



MONASH University

**Impact of climate change on a sub-Antarctic keystone cushion plant,
Azorella macquariensis (Apiaceae)**

Catherine Ruth Dickson
B.App.Sc (Hons)

A thesis submitted for the degree of Doctor of Philosophy at
Monash University in 2019
School of Biological Sciences

Copyright notice

© Catherine Ruth Dickson (2019).

Abstract

Mass plant mortality is increasingly common under anthropogenic climate change, typically affecting foundation species and potentially signalling the start of regime change. The first sub-Antarctic example was observed with the landscape-scale dieback of dominant keystone species Macquarie cushions (*Azorella macquariensis*, Apiaceae) commencing 2008/2009. The rapid onset and extent of dieback resulted in the endemic species' listing as critically endangered in 2010. It was hypothesised that the dieback was primarily driven by a change in the regional climate, resulting in reduced plant available water that facilitated a secondary pathogenic infection of weakened cushions. In this thesis, I quantify the condition of *A. macquariensis* and its fellfield (alpine) microclimate on Macquarie Island eight years after the onset of its decline in condition, and investigate associated ecosystem interactions to inform strategic conservation management actions. Field sampling was undertaken at sites across the extent of the island, randomly stratified by terrain class and geographic location, to capture the suite of putative microclimates experienced by *A. macquariensis*. First, I quantified the extent and variation of cushion dieback, showing that although variable, dieback remained pervasive and more extensive in the north. Topographic modelling showed a significant latitudinal dieback gradient, while derived terrain variables associated with water stress were unimportant. Second, microclimate modelling was used to clarify the role of microclimate stress and potential interactions with the currently unidentified pathogen/s. This revealed that cushion dieback was driven by microclimate extremes broadly known to promote (humidity) or suppress (freezing) pathogen activity. Variables associated with water stress remained unimportant. Fine-scale condition classes showed a latitudinal gradient in cushion condition where the most advanced dieback occurred in the north, consistent with the location of less extreme cold conditions. Third, qualitative network models were used to improve understanding of fellfield interactions. These demonstrated the loss of interactions and ecosystem resilience as the keystone cushion's condition declined. Using insights from the previously described models and published literature, a qualitative mechanistic state-transition model was built to formalise the transitions between condition classes, capturing knowledge about the system. Finally, I discuss potential management options for *A. macquariensis* and the associated fellfield, under a framework of management intervention level and potential to effect lasting change, including the risk of not acting. In summary, secondary interactions with the currently unknown pathogen/s have been shown to be more important in determining the

condition of *A. macquariensis* than water stress variables. Refined condition classes and microclimate data provided an improved baseline, revealing important insights about dieback progression and location, including that natural refugia in the south are protected by significantly colder microclimates. Under the current and projected climate conditions, it is expected that dieback will remain pervasive, removing cover of this keystone species over time. If the fellfield ecosystem and the associated iconic terraces are to be maintained as a prominent landform on the island, adaptive intervention management actions will need to be considered and implemented within a suitable timeframe. These findings have broader implications for managing sub-Antarctic fellfield ecosystems and *Azorella* species more generally under future climates.

Publications during enrolment

Dickson, C.R., Baker, D.J., Bergstrom, D.M., Bricher, P.K., Brookes, R.H., Raymond, B., Selkirk, P.M., Shaw, J., Terauds, A., Whinam, J., McGeoch, M.A., 2019. Spatial variation in the ongoing and widespread decline of keystone plant species. *Austral Ecology* **44**, 891-905. doi:10.1111/aec.12758

Thesis including published works declaration

I hereby declare that this thesis contains no material which has been accepted for the award of any other degree or diploma at any university or equivalent institution and that, to the best of my knowledge and belief, this thesis contains no material previously published or written by another person, except where due reference is made in the text of the thesis.

This thesis includes one original paper published in a peer-reviewed journal and three unpublished publications. The core theme of the thesis is ecology and conservation biology. The ideas, development and writing up of all the papers in the thesis were the principal responsibility of myself, the student, working within the School of Biological Sciences under the supervision of Prof. Melodie McGeoch, Dr. Dana Bergstrom and Dr. Rowan Brookes.

The inclusion of co-authors reflects the fact that the work came from active collaboration between researchers and acknowledges input into team-based research.

In the case of chapters 1, 2, 3, and 4 my contribution to the work involved the following:

Thesis Chapter	Publication Title	Status	Nature and % of student contribution	Co-author name(s) Nature and % of Co-author's contribution*	Co-author(s), Monash student Y/N*
1	Spatial variation in the ongoing and widespread decline of a keystone plant species	Published	85% Design, data collection, data analysis, manuscript write-up	1. MA McGeoch, design, input to manuscript 5% 2. DJ Baker, data analysis, input to manuscript 2.5% 3. DM Bergstrom, design, input to manuscript 2.0% 4. J Whinam, design, input to manuscript 2% 5. PK Bricher, data layers, input to manuscript 1% 6. RH Brookes, input to manuscript 0.5% 7. B Raymond, input to manuscript 0.5% 8. PM Selkirk, input to manuscript 0.5% 9. A Terauds, input to manuscript 0.5% 10. JD Shaw, input to manuscript 0.5%	No

Thesis Chapter	Publication Title	Status	Nature and % of student contribution	Co-author name(s) Nature and % of Co-author's contribution*	Co-author(s), Monash student Y/N*
2	Fine-scale variability and drivers of dieback in a keystone cushion plant on sub-Antarctic Macquarie Island	Not submitted	85% Design, data collection, data analysis, manuscript write-up	1. MA McGeoch, design, input to manuscript 7% 2. DJ Baker, data analysis, input to manuscript 3% 3. DM Bergstrom, design, input to manuscript 2% 4. J Whinam, design, input to manuscript 2% 5. RH Brookes, input to manuscript 1%	No
3	Understanding ecosystem change using qualitative modelling: sub-Antarctic fellfield on Macquarie Island	Not submitted	85% Design, data collection, data analysis, manuscript write-up	1. B Raymond, data analysis, input to manuscript 5% 2. MA McGeoch, design, input to manuscript 5% 3. DM Bergstrom, design, input to manuscript 2% 4. J Whinam, design, input to manuscript 2% 5. RH Brookes, input to manuscript 1%	No
4	Conservation options for a sub-Antarctic keystone species threatened by climate change	Not submitted	90% Design, data collection, data analysis, manuscript write-up	1. MA McGeoch, design, input to manuscript 7% 2. DM Bergstrom, design 3%	No

I have renumbered sections of submitted or published papers in order to generate a consistent presentation within the thesis.

Student signature:



Date: 6/12/2019

The undersigned hereby certify that the above declaration correctly reflects the nature and extent of the student's and co-authors' contributions to this work. In instances where I am not the responsible author I have consulted with the responsible author to agree on the respective contributions of the authors.

Main Supervisor signature:



Date: 6/12/2019

Acknowledgements

I would like to thank my supervisors, Melodie McGeoch, Dana Bergstrom and Rowan Brookes, for guiding me through my PhD journey. In particular Melodie, who has provided valuable insights, regular encouragement, and mentorship, whether it was while I was in the field or in the office. I always appreciated and enjoyed our wide-ranging conservation science discussions, which often ended in a whiteboard solution. Thank you to Dana, who shared her passion for the sub-Antarctic, encouraged me to think outside the square, and was always there to talk *Azorella* and Macquarie Island. To Rowan, thank you for providing the balance, perspective and (almost) curtailing my long sentences. I am also grateful to Jennie Whinam and Patricia Selkirk, who were generously available to talk through *Azorella* and Macquarie Island whenever necessary, provide support and similarly share their passion for this wind-swept island. Thank you to my panel members, Richard Reina, Carly Cook, and Cecilia Blomstedt for their helpful advice.

This PhD would not have been possible without the generous support of a large number of people and organisations. Thank you to my collaborators at the Australian Antarctic Division, University of Queensland, University of Tasmania and Monash University. In particular, thank you to Ben Raymond for teaching me about qualitative models, asking the pertinent questions, and having patience while I navigated R. Thank you to Aleks Terauds and Justine Shaw for talking through ideas about Macquarie Island ecology and providing helpful direction when needed. Thank you to Pip Bricher for valuable future Macquarie Island and PhD advice over coffees or via email, and getting me started with the first topographically-derived layers for the island. I am particularly grateful to David Baker who helped me further wrangle R, statistics, talk through ideas and endlessly discuss cushion plants.

The two summer field seasons on Macquarie Island were a highlight and made even more enjoyable by the people. Thank you to Dana and Jennie for introducing me to the island, hut life, and for establishing data loggers and trialling the study design with me. I am very grateful to John Burgess, whose unfailing good spirit and will, meant that together we established monitoring sites all over the island in 2016/17. Similarly to Rowena Hannaford in 2017/18, thank you for spending your summer helping me to collect data across the plateau, fitting in just one more site for the day and making the adventures fun. Thank you to George Brettingham-Moore, Alison Skinn, and Alex Fergus for all their help with *Azorella* surveys. In addition, more generally to the Macquarie Island 69th and 70th ANARE teams, who carried gear

all over the island, provided words of local advice and support. Being on Macquarie Island with a tribe of botanists was a delight – thanks for all the botanising between sites and around station. Special mention to the sub-Antarctic skuas who quickly demonstrated that the data logger housings were not quite fit-for-purpose, which resulted in an over-engineered solution, heavy packs, but most importantly a full data set. Thank you to Amie Turner-Brown for systematically scanning tiny leaves and counting spines in the lab with such great humour.

