent snow cover on Macquarie Island, the magnitude of fog precipitation is likely to be comparable or greater than the Otago uplands.

Cloud cover can influence plant growth in an environment where temperature is limiting since radiative heating from direct sunlight considerably increases leaf temperatures (Little *et al.* 2016; Walton 1984). Conversely, cloud cover can reduce water stress by decreasing evapotranspiration (Foster 2001; Price 1991). However, on Macquarie Island, where transpiration, temperature and nutrients are rarely limiting, radiation is the key limiting factor for the growth of the dominant plant species (Jenkin 1972). Cloud cover, therefore, is likely to reduce plant productivity.

### *Other climatic factors*

Based on the meteorological record, frequent rainfall and high humidity suggest that the Macquarie Island vegetation is infrequently if ever subject to water stress. However, the combination of skeletal soils and exposure to strong winds means that many high elevation parts of the island may dry out quickly and be subject to water stress within hours or days of precipitation. Conversely, lower elevations where drainage is concentrated and deep organic soils have formed can be periodically or permanently saturated. Plant species which are not adapted to waterlogging will be excluded from these sites due to physiological intolerance or competitive disadvantage. Although water availability was not investigated in the present study, topographic variables used in the species distribution models provide a proxy for the spatial variation in precipitation volume and form (relative frequencies of rain and snow) and for plant available water as determined by drainage and soils.

Solar radiation is an important driver of plant productivity and growing season (Caldwell *et al.* 1978). Overhead cloud cover measured at the BOM station shows that average cloud cover is high with a consequent reduction in incoming solar radiation reaching the land surface. High and middle level clouds such as altocumulus and cirrostratus will reduce sunlight reaching the entire island. However, low level cloud may have more localized effects. For example, this study observed cap clouds frequently present on the higher points of the island (Chapter 3), often when direct sunlight is present elsewhere.

Observations of incoming solar radiation at the summit of Mt Elder were similar to radiation recorded near sea level (Tweedie 2000). This suggests that orographic cloud may not have much influence on solar radiation received on peaks subject to cap clouds, or that other factors may compensate to overall averages, such as reduced cloud thickness compared to lower



elevations when low-level stratus occurs. Tweedie (2000) also observed higher relative humidity and lower vapour pressure deficit at the summit of Mt Elder than at lower elevations in the summer months, which is consistent with our observations of increased cloud frequency at higher elevations.

### Effects of introduced herbivores on Macquarie Island vegetation

Observations of landscape change from photographs covering a 34 year period revealed vegetation change consistent with the impact of a high rabbit population followed by initial signals of vegetation change associated with release from grazing pressure caused by rabbit eradication in 2011 (Chapter 4). Responses to release of grazing pressure varied between vegetation types and, within vegetation types, by location in the landscape. In some cases, no vegetation change was observed in the 2009—2014 period. Lack of change indicates either a stable state, a time lag in response to cessation of grazing or a slow rate of change, below detectable thresholds using the methods applied in this study.

Apart from feldmark environments, where it was difficult to detect change, the changes observed elsewhere on Macquarie Island agree with the magnitude and type of rabbit impacts on native vegetation observed in previous more localized studies (e.g. Carmichael 2008; Copson & Whinam 1998; Scott & Kirkpatrick 2012; Whinam *et al.* 2014a). Comparison of photographs from 2009 (two years before rabbit eradication) and 2014 (three years after) show changes in the vegetation, such as increases in tussock grass, that appear to be an early phase of vegetation transition from grazed to ungrazed. Chapter 4 illustrates the initial phase of vegetation recovery which is a key outcome of the successful eradication of feral herbivores from Macquarie Island and therefore joins a growing body of research demonstrating the ecological benefits of pest eradication projects in the subantarctic islands and elsewhere (Keitt *et al.* 2011; Schweizer *et al.* 2016).

### Effects of invasive species eradication

Macquarie Island has a history of successful eradications of established populations of vertebrate pest species (wekas, cats, rabbits, rats, mice) and incipient invasions of weed species (e.g. *Anthoxanthum odoratum*, *Agrostis* spp., *Rumex crispus*) which demonstrate the value of active management for restoring and maintaining the terrestrial ecosystem

(Carmichael 2007; Sindel *et al.* 2017). The eradication of rodents and rabbits is a massive contribution to protecting the natural values of this Nature Reserve and World Heritage Area.