Specifically for the following chapters. **Chapter 1:** Thank you to the Department of Primary Industries, Parks, Water and Environment (DPIPWE) for the provision of historical *Azorella* site data (2 m x 2 m) and provision of permits for both field seasons (TFL16276 and TFL17165). **Chapter 3:** I would like to thank all the workshop participants for their insights and contribution. Australian Antarctic Division (AAD): Dana Bergstrom, Ben Raymond, Kate Kiefer, Aleks Terauds. DPIPWE: Micah Visoiu. Royal Tasmanian Botanical Gardens (RTBG): Natalie Tapson. Macquarie University: Patricia Selkirk. Monash University: Melodie McGeoch. University of Tasmania (UTas): Phillippa Bricher, Jennie Whinam. University of Queensland (UQ): Justine Shaw. **Chapter 4:** Similarly, I would like to thank all of the final *A. macquariensis* workshop participants for their contribution and valuable discussion points. AAD: Dana Bergstrom, Ben Raymond, Aleks Terauds. DPIPWE: Noel Carmichael, Micah Visoiu. RTBG: Lorraine Perrins, Natalie Tapson, James Wood. Dept. of Environment and Energy: Peter Latch. UTas: Jennie Whinam. Monash: Melodie McGeoch.

This research was supported by an Australian Government Research Training Program (RTP) Scholarship and an Australian Government grant under an Australian Antarctic Science Program Grant no. 4312. Additional support was provided by The Holsworth Wildlife Research Endowment and The Ecological Society of Australia, and the Denis and Maisie Carr Award, which allowed me to stay dry in the field, and travel to interstate conferences and the AAD to progress my research.

I would particularly like to thank my friends who supported me through PhD life. Specifically, thank you to the McGeoch lab, past and present, for numerous coffee problem-solving chats. More widely to all the great friends who joined me along the way, in Melbourne, South Australia, and Hobart, providing much-needed bushwalking, phone calls and café interludes, with friendly faces, cake and Hobart accommodation whenever required. Finally, thank you to Mum, and my Melbourne and New Zealand families, for all the love and support throughout the years.

Table of Contents

Abstract	ii
Publications during enrolment	iv
Thesis including published works declaration	v
Acknowledgements	vii
General Introduction	1
Background	1
Southern ocean islands and Macquarie Island.....	4
Rationale and thesis aims	5
Study system and <i>Azorella</i> as a keystone species	8
Thesis outline	10
References	13
Chapter 1. Spatial variation in the ongoing and widespread decline of a keystone plant species	21
Abstract	22
Introduction	22
Methods	23
Results	27
Discussion	29
Prospects	33
Acknowledgements	34
References	34
Appendix A (S1.)	37
Appendix A (S2.)	52
Chapter 2. Fine-scale variability and drivers of dieback in a keystone cushion plant on sub-Antarctic Macquarie Island	56
Introduction	57
Materials and methods	60
Results	73
Discussion	81
Conclusion	87
References	88
Appendix B	95

Chapter 3. Understanding ecosystem change using qualitative modelling: sub-Antarctic fellfield on Macquarie Island

107

Introduction	108
Study system.....	110
Modelling methods	112
Results	120
Discussion	134
Conclusion	137
References	139
Appendix C1	145
Appendix C2	155

Chapter 4. Conservation options for a sub-Antarctic keystone species threatened by climate change

159

Introduction	160
Methods	163
Results and discussion	166
(i) Clarification of the decision context.....	166
(ii) Definition of the conservation vision, management objectives and desired outcomes	177
(iii) Develop alternatives and (iv) estimate consequences	177
The way forward	197
References	199
Appendix D	209

General Discussion

212

Conclusion	216
References	218

General introduction

Background

Accelerated global climate change has occurred since the mid-20th century and has resulted in increased variability, higher temperatures and altered precipitation regimes (Field et al. 2014). These changes occur as either long-term climate ‘presses’ (i.e. consistent rise in temperatures, sea level, or a decrease in rainfall) or alternatively as extreme climate ‘pulses’ (i.e. floods, fire, cyclones, or heat waves) (Harris et al. 2018). The largest contribution to the drivers of global climate change is the increase in the anthropogenic atmospheric concentration of CO₂ (Intergovernmental Panel on Climate Change, IPCC 2013). Since the late 19th century there has been a consistent rise in the global average of the combined land and ocean surface temperature of 0.78°C (range 0.72 to 0.85) (IPCC 2013). Climate models show that under all representative concentration pathways (RCP), except for the conservative RCP2.6 scenario, the climate will continue to warm during the 21st century, exceeding 1.5 °C above the historical average. These changes to temperature will include increasingly high extreme maximum temperatures and decreasing extreme minimum temperatures. The climate has also become more variable with more extreme events since 1950. The climate has also become more variable with more extreme events since 1950, for example, increased heavy precipitation events, increased warm days and nights, and a decline in freezing events (IPCC 2013). The occurrence of extreme climatic events is expected to continue (IPCC 2013). The precipitation response under projected change will vary across the world, but continue to become increasingly variable, where historically dry regions will get drier and wet regions wetter (IPCC 2013)

The change in climate, and in particular the increased variation with an increasing number of extreme events, are altering species’ distributions, abundance and phenology (Parmesan and Yohe 2003; Pecl et al. 2017; Harris et al. 2018). Those species with limited dispersal ability or with narrow distributions, such as those in alpine zones or on islands, are most at risk from changes in climate variability and extremes (Settele et al. 2014). Despite the large change in climatic variables, species’ extinctions, or substantial reductions in their conservation status, are often driven by the indirect consequences of climate change (Cahill et al. 2013; Ockendon et al. 2014). Common indirect effects of climate change include changes in habitat availability, food resources, predation, phenology, pollination interactions, and pathogen exposure (Cahill

et al. 2013; Ockendon et al. 2014). For example, a well-known example of both direct and indirect climate threats affecting multiple taxa on a landscape-scale is the decline in amphibian distribution and abundance across Central and South America, in response to increased climate variability and temperature, and the indirect threat of improved conditions for the amphibian chytrid fungus *Batrachochytrium dendro* (Rohr and Raffel 2010). Increasingly, climate change is also resulting in cases of mass plant mortality across a diverse range of ecosystems (see Harris et al. 2018; Hoffmann et al. 2019), and often of foundation species (i.e. dominant species that determine the diversity of associated taxa and modulate nutrients or energy within the system, Ellison 2019). Global examples of mass plant mortality in response to climate change include: (i) the death of 7 400 ha of tropical mangroves in northern Australia in 2015/16 in response to drought, extreme temperatures and a drop in sea level (Duke et al. 2017); (ii) dieback of 20 % of trembling aspen (*Populus tremuloides* Michx.) during severe drought in western North America (Michaelian et al. 2011); and (iii) widespread canopy mortality affecting 1.5% of dominant eucalypt and banksia species over 1 350 ha in Southwest Western Australia, following drought and extreme heat (Matusick et al. 2013). The negative consequences of current and projected climate change, such as the loss of long-lived foundation species, will be substantial for biodiversity, their biotic interactions and ecosystem services (Settele et al. 2014; Valiente-Banuet et al. 2015; Pecl et al. 2017).

Under a changing climate, climate refugia are increasingly important for the survival of long-lived species (Ashcroft 2010; Keppel et al. 2015). Climate refugia are created by complex topography, which decouples the local microclimate from the surrounding macroclimate, through a change in elevation, slope or aspect (Ashcroft 2010; Dobrowski 2011). Therefore, topographically complex areas with a large elevation change are more buffered from climate change effects, potentially allowing species to persist under more suitable, stable climate conditions (Suggitt et al. 2011; Graae et al. 2018). Considering climate at an appropriately fine-scale is important for determining appropriate conservation actions and refugia, because species' condition and distribution respond closely to fine-scale climate variation (Körner and Hiltbrunner 2018). In alpine systems, plants such as cushion-plants and bryophytes are very low growing and particularly influenced by near-ground and soil temperatures, and hence respond strongly to the associated microclimates (Körner and Hiltbrunner 2018). Consequently, microrefugial models are increasingly used to determine areas of conservation significance (Lenoir et al. 2017; Lembrechts et al. 2019; Maclean 2020), despite the challenges of capturing fine-scale climate variation and linking local scale variation to coarse-resolution simulations

of future climates (Baker et al. 2017). The identification and management of future climate refugia, at an appropriately fine-scale, is essential for effective conservation management to maintain biological diversity over the long-term (Keppel et al. 2015).

To identify effective refugia, it is important to understand the ecological requirements and necessary biotic interactions of the focal species. The interactions between biotic systems and climate change variables are notoriously complex, and often have nonlinear responses that have limited predictability with sudden changes (Folke et al. 2004; Walther 2010). These non-linear and sudden responses to climate change may lead to a regime shift, where the system moves from one stable state to another (Folke et al. 2004; Walther 2010), which can ultimately result in ecological collapse (Bland et al. 2018). Biotic interactions may help buffer against ecological collapse, by mediating some of the direct and indirect effects of climate through individual species, and therefore improving ecosystem resilience (Valiente-Banuet et al. 2015). The loss of one keystone¹ species, a species that has a disproportionate effect on the ecological function of the system (Jones et al. 1994), or foundation species, a dominant species that similarly facilitates biotic diversity but also stabilises ecosystem processes (Ellison et al. 2005), can therefore result in the subsequent loss of multiple dependent species (Valiente-Banuet et al. 2015). This loss of the keystone or foundation species may then potentially trigger the initiation of a regime shift. However, regime shifts, and ultimately ecosystem collapse, are particularly hard to predict, because of the complexity of biotic interaction and the potential for multiple drivers of change (Petraitis 2013).

To undertake evidence-based conservation that effectively addresses climate change threats, a strong evidence base is required to facilitate effective and strategic conservation decisions (Sutherland et al. 2004). Conservation evidence is particularly important when managing species threatened by climate change, because the outcomes of potential recovery actions have a high level of associated uncertainty, due to the potential for complex non-linear interactions between multiple species (see Hoepfner and Hughes 2019). To develop an evidence-base, strategic (often long-term) biotic and abiotic monitoring is needed, which clearly defines the question and has a rigorous study design with the power to answer the associated question

¹ I use the term keystone here, as it has been previously been used to describe the role of *Azorella* species, which have properties of a keystone species (Hugo et al. 2004, le Roux et al. 2005, Nyakatia & McGeoch 2008). More recently, dominant plants that fulfil this role and stabilise ecosystem processes have been referred to as foundation species, with the use of 'keystone' restricted to herbivores and predators only (Ellison et al. 2005, Ellison 2019). While *Azorella* species may be the dominant vascular species in fellfield ecosystems, they have highly variable cover that at times is very low, particularly in comparison to the non-vascular bryophytes (Selkirk 2012), requiring the term foundation species to be used with nuance.

(Lindenmayer and Likens 2010). The resultant baseline data can then be used in qualitative and quantitative models, to clarify the ecosystem structure, interaction strengths, and identify drivers and thresholds of change (see examples in Petraitis 2013; Bland et al. 2018). Similarly, baseline biotic and abiotic data provides the ability to develop microrefugial models, identifying areas within the landscape where the species or ecosystem may persist in the future (see Ashcroft and Gollan 2013; Lenoir et al. 2017; Maclean et al. 2017). Baseline data, together with model outcomes and considered engagement with key stakeholders, can then be used to make strategic evidence-based conservation management decisions, to provide the highest likelihood of success and the most effective use of the increasingly limited conservation funding (see Sutherland et al. 2004).

Southern ocean islands and Macquarie Island

The effect of climate change is particularly apparent at high latitudes, with accelerated warming of more than 1°C in the last 40 to 50 years in the Antarctic Ocean and southern ocean islands (SOI) in the sub-Antarctic (Frénot et al. 2005). Historically the sub-Antarctic islands were described as cool, windy and wet environments with highly equable climates (Adamson et al. 1988; Bergstrom and Chown 1999; Pendlebury and Barnes-Keoghan 2007). However, since the 1960s the climate of many sub-Antarctic islands is changing to one that is warmer, windier, predominantly drier, and with greater variation in weather extremes (Adamson et al. 1988; Frénot et al. 1997; Tweedie and Bergstrom 2000; le Roux and McGeoch 2008a; Adams 2009). The change in climate across the sub-Antarctic islands is not consistent. For example, the change in precipitation is particularly variable between islands, with Îles Kerguelen, Marion and Prince Edward Islands experiencing significantly decreased annual precipitation (Frénot et al. 1997; le Roux and McGeoch 2008a; Lebouvier et al. 2011), while the more southerly Macquarie Island has 55% more precipitation during winter, and 30% higher annual precipitation (Bergstrom et al. 2015). Some of the most well-documented changes have occurred on Marion Island, which has had an above average 1.2 °C increase in mean temperatures since 1966, and an annual decrease in rainfall of 25 mm.yr⁻¹ to 2000 (le Roux and McGeoch 2008a). It is likely that the greatest impact on Marion Island species has occurred from a significant increase in climatic variability in combination with a drier climate (le Roux and McGeoch 2008a).

Similar to global trends, the change in climate is resulting in altered species distributions, abundance, and condition on the southern ocean islands. On the rapidly warming Marion Island,

vascular plants have moved up elevation at a rate of $3.4 \pm 0.8 \text{ m.yr}^{-1}$ from 1966, resulting in a reorganisation of communities on the island (le Roux and McGeoch 2008b). On Macquarie Island coastal plant species have increased in cover and / or abundance with a changing climate (Scott and Kirkpatrick 2013). While the resultant trend of changing climates is not as clear on Îles Kerguelen, affecting different species differently, *Acaena magellanica* (Lam.) Vahl (Rosaceae) has also increased in distribution with warming climates (Frénét et al. 1997). In contrast, dieback occurred in *Azorella selago* Hook. (Apiaceae) populations on several islands in Îles Kerguelen following a period of low annual rainfall in the mid-late 1990s, which was the first observation indicating this species might be sensitive to drought (Frénét et al. 1997). Experimental research on *A. selago* on Marion Island that simulated the potential climate change impacts of reduced rainfall and increased shade (an indirect effect of increased temperature), resulted in increased stem death, confirming the sensitivity of *A. selago* to changing conditions (le Roux et al. 2005). The milder climate on the southern ocean islands is increasing invasive species' ability to establish (Frénét et al. 2005; Lebouvier et al. 2011; Chown et al. 2012; Perterra et al. 2016) and exacerbating their impact (Phiri et al. 2009; McClelland et al. 2018). The changing distribution of native species, and the increasing potential of establishment and impact of invasive species are resulting in unexpected biological responses to climate on these islands. These species' responses provide a valuable opportunity to undertake research in a comparatively biotically simple system. Providing a better understanding of the complex biotic responses to climate change, which will have application not only across the other southern ocean islands but more generally across more complex global systems (Bergstrom and Chown 1999).

Rationale and thesis aims

Over the past 40 years the climate of sub-Antarctic Macquarie Island (Fig. 1) has changed (Bergstrom et al. 2015). Observations suggest the climate is moving to a system with higher wind speed, increased but more episodic rainfall, a drier background atmosphere (Adamson et al. 1988; Adams 2009), with less cloud cover and more sunshine hours (Bergstrom et al. 2015). In the 2008/2009 Austral summer, the keystone endemic species *Azorella macquariensis* Orchard (Macquarie cushions, Apiaceae, Fig. 2a-d) and bryophytes in the associated fellfield (also referred to as fjeldmark or feldmark) ecosystem underwent a rapid decline in condition

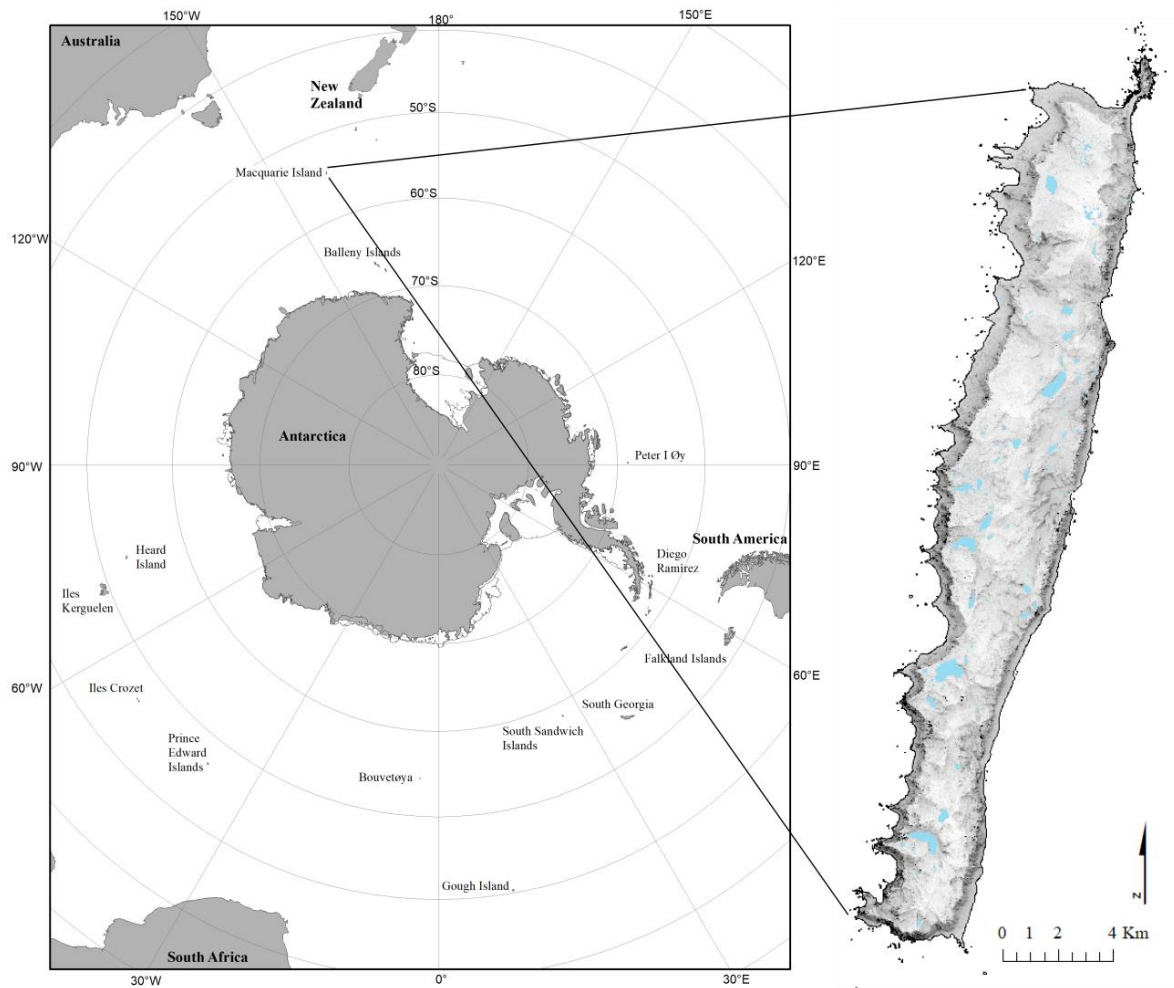


Fig. 1. The location of Macquarie Island, in the context of the southern ocean islands (S40° – S50°), with a more detailed hill-shaded relief of Macquarie Island, showing the general topography across the undulating plateau.