The remaining invasive species on the island, comprising two bird species and three plant species, appear to have minor or localized impacts on the terrestrial ecosystem with no evidence of ecosystem transforming impacts of the magnitude of cats, rats and rabbits. However, the two self-introduced alien bird species (starlings *Sturnus vulgaris* and common redpolls *Carduelis flammea*) are predicted to increase in numbers following rodent and rabbit eradication, with unknown ecological consequences (Raymond *et al.* 2011).

While there is a desire to control the weed populations, eradication is unlikely to be a viable option for at least some of the weed species (Sindel *et al.* 2017). Monitoring of weed populations is necessary to determine whether they are declining or expanding in the absence of rabbit disturbance. Climate change might also facilitate the expansion of existing and new weed invasions in the subantarctic, highlighting the need for ongoing monitoring and biosecurity (le Roux *et al.* 2013).

### Distribution and dynamics of native vegetation on Macquarie Island

Topographic patterns in vegetation dynamics related to changes in grazing pressure and patterns in the distribution of dominant species were apparent (Chapters 4, 5). However, it was difficult to determine causal climatic factors due to the multiple potential bioclimatic drivers and the confounding influence of different rabbit grazing histories.

*Poa foliosa*- tall tussock grassland and *Stilbocarpa polaris* herbfield have a modelled distribution encompassing most of the coastal terraces and steep coastal slopes. *Poa foliosa* and the core range of *S. polaris* are limited to low elevations where productivity is high due to warmer temperatures and generally higher nutrient levels. As the largest and tallest plants on Macquarie Island, these species are able to outcompete smaller plants in productive environments. Both these species were observed to decline prior to rabbit eradication. Subsequent recovery was evident in *P. foliosa* in most cases, but not in *S. polaris*, which suggests different rates of re-establishment (Chapter 4).

Modelled core ranges of both species, and *S. polaris* in particular, are probably underestimates because the species are undergoing range expansion consistent with release of grazing

pressure, from perhaps their historically lowest extent prior to rabbit eradication. Since primary productivity declines with elevation (Tweedie 2000), recovery will be slower at higher elevations and there may be a substantial time lag before the upper elevation limits of *P. foliosa* and *S. polaris* dominated vegetation are established by upslope migration and establishment. Given similar lapse rates on western and eastern sides of the island (Chapter 3) the elevation limits should not vary with aspect, unless wind exposure is influential on the western slopes.

The environmental envelopes of *P. foliosa* and *S. polaris* overlap substantially with the seral communities short grassland and herbfield. Species characteristic of short grassland and *Acaena* herbfield are mostly widespread generalists which have been resilient to rabbit grazing. Therefore, the total ranges of these species are likely to be accurately captured in the modelling and the core ranges should be representative of the environmental envelope in which they can be dominant components of the vegetation (Chapter 5). While short grassland and *Acaena* herbfield are potentially dominant across most lowland habitats the environmentally similar and expanding ranges of *P. foliosa* and *S. polaris* suggest that there will be few places where the shorter vegetation communities will persist without a continuation of widespread disturbance (Chapter 5).

*Pleurophyllum hookeri* is a generalist species which can occur as a co-dominant. The core range of *P. hookeri* appears to be topographically controlled, being defined by a combination of elevation, slope and aspect (Chapter 5). *Pleurophyllum* herbfield is abundant in mid altitude locations in the north of the plateau and infrequent in other environments. Increase in *P. hookeri* after 2009 mostly occurred at higher elevations in the north of Macquarie Island, which is consistent with the main extent of modelled *Pleurophyllum* herbfield (Chapters 4, 5). If low temperatures were limiting for *P. hookeri* the species would be expected to increase more at lower elevations (Chapter 4). At most locations covered by the rephotography analysis, *P. hookeri* increased in abundance prior to rabbit eradication (Chapter 4), which suggests it has some resilience to grazing.