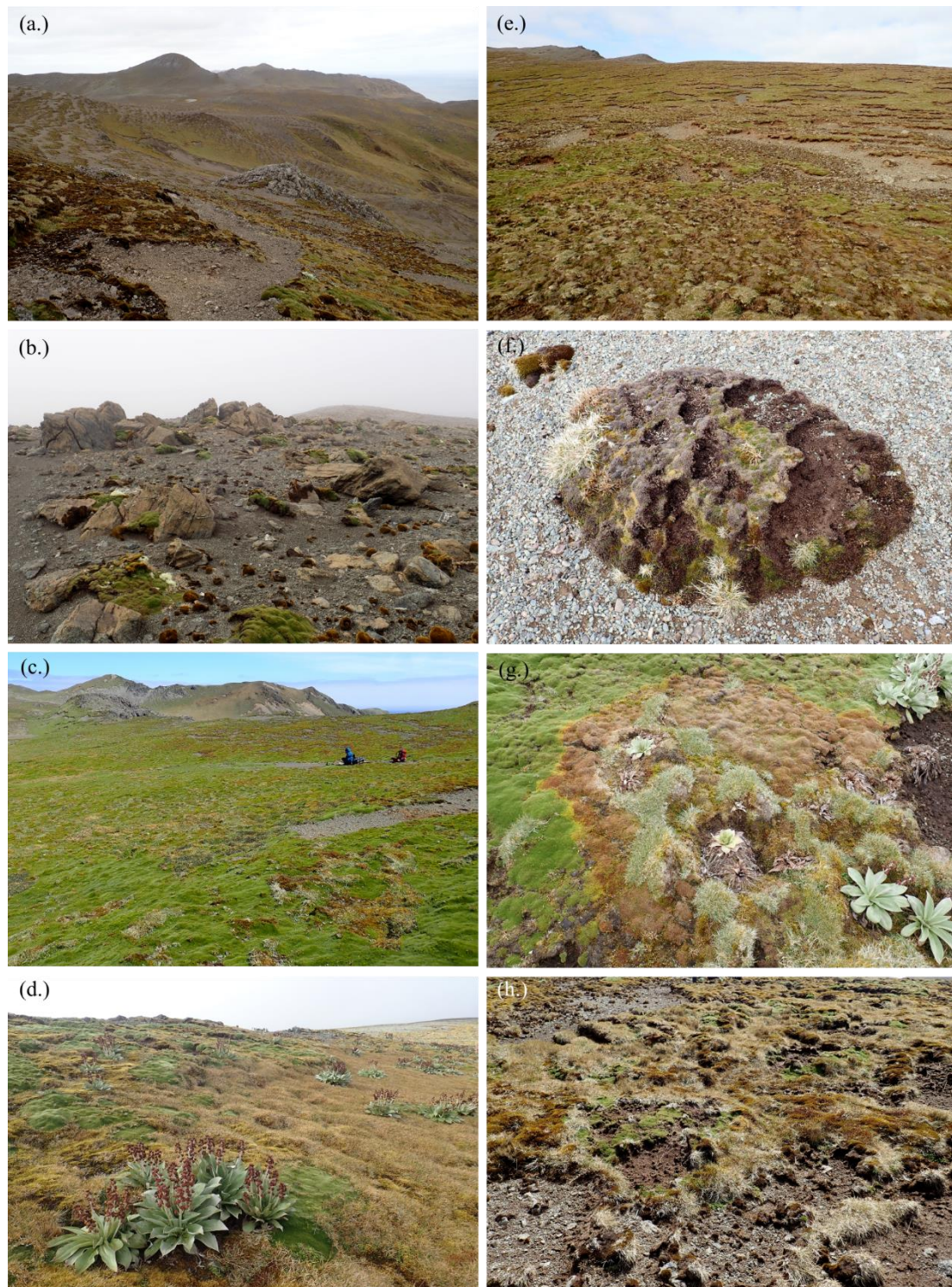


Fig. 2. The patterned Macquarie Island fellfield landscape dominated by *Azorella macquariensis* (Macquarie cushions) and associated bryophytes (a.), sparse cushions on Boot Hill (b.), extensive *A. macquariensis* carpets in the south of the island (c.), and cushions within a short-grassland ecosystem (d.). Examples of *A. macquariensis* dieback across a variety of habitats (e. – h.), noting the large area of dieback radiating out from the camera and additional dieback areas in the background naturally thin carpets (e.), the loss of canopy integrity (f.), the simultaneous dieback of *A. macquariensis* and *Pleurophyllum hookeri* Hook. (Asteraceae) (g.) and, the peat ‘holes’ in a short-grassland, previously occupied by cushions (h.).

across the island (Whinam et al. 2014; Bergstrom et al. 2015). Dieback (Fig. 2e-h) was recorded at 88% of 115 island-wide sites in 2008/2009 (Bergstrom et al. 2015). This change resulted in its listing as critically endangered under the Environment Protection and Biodiversity Conservation (EPBC) Act 1999 (TSSC 2010). Initial research hypothesised that 17 consecutive years of low summer plant available water leading up to the event was the primary driver of *A. macquariensis* dieback (Bergstrom et al. 2015). The weakened plants were hypothesised to be more susceptible to a secondary pathogenic infection as a result of climatic stress (Bergstrom et al. 2015). What appears to be the main pathogen is expressed as a yellow chlorosis line that moves across the cushion (Whinam et al. 2014). However, the drivers of dieback and the response of the ecosystem remained untested, which limited the ability to provide well-informed conservation advice.

In this thesis, I aim to overcome key limits to understanding the system by quantifying the response, changing interactions and condition of *Azorella macquariensis* and the surrounding fellfield ecosystem to the changing climate. I then draw on this new evidence to inform strategic conservation management through the provision of recommended recovery actions and research priorities.

Study system and *Azorella* as a keystone species

Macquarie Island (54°30'S, 158°55'E) is a small sub-Antarctic Island of 12,390 ha, 34 km long and no more than 5km wide, orientated slightly northeast to southwest (Selkirk et al. 1990) (Fig.1). The island is one of three Australian sub-Antarctic islands, located approximately 1500 km southeast from Tasmania to Antarctica. Macquarie Island was listed as World Heritage in 1997 for its unique geological features (criterion viii), and its exceptional natural beauty and phenomena (criterion vii) (Parks and Wildlife Service 2006).

The island is characterised by a low undulating alpine plateau interspersed with lakes, tarns, and bogs, ranging from 200 m above sea level (asl) and to 435m asl at the highest point in the south of the island (Selkirk et al. 1990). Macquarie Island supports 47 vascular flora species (Flora of Australia 1993; Selkirk 2012), including three extant weed species (Williams et al. 2019). However, the highest flora diversity is recorded in the non-vascular species, with a further 86 species of mosses and 51 species of liverworts (Selkirk et al. 1990). The sparse fellfield ecosystem (< 50% cover) dominates the Macquarie Island plateau, supporting a low

diversity of both vascular and non-vascular flora, including 18 vascular plant species, 18 mosses, 12 liverworts and 14 lichen species (Selkirk 2012). The study species, *Azorella macquariensis*, is the dominant vascular plant on the plateau, with a highly variable cover that typically ranges between 0.60 – 49.85 % (Selkirk 2012) (Fig 2a-d).

The genus *Azorella* Lamarck (Apiaceae) contains 27 species that are widespread across fellfield (alpine – sub-alpine) ecosystems in the sub-Antarctic, southern South American steppes and altiplano highlands of the southern and central Andes (Nicolas and Plunkett 2012). Following new phylogenetic analyses of nuclear rDNA spacers (ITC and ETS), the taxonomy of this genus has been reassessed and a case made for the inclusion of the *Huanaca*, *Mulinum*, *Schizeilema*, *Laretia* and *Stilbocarpa* genera within the *Azorella* genus, resulting in *Azorella* containing 58 species in 10 sections (Plunkett and Nicolas 2017). This thesis follows the taxonomy used by the Royal Tasmanian Botanical Gardens (Australia), who have yet to adopt Plunkett and Nicolas (2017). *Azorella* are long-lived species with slow growth rates (Frénot et al. 1993; Frénot et al. 1998), where many individuals have been estimated to be older than 80 years (le Roux and McGeoch 2004) and in some cases estimated to be up to ~700 years (Kleier and Rundel 2004). The cushion growth form of *Azorella* is common to many other alpine or desert species and is important for ameliorating water loss and temperature within the cushion, through the overall reduction of mechanical wind stress (Ashton and Gill 1965; He et al. 2014).

Azorella species are an important component of the fellfield ecosystem and are also considered ecosystem engineers, i.e. that the species create, modify and maintain a habitat that facilitates other species, or landscape processes, through the modification of both abiotic and biotic components of a system (see Jones et al. 1994). *Azorella* have been shown to ameliorate extreme temperatures, water availability and concentrate nutrient and soil organic carbon resources within their canopy (Barendse and Chown 2001; Arroyo et al. 2003; Cavieres et al. 2007; Nyakatya and McGeoch 2008; Almeida et al. 2013). The genus is well known to have an overall positive effect on the species richness of the surrounding vascular flora community under increasing abiotic stress, significantly affecting community diversity and structure in the Andes and sub-Antarctic (e.g. Arredondo-Nunez et al. 2009; Cavieres and Badano 2010; le Roux et al. 2013; Raath-Krüger et al. 2019). *Azorella* species are also important for microarthropod communities, with significantly higher abundance and a different composition beneath *Azorella* cushions in comparison to the surrounding fellfield ecosystems (Barendse and Chown 2001; Hugo et al. 2004; Bergstrom et al. 2015).

Thesis outline

This thesis focusses on quantifying the environmental conditions that drive dieback severity and extent, and the consequence of these relationships for the fellfield ecological community. In the thesis the first two chapters quantify the variation in island-wide dieback at different scales, with the purpose of identifying physical correlates of dieback extent under current climate conditions. The third chapter uses qualitative models to better understand the drivers of change in cushion condition and the complex response of the fellfield ecosystem to climate change. The fourth chapter uses a strategic decision making framework, integrating the knowledge gained from this thesis, together with published case studies, to provide recommended recovery actions for *A. macquariensis* and the associated fellfield ecosystem. Each of the four data chapters are written as standalone publications, hence, there is some repetition of the study system description and key threatening processes across the chapters.

In **Chapter 1**, the variation of *A. macquariensis* cover and condition (dieback) were quantified across both geographic and environmental space, to provide a spatially representative baseline for monitoring future change, and the first island-wide assessment of condition since 2012. Bergstrom et al. (2015)'s original hypothesis suggested that dieback extent was positively related to high evapotranspiration rates. Clarifying the relationship between local climate variation and dieback would provide important evidence for the role of climate change in the ongoing dieback of *A. macquariensis*, and provide the ability to identify climate refugia for *A. macquariensis*. In this chapter I test the relationship between dieback extent and high evapotranspiration rates, using topographically-derived proxies for evapotranspiration (27 m² resolution), based on the well-described relationship between topography and microclimate (see Dobrowski 2011).

In **Chapter 2**, fine-scale cushion condition classes were developed and used in combination with microclimate data, to provide a better understanding of the drivers of dieback progression across Macquarie Island. The condition and distribution of plants are known to vary in response to climate on a fine-scale. Therefore to draw appropriate conclusions about a species' response to local change, it is necessary to use data at an appropriately fine-scale (Körner and Hiltbrunner 2018). Microclimate was modelled at a site scale (27 m²) to allow for both an island-wide coverage and comparatively fine site-scale air measurements at the height representative of *A. macquariensis* canopies. Although the pathogen or pathogens involved clearly play a significant role, attempts by other research groups to date to identify them have

been largely unsuccessful. Pursuing the identity and biology of the apparent pathogen complex was not part of the aim of this thesis. In this chapter, a microclimate model was used to test support for two conceptual mechanistic dieback models, where dieback extent was either related to microclimate conditions that (i) cause plant water-stress, and/or (ii) pathogen activity, which might be acting additively or synergistically. The results of the chapter provide a better understanding of the progression of *A. macquariensis* dieback and the characteristics of natural southern refugia, to better inform baseline information for future monitoring.

In **Chapter 3**, qualitative modelling methods are used to describe and test the response of the *Azorella*-centred fellfield ecosystem to the direct and indirect threats of climate change. A state-transition diagram incorporates the knowledge gained from the qualitative models and previous chapters to describe the transition of cushion condition in response to multiple drivers of change on the fellfield. Predicting the response of biotic systems to climate change is complex (Petraitis 2013), therefore the comparatively biotically simple Macquarie Island fellfield (Selkirk et al. 1990) provided a good model system to test and describe such responses. The models used in chapter 3 provide a more structured and precise understanding of the complex interactions on the fellfield, including the response of keystone *A. macquariensis* to current and predicted environmental change. This articulation of the process of fellfield ecosystem collapse, through the loss of underpinning keystone interactions, provides an important step in describing the risk of ecosystem collapse by clarifying and communicating assumptions (see Bland et al. 2018). The outcomes of this chapter provide clear future hypotheses to be tested, but most importantly demonstrate the need for time-critical management and research.

Chapter 4 synthesises the new knowledge gained from Chapters 1 to 3, updating the causal pathway model (Hoffmann et al. 2019) describing direct and indirect drivers of *A. macquariensis* dieback, and subsequently recommends recovery actions to maintain ecosystem function. While a growing number of Australian and international threatened species and ecological community recovery plans discuss the threats of climate change, very few plans recommend actions to address climate threats or have the boldness to improve the species' conservation status in the long-term (Hoeppner and Hughes 2019). I use a structured decision making framework (Gregory et al. 2012) to identify the full range of potential recovery actions for *A. macquariensis* and fellfield ecosystem to maintain ecosystem function. I go on to discuss the associated advantages and potential risks of uncertain outcomes for high intervention recovery actions, to facilitate informed future conservation management decisions. Given the

ongoing, pervasive dieback described in Chapters 1 to 3, Chapter 4 emphasises the need for research and recovery actions to be time-critical and undertaken simultaneously.

Finally, in the **general discussion**, I discuss the implications of the results of this thesis more broadly for the sub-Antarctic and high altitude ecological communities under current and projected climate change, and the subsequent consequences for their conservation status.

References

- Adams, N., 2009. Climate trends at Macquarie Island and expectations of future climate change in the sub-Antarctic. *Papers and proceedings of the Royal Society of Tasmania* 143, 1-8.
- Adamson, D., Whetton, P., Selkirk, P.M., 1988. An analysis of air temperature records for Macquarie Island: decadal warming, ENSO cooling and southern hemisphere circulation patterns. *Papers and proceedings of the Royal Society of Tasmania* 122, 107-112.
- Almeida, J.P., Montufar, R., Anthelme, F., 2013. Patterns and origin of intraspecific functional variability in a tropical alpine species along an altitudinal gradient. *Plant Ecology & Diversity* 6, 423-433.
- Arredondo-Nunez, A., Badano, E.I., Bustamante, R.O., 2009. How beneficial are nurse plants? A meta-analysis of the effects of cushion plants on high-Andean plant communities. *Community Ecology* 10, 1-6.
- Arroyo, M.T.K., Cavieres, L.A., Penaloza, A., Arroyo-Kalin, M.A., 2003. Positive associations between the cushion plant *Azorella monantha* (Apiaceae) and alpine plant species in the Chilean Patagonian Andes. *Plant Ecology* 169, 121-129.
- Ashcroft, M.B., 2010. Identifying refugia from climate change. *Journal of Biogeography* 37, 1407-1413.
- Ashcroft, M.B., Gollan, J.R., 2013. Moisture, thermal inertia, and the spatial distributions of near-surface soil and air temperatures: Understanding factors that promote microrefugia. *Agricultural and Forest Meteorology* 176, 77-89.
- Ashton, D.H., Gill, A.M., 1965. Pattern and Process in a Macquarie island Feldmark. *Proceedings Of The Royal Society Of Victoria* 79, 235-248.
- Baker, D.J., Hartley, A.J., Pearce-Higgins, J.W., Jones, R.G., Willis, S.G., 2017. Neglected issues in using weather and climate information in ecology and biogeography. *Diversity and Distributions* 23, 329-340.
- Barendse, J., Chown, S.L., 2001. Abundance and seasonality of mid-altitude fellfield arthropods from Marion Island. *Polar Biology* 24, 73-82.
- Bergstrom, D.M., Bricher, P.K., Raymond, B., Terauds, A., Doley, D., McGeoch, M.A., (. . .) Ball, M.C., 2015. Rapid collapse of a sub-Antarctic alpine ecosystem: the role of climate and pathogens. *Journal of Applied Ecology* 52, 774-783.
- Bergstrom, D.M., Chown, S.L., 1999. Life at the front: history, ecology and change on southern ocean islands. *Trends in Ecology & Evolution* 14, 472-477.

- Bland, L.M., Rowland, J.A., Regan, T.J., Keith, D.A., Murray, N.J., Lester, R.E., (. . .)
Nicholson, E., 2018. Developing a standardized definition of ecosystem collapse for risk
assessment. *Frontiers in Ecology and the Environment* 16, 29-36.
- Cahill, A.E., Aiello-Lammens, M.E., Fisher-Reid, M.C., Hua, X., Karanewsky, C.J., Yeong
Ryu, H., (. . .) Wiens, J.J., 2013. How does climate change cause extinction? *Proceedings
of the Royal Society B: Biological Sciences* 280, 20121890.
- Cavieres, L.A., Badano, E.I., 2010. Consequences of Facilitation on Species Diversity in
Terrestrial Plant Communities. *Positive Plant Interactions and Community Dynamics*, 39-
57.
- Cavieres, L.A., Badano, E.I., Sierra-Almeida, A., Molina-Montenegro, M.A., 2007.
Microclimatic modifications of cushion plants and their consequences for seedling survival
of native and non-native herbaceous species in the high Andes of central Chile. *Arctic
Antarctic and Alpine Research* 39, 229-236.
- Chown, S.L., Huiskes, A.H.L., Gremmen, N.J.M., Lee, J.E., Terauds, A., Crosbie, K., (. . .)
Bergstrom, D.M., 2012. Continent-wide risk assessment for the establishment of
nonindigenous species in Antarctica. *Proceedings of the National Academy of Sciences* 109,
4938-4943.
- Dobrowski, S.Z., 2011. A climatic basis for microrefugia: the influence of terrain on climate.
Global Change Biology 17, 1022-1035.
- Duke, N.C., Kovacs, J.M., Griffiths, A.D., Preece, L., Hill, D.J.E., van Oosterzee, P., (. . .)
Burrows, D., 2017. Large-scale dieback of mangroves in Australia's Gulf of Carpentaria: a
severe ecosystem response, coincidental with an unusually extreme weather event. *Marine
and Freshwater Research* 68, 1816-1829.
- Ellison, A.M., 2019. Foundation Species, Non-trophic Interactions, and the Value of Being
Common. *iScience* 13, 254-268.
- Ellison, A.M., Bank, M.S., Clinton, B.D., Colburn, E.A., Elliott, K., Ford, C.R., (. . .) Webster,
J.R., 2005. Loss of foundation species: consequences for the structure and dynamics of
forested ecosystems. *Frontiers in Ecology and the Environment* 3, 479-486.
- Field, C.B., Barros, V.R., Mach, K.J., Mastrandrea, M.D., Aalst, M.v., Adger, W.N., (. . .)
Yohe, G.W., 2014. Technical Summary, In *Climate Change 2014: Impacts, Adaptation, and
Vulnerability. Part A: Global and Sectoral Aspects. Contribution of Working Group II to the
Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. eds C.B. Field,
V.R. Barros, D.J. Dokken, K.J. Mach, M.D. Mastrandrea, T.E. Bilir, (. . .) L.L. White, pp.
35-94. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