Sites where *P. hookeri* increased post-2009 were very different from the environments in which *P. foliosa* increased, being higher, windier, and wetter (Chapter 4). A combination of elevated and waterlogged seems to benefit *P. hookeri*, while *P. foliosa* was more successful on well-drained low elevation sites (Chapter 5). This suggests that *Pleurophyllum* herbfield may

be a climax community in some situations, although the potential for *S. polaris* to become a co-dominant or dominant in these situations is not clear.

The distribution of *Azorella macquariensis* and the feldmark community is best defined by the low abundance of other taller plant species, since *A. macquariensis* is tolerant of harsh climate but is not successful in situations with interspecific competition. This explains why elevation and latitude were strongly associated with *A. macquariensis* distribution (Chapter 5), rather than other more localized topographic features which might reflect an actual topoclimatic niche.

The present study found strong elevational gradients in vegetation patterns on Macquarie Island. There is also an interesting latitudinal effect. Smaller scale topographic influences on species distributions were less evident but may become more apparent as the legacy of grazing impacts diminishes and dominant species distributions become primarily determined by interspecific competition. Despite the extremely windy environment (Chapter 2), there was little evidence for wind exposure as a limiting factor for species distributions (Chapter 5). This may be due to complex wind flows caused by high wind speeds and steep topography (e.g. Born *et al.* 2012) which are not adequately modelled without sophisticated fluid dynamics models. Even with better spatial modelling of wind flows across Macquarie Island, microtopographic effects and the influence of vegetation on boundary layer flows will be relevant at the scale of individual plants.

Although there are many similarities in environment and ecology between the subantarctic islands, there are differences which might make it difficult to make generalisations or to extrapolate observations from one island to another. For example, plant species that are widespread in the subantarctic, such as *Blechnum penna-marina*, *Crassula moschata* and *Agrostis magellanica*, can form unique communities on different islands (Smith & French 1988).

## Possible future trajectories of Macquarie Island vegetation

### *Release from grazing pressure*

There is no evidence of long-term damage to the Macquarie Island ecosystem from more than 150 years of rabbit impacts. No plant species are known to have gone extinct on the island and

there appear to be no barriers to range expansion and recruitment of plant species which were reduced to low numbers or local extinction by rabbits (e.g. *Huperzia australiana*, *Stilbocarpa polaris*). The expected widespread transition from short grassland and herbfield to taller vegetation dominated by *Pleurophyllum hookeri*, *Poa foliosa* and *Stilbocarpa polaris* is discussed in Chapter 5. Whether this transition will follow a linear climax succession pathway or the vegetation reaches a dynamic equilibrium is not known. Other unknown factors include the future distribution and synecology of the large fern *Polystichum vestitum* which presently has a very restricted distribution and appears able to coexist with *Poa foliosa* and *Stilbocarpa polaris* in some situations.

### *Climate change*

Key factors determining the distribution of plant species and communities on the island are soil depth, waterlogging and wind exposure (Selkirk 2012; Taylor 1955). These and other likely important environmental determinants, such as air temperature and soil freeze-thaw cycles are broadly related to elevation, resulting in altitudinal zonation in plant communities. Climatic variables relevant to plant growth, including air temperature and effective precipitation, show clear altitudinal gradients (Tweedie 2000). Therefore, it is not surprising that elevation was among the most important explanatory variables for most species in the SDMs reported in Chapter 5.

Macquarie Island's topography and climate exhibit considerable variation over distances of hundreds of metres. While there are no data for shifting elevational distribution of plant species on Macquarie Island, there has been sufficient warming in the the 20th century for species to migrate upslope (Tweedie & Bergstrom 2000) as has been observed on Marion Island (le Roux & McGeoch 2008a). However, the present hiatus in atmospheric warming at Macquarie Island due to a time lag in the response of the Southern Ocean to global warming means elevation changes in vegetation are unlikely to be occurring now. Nevertheless, they will probably occur during this century and, moreover, long-term projections for the region are extreme on a multi-century scale (Turner *et al.* 2009). If lapse rates remain steep the altitudinal shift in thermal environments will be substantial, with 1°C warming equivalent to nearly 100 m elevation difference on an island with a maximum elevation range of 420 m (Chapter 3).

Wind regimes are changing on Macquarie Island due to global climate change (Hande *et al.* 2012). *Azorella macquariensis* plants are slow growing and can form large asymmetric cushions when their growth rate exceeds the rate of biomass loss due to factors such as wind erosion. Since southwesterly and westerly winds are the most damaging to cushion plants (Chapter 2), the increasing frequency and intensity of northwesterly winds may have little effect in feldmark vegetation. However, if northwesterly winds become more damaging and overall wind intensity is increased, individual cushion plants might suffer more severe damage and more widespread damage. This would reduce the size and integrity of *Azorella* plants and limit recruitment of plants in wind-exposed locations. As a dominant species in feldmark environments, decline in *A. macquariensis* would potentially impact on co-occurring plants which are facilitated by *Azorella* cushions (Cerfonteyn *et al.* 2011) and on the geomorphology, since *Azorella* cushions stabilize terrace formations (Selkirk-Bell & Selkirk 2013). However, wind speeds have increased over at least the last 20 years without a consistent trend of change in feldmark environments (Chapter 4).

Strong winds are frequently cited as an environmental determinant of feldmark distribution (e.g. Kirkpatrick 1997). Strengthening winds might therefore promote the downslope migration of feldmark. Yet a warming climate would promote greater vegetation cover by increasing primary productivity and reducing frost heave of bare ground, which presently limits recruitment and expansion of plants, thus promoting a transition from feldmark to closed vegetation. However, soil freeze-thaw cycles are also influenced by cloud cover and may increase in frequency if clear skies become more frequent, as is occurring on Marion Island (Boelhouwers *et al.* 2007). The projected warmer, windier climate therefore would seem to have opposing influences on feldmark. Long-term monitoring of feldmark ecotones would be a useful approach to detect potential vegetation change.

Feedbacks between plants and climate could accelerate conversion of feldmark to grassland and herbfield. Greater ground cover of plants will reduce frost heave and promote soil development while increased leaf area will enhance effective precipitation by fog interception. A further complication is the phenomenon of *Azorella* dieback on Macquarie Island, which has transformed some feldmark sites. Clearly, a simple explanation like wind exposure is inadequate and interactions between multiple climatic factors, soils, landforms and vegetation

need to be taken into account to understand vegetation distribution and response to climate change in higher elevation subantarctic environments.

Rainfall is not likely to be a limiting factor for most plant species on Macquarie Island, particularly if total rainfall continues to increase. However, changes in rainfall patterns, notably an increase in periods without rain, could have adverse effects on the vegetation. Indeed, such conditions appear to be increasing on Macquarie Island and even relatively short periods without precipitation can lead to moisture stress for plant species adapted to humid environments (Bergstrom *et al.* 2015). Feldmark environments appear to be most susceptible to water stress given their lack of soil water holding capacity, good drainage and exposure to drying winds. Increased wind speeds would further exacerbate water stress. The role of fog interception in the water balance of terrestrial ecosystems on Macquarie Island is another unknown component that warrants investigation along with changes in rainfall patterns and water relations at the organism and vegetation community scale.

Predicted changes to Macquarie Island's climate include a decrease in fog days and an increase in the cloud base associated with rising sea surface temperatures (Tweedie 2000). Bergstrom *et al.* (2015) note a long-term reduction in cloud cover, however these observations of sky coverage visible from Macquarie Island station are not a good indication of localized orographic cloud on the plateau. Low elevation mires fed by rainfall and fog interception at higher elevations might be most affected by an increase in cloud base height (Tweedie 2000). Dieback in the Macquarie Island cushion plant (*A. macquariensis*) is thought to be partly attributable to water stress due to increased evapotranspiration which may be exacerbated by reduced cloud cover and fog precipitation (Bergstrom *et al.* 2015).

Another likely consequence of changed rainfall patterns is an increase in landslides associated with high intensity rainfall events, such as in summer 2014-15, but how this phenomenon will interact with changes in vegetation (e.g. a shift from short grassland to tussock grass) is not known.