- Flora of Australia, 1993. Flora of Australia, vol. 50, Oceanic Islands 2. Australian Government Publishing Service, Canberra.
- Folke, C., Carpenter, S., Walker, B., Scheffer, M., Elmqvist, T., Gunderson, L., Holling, C.S., 2004. Regime Shifts, Resilience, and Biodiversity in Ecosystem Management. *Annual Review of Ecology, Evolution, and Systematics* 35, 557-581.
- Frénét, Y., Chown, S.L., Whinam, J., Selkirk, P.M., Convey, P., Skotnicki, M., Bergstrom, D.M., 2005. Biological invasions in the Antarctic: extent, impacts and implications. *Biological Reviews* 80, 45-72.
- Frénét, Y., Gloaguen, J., Trehen, P., 1997. Climate change in Kerguelen Islands and colonization of recently deglaciated areas by *Poa Kerguelensis* and *P. annua*. Antarctic communities: species, structure and survival, B. Battaglia, J. Valencia et DWH Walton eds., Cambridge University Press, Cambridge, 358-366.
- Frénét, Y., Gloaguen, J.C., Cannavacciuolo, M., Bellido, A., 1998. Primary succession on glacier forelands in the subantarctic Kerguelen Islands. *Journal of Vegetation Science* 9, 75-84.
- Frénét, Y., Gloaguen, J.C., Picot, G., Bougere, J., Benjamin, D., 1993. *Azorella selago* Hook - used to estimate glacier fluctuations and climatic history in the Kerguelen Islands over the last 2 centuries. *Oecologia* 95, 140-144.
- Graae, B.J., Vandvik, V., Armbruster, W.S., Eiserhardt, W.L., Svenning, J.-C., Hylander, K., (. . .) Lenoir, J., 2018. Stay or go – how topographic complexity influences alpine plant population and community responses to climate change. *Perspectives in Plant Ecology, Evolution and Systematics* 30, 41-50.
- Gregory, R., Failing, L., Harston, G., Long, G., McDaniels, T., Ohlson, D., 2012. Structured decision making: A practical guide to environmental management choices. Wiley-Blackwell, Chichester, West Sussex.
- Harris, R.M.B., Beaumont, L.J., Vance, T.R., Tozer, C.R., Remenyi, T.A., Perkins-Kirkpatrick, S.E., (. . .) Bowman, D.M.J.S., 2018. Biological responses to the press and pulse of climate trends and extreme events. *Nature Climate Change* 8, 579-587.
- He, Y., Kueffer, C., Shi, P., Zhang, X., Du, M., Yan, W., Sun, W., 2014. Variation of biomass and morphology of the cushion plant *Androsace tapete* along an elevational gradient in the Tibetan Plateau. *Plant Species Biology* 29, E64-E71.
- Hoepfner, J.M., Hughes, L., 2019. Climate readiness of recovery plans for threatened Australian species. *Conservation Biology* 33, 534-542.

- Hoffmann, A.A., Rymer, P.D., Byrne, M., Ruthrof, K.X., Whinam, J., McGeoch, M., (. . .) Williams, S.E., 2019. Impacts of recent climate change on terrestrial flora and fauna: Some emerging Australian examples. *Austral Ecology* 44, 3-27.
- Hugo, E.A., McGeoch, M.A., Marshall, D.J., Chown, S.L., 2004. Fine scale variation in microarthropod communities inhabiting the keystone species *Azorella selago* on Marion Island. *Polar Biology* 27, 466-473.
- IPCC, 2013. Summary for Policymakers, In *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. eds T.F. Stocker, D. Qin, G.-K. Plattner, M. Tignor, S.K. Allen, J. Boschung, (. . .) P.M. Midgley. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.
- Jones, C.G., Lawton, J.H., Shachak, M., 1994. Organisms as ecosystem engineers. *Oikos* 69, 373-386.
- Keppel, G., Mokany, K., Wardell-Johnson, G.W., Phillips, B.L., Welbergen, J.A., Reside, A.E., 2015. The capacity of refugia for conservation planning under climate change. *Frontiers in Ecology and the Environment* 13, 106-112.
- Kleier, C., Rundel, P.W., 2004. Microsite requirements, population structure and growth of the cushion plant *Azorella compacta* in the tropical Chilean Andes. *Austral Ecology* 29, 461-470.
- Körner, C., Hiltbrunner, E., 2018. The 90 ways to describe plant temperature. *Perspectives in Plant Ecology, Evolution and Systematics* 30, 16-21.
- le Roux, P.C., McGeoch, M.A., 2004. The use of size as an estimator of age in the subantarctic cushion plant, *Azorella selago* (Apiaceae). *Arctic Antarctic and Alpine Research* 36, 509-517.
- le Roux, P.C., McGeoch, M.A., 2008a. Changes in climate extremes, variability and signature on sub-Antarctic Marion Island. *Climatic Change* 86, 309-329.
- le Roux, P.C., McGeoch, M.A., 2008b. Rapid range expansion and community reorganization in response to warming. *Global Change Biology* 14, 2950-2962.
- le Roux, P.C., McGeoch, M.A., Nyakatya, M.J., Chown, S.L., 2005. Effects of a short-term climate change experiment on a sub-Antarctic keystone plant species. *Global Change Biology* 11, 1628-1639.
- le Roux, P.C., Shaw, J.D., Chown, S.L., 2013. Ontogenetic shifts in plant interactions vary with environmental severity and affect population structure. *New Phytologist* 200, 241-250.

- Lebouvier, M., Laparie, M., Hulle, M., Marais, A., Cozic, Y., Lalouette, L., (. . .) Renault, D., 2011. The significance of the sub-Antarctic Kerguelen Islands for the assessment of the vulnerability of native communities to climate change, alien insect invasions and plant viruses. *Biological Invasions* 13, 1195-1208.
- Lembrechts, J.J., Lenoir, J., Roth, N., Hattab, T., Milbau, A., Haider, S., (. . .) Nijs, I., 2019. Comparing temperature data sources for use in species distribution models: From in-situ logging to remote sensing. *Global Ecology and Biogeography* 28, 1578-1596.
- Lenoir, J., Hattab, T., Pierre, G., 2017. Climatic microrefugia under anthropogenic climate change: implications for species redistribution. *Ecography* 40, 14.
- Lindenmayer, D.B., Likens, G.E., 2010. The science and application of ecological monitoring. *Biological Conservation* 143, 1317-1328.
- Maclean, I.M.D., 2020. Predicting future climate at high spatial and temporal resolution. *Global Change Biology* 26, 1003-1011.
- Maclean, I.M.D., Suggitt, A.J., Wilson, R.J., Duffy, J.P., Bennie, J.J., 2017. Fine-scale climate change: modelling spatial variation in biologically meaningful rates of warming. *Global Change Biology* 23, 256-268.
- Matusick, G., Ruthrof, K.X., Brouwers, N.C., Dell, B., Hardy, G.S.J., 2013. Sudden forest canopy collapse corresponding with extreme drought and heat in a mediterranean-type eucalypt forest in southwestern Australia. *European Journal of Forest Research* 132, 497-510.
- McClelland, G.T.W., Altwegg, R., Aarde, R.J., Ferreira, S., Burger, A.E., Chown, S.L., 2018. Climate change leads to increasing population density and impacts of a key island invader. *Ecological Applications* 28, 212-224.
- Michaelian, M., Hogg, E.H., Hall, R.J., Arsenault, E., 2011. Massive mortality of aspen following severe drought along the southern edge of the Canadian boreal forest. *Global Change Biology* 17, 2084-2094.
- Nicolas, A.N., Plunkett, G.M., 2012. Untangling generic limits in *Azorella*, *Laretia*, and *Mulinum* (Apiaceae: Azorelloideae): Insights from phylogenetics and biogeography. *Taxon* 61, 826-840.
- Nyakatya, M.J., McGeoch, M.A., 2008. Temperature variation across Marion Island associated with a keystone plant species (*Azorella selago* Hook. (Apiaceae)). *Polar Biology* 31, 139-151.
- Ockendon, N., Baker, D.J., Carr, J.A., White, E.C., Almond, R.E.A., Amano, T., (. . .) Pearce-Higgins, J.W., 2014. Mechanisms underpinning climatic impacts on natural populations:

- altered species interactions are more important than direct effects. *Global Change Biology* 20, 2221-2229.
- Parks and Wildlife Service, 2006. Macquarie Island Nature Reserve and World Heritage Area Management Plan, ed. Parks and Wildlife Service, Department of Tourism, Arts and the Environment, p. 189, Hobart, Australia.
- Parnesan, C., Yohe, G., 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421, 37-42.
- Pecl, G.T., Araújo, M.B., Bell, J.D., Blanchard, J., Bonebrake, T.C., Chen, I.-C., (. . .) Williams, S.E., 2017. Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. *Science* 355, eaai9214.
- Pendlebury, S.F., Barnes-Keoghan, I.P., 2007. Climate and climate change in the sub-Antarctic. *Papers and proceedings of the Royal Society of Tasmania* 141, 67-82.
- Pertierra, L.R., Baker, M., Howard, C., Vega, G.C., Olalla-Tarraga, M.A., Scott, J., 2016. Assessing the invasive risk of two non-native *Agrostis* species on sub-Antarctic Macquarie Island. *Polar Biology*, 1-11.
- Petraitis, P., 2013. Multiple stable states in natural ecosystems, 1st ed. edn. Oxford : Oxford University Press, Oxford.
- Phiri, E.E., McGeoch, M.A., Chown, S.L., 2009. Spatial variation in structural damage to a keystone plant species in the sub-Antarctic: interactions between *Azorella selago* and invasive house mice. *Antarctic Science* 21, 189-196.
- Plunkett, G.M., Nicolas, A.N., 2017. Assessing *Azorella* (Apiaceae) and its allies: Phylogenetics and a new classification. *Brittonia* 69, 31-61.
- Raath-Krüger, M.J., McGeoch, M.A., Schöb, C., Greve, M., le Roux, P.C., 2019. Positive plant–plant interactions expand the upper distributional limits of some vascular plant species. *Ecosphere* 10, e02820.
- Rohr, J.R., Raffel, T.R., 2010. Linking global climate and temperature variability to widespread amphibian declines putatively caused by disease. *Proceedings of the National Academy of Sciences* 107, 8269-8274.
- Scott, J.J., Kirkpatrick, J.B., 2013. Changes in the cover of plant species associated with climate change and grazing pressure on the Macquarie Island coastal slopes, 1980-2009. *Polar Biology* 36, 127-136.
- Selkirk, P.M., 2012. Plateau Vegetation On Sub-Antarctic Macquarie Island. *Papers and proceedings of the Royal Society of Tasmania* 146, 71-79.