Aside from impacts on the native biota, a warming climate will lead to an increased number of temperate plant species climatic envelopes extending to the subantarctic (Chown *et al.* 1998; Duffy *et al.* 2017) and existing alien plants will expand their ranges on subantarctic islands (le Roux *et al.* 2013). Presently, many plants capable of growing on Macquarie Island are not

present there due to lack of dispersal, suggesting that only a small proportion of species are likely to successfully migrate to the island. While climate change might alter dispersal vectors such as winds and bird movements (Moon et al. 2017), limits to dispersal are likely to remain the main filter determining the flora of Macquarie Island. However, even a single new species could dramatically alter the vegetation ecology of the island.

### Contributions to methods and practical implications of the research

This thesis research utilized a variety of methods including novel and modified techniques.

The wind distortion interpretation (Chapter 2) involved re-analysis of photographic plots from previous studies. Azimuthal photographs of quadrats are practical for very low growing vegetation such as feldmark and, provided the orientation of the plot or photograph is known, are suitable for observing directional growth, distortion or damage in plants. This highlights the value of systematic photography for uses other than the original research topic. This research also showed that some non-woody plants, specifically graminoids and cushion plants, can be used to infer the dominant direction of wind influence on vegetation, which has utility in remote alpine and subantarctic environments where woody plants and meteorological data are non-existent.

Using an extensive archive of webcam images to determine the frequency of different cloud base level classes is a novel approach to understanding variation in cloud level as it relates to an elevation gradient in the landscape (Chapter 3). Automated image classification was trialled to detect the relative brightness of cloud in each of four zones within the image, representing the elevation classes. This method compared the histogram (representing brightness) for each zone within each photograph to histograms of reference images with known cloud presence or absence in each zone. However, this approach failed due to the highly variable lighting conditions and occasional distorting effects of water or snow on the webcam lens the images were readily classified manually using a superimposed graticule.

In order to consider the major synoptic weather patterns in relation to lapse rates and cloud cover it was necessary to classify hourly meteorological observations of multiple variables (e.g. air temperature, wind speed, wind direction, mean sea level pressure) into broad weather patterns (Chapter 3). Synoptic types can be classified using a subjective scheme (e.g. Pepin 2001) but this approach is impractical for large datasets. There may be a particular variable,



such as air pressure or wind direction, which is an indicator of synoptic type but without knowing if this is the case it seems sensible to use several key meteorological variables, all of which may contribute to characterising a synoptic type. We therefore used an ordination and classification approach commonly employed for ecological data analysis to group each hourly set of weather observations into relatively homogenous classes representing synoptic types.

Rephotography is an established method for assessing landscape and vegetation change, either from historical photography or purpose designing monitoring programs (Pickard 2002; Webb *et al.* 2010). Availability of an archive of photographs with extensive geographic and temporal scope on Macquarie Island presented an opportunity for a rephotography analysis with the main challenge being how to geolocate sites where change (or no change) was observed in the photographs (Chapter 4). While the location of the photographer was known in each case it was the locations within the photographic scene that were of interest and these were determined by interpretation of maps, including combining satellite imagery with contours and calculated viewsheds to provide sufficient information to confidently assign a point in a photograph to a point on the map. While the photograph analysis involved drawing polygons on the photographs representing homogenous zones it was not possible to replicate these polygons on the map due to issues of distortion and perspective in transferring from an oblique 3-dimensional image to an azimuthal 2-dimensional image.

In most cases, the combination of visual interpretation with layers manipulated in a geographic information system proved effective for geolocating points to represent the centre of each polygon. These geolocated points were then attributed with several terrain variables derived from a digital elevation model of Macquarie Island to allow an objective analysis of vegetation change in relation to topography. This approach derives a substantial amount of information from the repeat photography combined with topographic data within the typical limitations of the rephotography method (e.g. with only change direction, not magnitude, data) and could be used in many other contexts.

Species distribution models (SDMs) are a very widely used tool in ecology, biogeography and conservation biology, however their use and interpretation should be mindful of the limitations of the method and appropriate to the ecological questions being examined (Austin 2007; Franklin 2009). SDMs typically produce a predicted probability of presence or a binary

presence/absence for a modelled species. On Macquarie Island where most of the dominant vascular plant species are widespread generalists a typical binary species model would show most of these species co-occurring across large areas of the island. However, the distribution of vegetation types and the highly variable abundance of individual species on the island suggests that species may be a dominant component of the vegetation within a subset of their total range.