- Selkirk, P.M., Seppelt, R.D., Selkirk, D.R., 1990. Subantarctic Macquarie Island: environment and biology. Cambridge Press University Press, Cambridge.
- Settele, J., Scholes, R., Betts, R., Bunn, S.E., Leadley, P., Nepstad, D., (. . .) Taboada, M.A., 2014. Terrestrial and inland water systems, In Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part A: Global and Sectoral Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel of Climate Change. eds C.B. Field, V.R. Barros, D.J. Dokken, K.J. Mach, M.D. Mastrandrea, T.E. Bilir, (. . .) P.R. Mastrandrea, pp. 271-359. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.
- Suggitt, A.J., Gillingham, P.K., Hill, J.K., Huntley, B., Kunin, W.E., Roy, D.B., Thomas, C.D., 2011. Habitat microclimates drive fine - scale variation in extreme temperatures. *Oikos* 120, 1-8.
- Sutherland, W.J., Pullin, A.S., Dolman, P.M., Knight, T.M., 2004. The need for evidence-based conservation. *Trends in Ecology & Evolution* 19, 305-308.
- TSSC, 2010. Advice to the Minister for Environment Protection, Heritage and the Arts from the Threatened Species Scientific Committee (the Committee) on amendment to the list of threatened species under the Environmental Protection and Biodiversity Conservation Act 1999 (EPBC Act): *Azorella macquariensis* (Macquarie Cushions), ed. Department of Environment Protection, Heritage and the Arts, Canberra. <http://www.environment.gov.au/biodiversity/threatened/species/pubs/21846-listing-advice.pdf>.
- Tweedie, C.E., Bergstrom, D.M., 2000. A climate change scenario for surface air temperature at subantarctic Macquarie Island (ed.), In Antarctic Ecosystems: Models for Wider Understanding. eds W. Davison, C. Howard-Jones, P. Broady, pp. 272-281. Canterbury University Press, Canterbury.
- Valiente-Banuet, A., Aizen, M.A., Alcántara, J.M., Arroyo, J., Cocucci, A., Galetti, M., (. . .) Zamora, R., 2015. Beyond species loss: the extinction of ecological interactions in a changing world. *Functional Ecology* 29, 299-307.
- Walther, G.-R., 2010. Community and ecosystem responses to recent climate change. *Philosophical Transactions of the Royal Society B: Biological Sciences* 365, 2019-2024.
- Whinam, J., Abdul-Rahman, J.A., Visoiu, M., di Folco, M.B.F., Kirkpatrick, J.B., 2014. Spatial and temporal variation in damage and dieback in a threatened subantarctic cushion species. *Australian Journal of Botany* 62, 10-21.

Williams, L.K., Fergus, A.J., Shaw, J.D., Terauds, A., Kristiansen, P., Wilson, S.C., (. . .)
Sindel, B.M., 2019. Quantifying site and species factors to inform the feasibility of
eradication of alien plants from Southern Ocean Islands: *Stellaria media* on Macquarie Island.
Biological Invasions 21, 993–1005.


Chapter 1

Spatial variation in the ongoing and widespread decline of a keystone plant species

This thesis chapter is in the published format of the peer-reviewed journal *Austral Ecology*.
The full reference for the published paper is:

Dickson, C.R., Baker, D.J., Bergstrom, D.M., Bricher, P.K., Brookes, R.H., Raymond, B., Selkirk, P.M., Shaw, J., Terauds, A., Whinam, J., McGeoch, M.A., 2019. Spatial variation in the ongoing and widespread decline of keystone plant species. *Austral Ecology* **44**, 891-905. doi:10.1111/aec.12758

Spatial variation in the ongoing and widespread decline of a keystone plant species

CATHERINE R. DICKSON,^{1*}  DAVID J. BAKER,¹ DANA M. BERGSTROM,² PHILLIPPA K. BRICHER,³ ROWAN H. BROOKES,¹ BEN RAYMOND,² PATRICIA M. SELKIRK,⁴ JUSTINE D. SHAW,⁵ ALEKS TERAUDS,² JENNIE WHINAM⁶ AND MELODIE A. MCGEOCH¹

¹*School of Biological Sciences, Monash University, Clayton 3800, Victoria, Australia (Email: Catherine.Dickson@monash.edu);* ²*Australian Antarctic Division, Kingston, Tasmania, Australia;*

³*Southern Ocean Observing System and Antarctic Gateway Partnership, University of Tasmania,*

Hobart, Tasmania, Australia; ⁴*Department of Biological Sciences, Macquarie University, Sydney, New South Wales, Australia;* ⁵*School of Biological Sciences, University of Queensland, Brisbane, Queensland,*

Australia; and ⁶*School of Technology, Environments and Design, University of Tasmania, Hobart, Tasmania, Australia*

Abstract Extensive dieback in dominant plant species in response to climate change is increasingly common. Climatic conditions and related variables, such as evapotranspiration, vary in response to topographical complexity. This complexity plays an important role in the provision of climate refugia. In 2008/2009, an island-wide dieback event of the keystone cushion plant *Azorella macquariensis* Orchard (Apiaceae) occurred on sub-Antarctic Macquarie Island. This signalled the start of a potential regime shift, suggested to be driven by increasing vapour pressure deficit. Eight years later, we quantified cover and dieback across the range of putative microclimates to which the species is exposed, with the aim of explaining dieback patterns. We test for the influence of evapotranspiration using a suite of topographic proxies and other variables as proposed drivers of change. We found higher cover and lower dieback towards the south of the island. The high spatial variation in *A. macquariensis* populations was best explained by latitude, likely a proxy for macroscale climate gradients and geology. Dieback was best explained by *A. macquariensis* cover and latitude, increasing with cover and towards the north of the island. The effect sizes of terrain variables that influence evapotranspiration rates were small. Island-wide dieback remains conspicuous. Comparison between a subset of sites and historical data revealed a reduction of cover in the north and central regions of the island, and a shift south in the most active areas of dieback. Dieback remained comparatively low in the south. The presence of seedlings was independent of dieback. This study provides an empirical baseline for spatial variation in the cover and condition of *A. macquariensis*, both key variables for monitoring condition and ‘cover-debt’ in this critically endangered endemic plant species. These findings have broader implications for understanding the responses of fellfield ecosystems and other *Azorella* species across the sub-Antarctic under future climates.

Key words: *Azorella*, climate change, dieback, sub-Antarctic, terrain variables.

INTRODUCTION

The effects of anthropogenic climate change have now been documented in ecosystems across the globe (Field *et al.* 2014). Many plant species, for example, are undergoing rapid changes in condition and distribution (Parmesan & Yohe 2003; Chen *et al.* 2011), and differing rates of species’ responses are resulting in the formation of novel communities (le Roux & McGeoch 2008; Chown *et al.* 2013). As climate conditions change, dominant species may become displaced by those better adapted to current conditions. This is well illustrated by the growing number of landscape-scale plant mortality events across different

ecosystems in Australia and elsewhere (Breshears *et al.* 2005; Allen *et al.* 2010; Carnicer *et al.* 2011; Duke *et al.* 2017; Harris *et al.* 2018; Hoffmann *et al.* 2019). Three such examples include (i) dieback of overstorey species extending across 12 000 km² of south-western North American woodlands, driven by the interactions of drought and bark beetle infestations (Breshears *et al.* 2005), (ii) extensive northern Australian mangrove dieback along 1000 km of coastline, as a response to climate change and extreme events (Harris *et al.* 2018), and (iii) increase in arctic browning across Alaskan boreal forests (reduction in the normalised difference vegetation index, NDVI) between 1982 and 2003, which may be attributed to multiple factors including drought stress, insect damage, disease, wild-fire and changes in resource allocation (Verbyla 2008). The first case of a landscape-scale plant mortality

*Corresponding author.

Accepted for publication March 2019.

event in the sub-Antarctic occurred on Macquarie Island in 2008/2009. Dieback of the keystone plant species *Azorella macquariensis* Orchard (Apiaceae, Macquarie cushion) was observed at 88% of sites surveyed across the island (Bergstrom *et al.* 2015). Dieback was found in even very spatially isolated individuals, with the few unaffected populations observed mainly at higher elevations and towards the south of the island (Bergstrom *et al.* 2015).