In order to understand the coexistence of different floristic and structural vegetation types within the Macquarie Island landscape and its possible future patterns following removal of rabbit grazing, we attempted to model the subset of each plant species range in which it could be a dominant species and thus characterise the vegetation types. This modification of the typical SDM process involved running two models for each species, one a standard presence/absence model and the other using only the presence data and splitting it into two classes: not-dominant and dominant. For each on-ground observation point used to train the models we had three categories for each species: absent, not-dominant (<25% foliage cover) and dominant (>25% foliage cover). The inclusion of absence data and two categories of presence makes these models more robust and provides much more useful information than a typical SDM based only on presence records.

### Future research directions

Several aspects of the bioclimatology, hydrology and plant ecology of the island require further study to better understand the ongoing response to feral mammal removal and potential impacts of climate change on the ecosystem.

Meteorological observations from the BOM station do not characterize the wind and cloud conditions which most of the island experiences. While the BOM data are representative of the coastal environment, there is a lack of systematic meteorological observations from the higher elevations of the island. Tweedie (2000) made an important contribution but did not record wind direction. An automated weather station on the plateau would provide valuable data representative of the climate of the majority of the island.

Hydrology and plant water relations on Macquarie Island deserve more attention, particularly at higher elevations where the interplay of fog precipitation, wind, topography (especially terrace features), snow cover, soils and vegetation is likely to be complex and to have

significant implications for the Critically Endangered species *Azorella macquariensis*. Influence of low cloud on microclimates is not well understood and could be investigated by recording solar radiation, fog precipitation, leaf and soil temperatures over time.

Combined with altitudinal vegetation transects, climatic data from the plateau would allow for improved monitoring of climate change impacts on this near-pristine ecosystem. Recent climate change on Macquarie Island has been different from other locations in the subantarctic (e.g. Richard *et al.* 2013) which means local studies are needed to better understand environmental change. Nevertheless, an improved understanding of local climate changes and associated ecological responses will contribute to the broader understanding and more responsive management of subantarctic and cool maritime environments, by establishing the similarities and differences that exist between these rare and vulnerable systems.

Tracking the ongoing vegetation change in response to grazing release is readily achievable given the existing long-term vegetation monitoring sites which are typically resurveyed every two years. Projected foliage cover is recorded for each vascular plant species in each permanent plot. However, the cover score classes are very wide, so substantial change in foliage cover is typically needed for a species to move between classes. Therefore, changes in plant species cover which are clearly visible to an observer may not be apparent in the data or there may be a time lag before change becomes detectable when a species passes a cover class threshold. Systematic photographs of the monitoring plots captured during each vegetation survey and the recently added nested subplots will be useful for observing change that does not appear in the 20 x 20 m quadrat dataset. Disturbance to some of these quadrats by landslides and streambank erosion provides an opportunity to document the impact of these natural events and the subsequent vegetation changes.

The rephotography series and the satellite imagery examined here (Chapter 4) provide a baseline covering the pre-eradication and the early post-eradication periods which can be continued in the future to examine landscape-scale change. The recent increase in availability of high-resolution satellite imagery covering Macquarie Island makes this now a practical option for environmental monitoring.

Finally, some aspects of the distribution and ecology of the Macquarie Island flora which are poorly understood might reward further investigation. These include the ecology of the fern

*Polystichum vestitum* and the grass *Poa litorosa*. The mysterious geographical trend where some species are absent or infrequent in the south of the island (e.g. *Blechnum penna-marina*, *Pleurophyllum hookeri*) merits investigation since the latitudinal range is not great and there are no obvious environmental correlates of this north-south biogeographic pattern.

## Conclusion

The work presented in this thesis adds to the substantial body of research investigating the vegetation of Macquarie Island since the mid-1900s. The present vegetation change following feral mammal eradication is a significant event in the vegetation history of the island, being a major step in the restoration of the most plant species rich subantarctic island ecosystem. Continuing monitoring of Macquarie Island's vegetation is vital to understand the ecological outcomes of the pest eradication project and the ongoing ecological response to climate change. There remains much scope for future research which, together with past and present research projects, will help inform the management of this Nature Reserve and World Heritage Area.

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