Two explanations were proposed to explain the dieback event. First, a pathogen may have emerged as a result of the change in climate (Whinam *et al.* 2014). No definitive relationship between a disease-causing pathogen and unhealthy cushions has been established to date. However, multiple potentially pathogenic taxa were identified, suggesting potential susceptibility to infection under stressful conditions (Bergstrom *et al.* 2015). Second, a significant change in the regional climate over the past ~40 years across Macquarie Island has resulted in a decadal reduction in plant available water (PAW) during the summer growing season (Bergstrom *et al.* 2015). The functional morphology of *A. macquariensis*, where it both quickly loses and takes-up water (Rolland *et al.* 2015), suggests that while it is well adapted to cope with small daily variations in weather, it may be susceptible to the current change in the regional climate, where extended periods between rainfall and increased evapotranspiration are increasingly common (Bergstrom *et al.* 2015). The closely related species *A. selago* has been shown experimentally to experience increased stem death and early senescence under reduced rainfall conditions, implying that the genus may be negatively impacted by climate change (see le Roux *et al.* 2005). These two hypotheses are not mutually exclusive as climate change may weaken plant condition facilitating a secondary pathogenic infection (Bergstrom *et al.* 2015; Hoffmann *et al.* 2019).

Regardless of the proximate cause of mortality, climate change is implicated in the widespread dieback of *A. macquariensis* on the island (Whinam *et al.* 2014; Bergstrom *et al.* 2015). Given the evidence, it is important to quantify the variation in *A. macquariensis* distribution and condition (dieback) across both geographic and environmental space. *Azorella* populations increase with elevation (Phiri *et al.* 2015), and *A. macquariensis* populations have been observed in higher densities, with lower levels of dieback in the south of the island (Bergstrom 2013, updated 2014), which is also higher in elevation. A strong correlation between local climate variation and *A. macquariensis* dieback would (i) provide evidence for the role of climate change in dieback and (ii) identify potential areas, or microrefugia, where *A. macquariensis* may best survive should the current climate trajectory continue. Such baseline data provide essential information for understanding the drivers of change and physiological and

ecological mechanisms responsible for observed declines in the states of ecosystems (Bland *et al.* 2018). Conservation and management decisions about regime change or ecosystem collapse in the *Azorella*-dominated fellfield ecosystems are best underpinned by knowledge of the system's past and current state, so that departure of ecosystems from historic baselines can be quantified (see Bland *et al.* 2018).

Here, we quantify the current distribution of *A. macquariensis* cover and dieback across both geographic and environmental space to generate a spatially representative baseline for monitoring future change, and to better understand the mechanisms driving *A. macquariensis* dieback. We simultaneously provide an update on the condition of *A. macquariensis* populations across Macquarie Island eight years after the dieback event was first observed and five years after the first island-wide assessment (Whinam *et al.* 2014; Bergstrom *et al.* 2015). Specifically, we expected: (i) *A. macquariensis* populations to increase in cover and condition with an increase in latitude and elevation (Bergstrom *et al.* 2015), with these variables representing island-wide macroscale gradients that are well known elsewhere to be related to various dimensions of microclimate (Dobrowski 2011), (ii) in addition, if dieback is driven by finer-scale topography that relates to high evapotranspiration, then the population condition will vary across Macquarie Island and be negatively related to variables associated with high moisture stress (i.e. high wind exposure or low topographic wetness index), (iii) *A. macquariensis* recruitment will be negatively related to the proportion of dieback, because if evapotranspiration negatively impacts adult plants in the form of dieback it may be expected also to affect recruitment. Based on the outcome, we discuss assessment and monitoring priorities to inform potential options for management of this species in the face of ongoing climate change.

METHODS

Macquarie Island (54°30'S, 158°55'E) is a small, narrow sub-Antarctic island of 12 390 ha (Selkirk *et al.* 1990) (Fig. 1). It is characterised by a low, undulating alpine plateau with numerous lakes, tarns and bogs, ranging between 200 and 433 m above sea level (asl) (Selkirk *et al.* 1990). The island has historically had a consistently cool, misty and windy climate, with the plateau regularly shrouded in cloud (Selkirk *et al.* 1990). However, over the past 40 years there has been a significant change in local climate resulting in a significant increase in evapotranspiration (Bergstrom *et al.* 2015). The island has experienced an increase in temperature (Adamson *et al.* 1988; Tweedie & Bergstrom 2000; Pendleybury & Barnes-Keoghan 2007), sunshine hours, average wind speeds (Bergstrom *et al.* 2015), and a higher number of annual cyclonic wind events (Adams 2009). Although there has been a 35% increase in total

precipitation to 1080 mm year⁻¹, it is now more episodic and primarily occurs during winter (Bergstrom *et al.* 2015).

Azorella macquariensis Orchard (Apiaceae) is a highly variable perennial herb that forms tight cushions or extensive mats, depending on the exposure of the site (Orchard 1989) (Fig. 2). *A. macquariensis* undergoes a winter dormancy, where the leaves brown from late March and new leaves emerge in September (Taylor 1955). The winter senescence suggests that the additional winter rainfall has little value for the species. Within the plateau ecosystems, the endemic *A. macquariensis* occurs as the dominant species on the east-facing higher slopes, fellfield and polar desert zones, and as sub-dominant species in short-grasslands at mid-elevations (Selkirk 2012; Bricher *et al.* 2013). *Azorella macquariensis* is considered a keystone species on the fellfield ecosystem because it facilitates a larger more diverse micro-arthropod population, accumulates soil carbon beneath the plant through the deposition of leaf litter (Bergstrom *et al.* 2015) and is likely to facilitate floristic diversity through the amelioration of climatic stress (see le Roux & McGeoch 2010).

Terrain variables

The data from the single weather station on Macquarie Island, located at sea level on the northern end of the island, are generally considered unrepresentative of conditions on the plateau (Fitzgerald & Kirkpatrick 2017). Therefore, we first considered the effect of two macroscale gradients (elevation and latitude) that are well known to serve as proxies for climate conditions, even across relatively short distances of <34 km (Dobrowski 2011). However, variation in climatic conditions between sites, and microclimates experienced at fine spatial scales, can be approximated at these finer scales by inferring the effects of topography on microclimate (Dobrowski 2011; Maclean *et al.* 2015). A suite of landscape variables (which we refer to as terrain variables) that are known to affect microclimate variation were therefore derived from the 5 m × 5 m resolution Macquarie Island Digital Elevation Model (DEM) (Broksma 2008). This model had a particular emphasis on those variables likely to influence plant condition via their effects on evapotranspiration rates (see Bricher *et al.* 2013 for methods). Soil variables and parent geology were considered for inclusion within the models. However, soil variables only had weak relationships with both cover and dieback ($r < -0.16$) and parent geology showed very little variation across sites on the island [dominated (73%) by two classes]. The ecological rationale for including each variable in either the terrain class model or statistical analyses is described in Appendix S1: Table S1.1. In the case of highly correlated variables ($r > 0.70$), one variable was excluded from analysis to minimise collinearity.

Site selection and field survey

Survey sites were randomly stratified by four terrain classes from the Terrain Class Model and eight geographic blocks (see Appendix S1: Figs S1.1–S1.8.). This resulted in 70 sites, including eight sites where *A. macquariensis* was absent. An additional 20 sites, bringing the total number of

sites to 90, were established to increase spatial representation in areas of core *A. macquariensis* habitat and were primarily collocated with historical sites. The position of sampled sites thus represented the range of topographies experienced by *A. macquariensis* on Macquarie Island, and consequently, the putative range of microclimates that exist on the island within those areas that *A. macquariensis* is known to occupy (Appendix S1: Fig. S1.5.). In addition, to characterise directly soil texture and gravel proportions as a potential determinant of cushion cover and condition, a soil pit was dug at each site through the top 250 mm of the soil profile (within the primary *A. macquariensis* root-zone). The proportion of four classes of gravel was visually estimated: coarse gravel (60–20 mm), medium gravel (20–6 mm), fine gravel (6–2 mm) and fine earth fraction (<2 mm) (Sonter *et al.* 2000).

To understand the area of *A. macquariensis* that could potentially be affected by dieback, the total cover (m²) of *A. macquariensis* at each site was quantified. Sites were surveyed during the active growing season of *A. macquariensis* (October to March), between January and March 2017. To obtain a representative sample over highly spatially variable *A. macquariensis* populations, a circular site (15 m radius, 706.86 m² in area) was established and split into four quadrants through the magnetic cardinal points (north, east, south, west). The total percentage cover of *A. macquariensis* at each quadrant was estimated visually using cover estimates of 1% increments for 1–10% cover, and 5% increments above 10%. Throughout the study, the same three people, with significant vegetation survey experience, recorded the visual percentage cover at each site to remove inter-observer error (Wintle *et al.* 2013; Morrison 2016). The area (m²) of *A. macquariensis* was calculated per quadrant (cushion quadrant percent cover multiplied by quadrant area, 176.72 m²) and summed to determine the total area (m²) of cover at the site. No attempt was made to determine the number of individuals within a site, given the high likelihood that most mat forms, and even discrete cushions, include multiple individuals (Mortimer *et al.* 2008; Cerfonteyn *et al.* 2011). The proportion (%) of *A. macquariensis* dieback (defined as stem death) (Fig. 2d–f) was estimated visually as a function of total *A. macquariensis* cover in each quadrant at each site, using the same method to estimate total *A. macquariensis* cover. The total proportion of *A. macquariensis* dieback (%) was then calculated for the site. To assess *A. macquariensis* regeneration under the presence of varying levels of dieback, the presence/absence of seedlings within each circular site was recorded.

Statistical analysis

To assess the potential effect of climate on *A. macquariensis* cover, we modelled the relationship between the proportion of *A. macquariensis* (Cover, between 0 and 1) and variables that (i) describe a site's position along the macroscale climate (Latitude (as measured by Northing), elevation, distance to west coast (West_Dist)) and (ii) the effects of local terrain on site conditions (topographic wetness index (Wetness_Index), topographically deflected wind speed (Wind_Speed), and solar radiation (Solar_Rad)) (see Appendix S1:

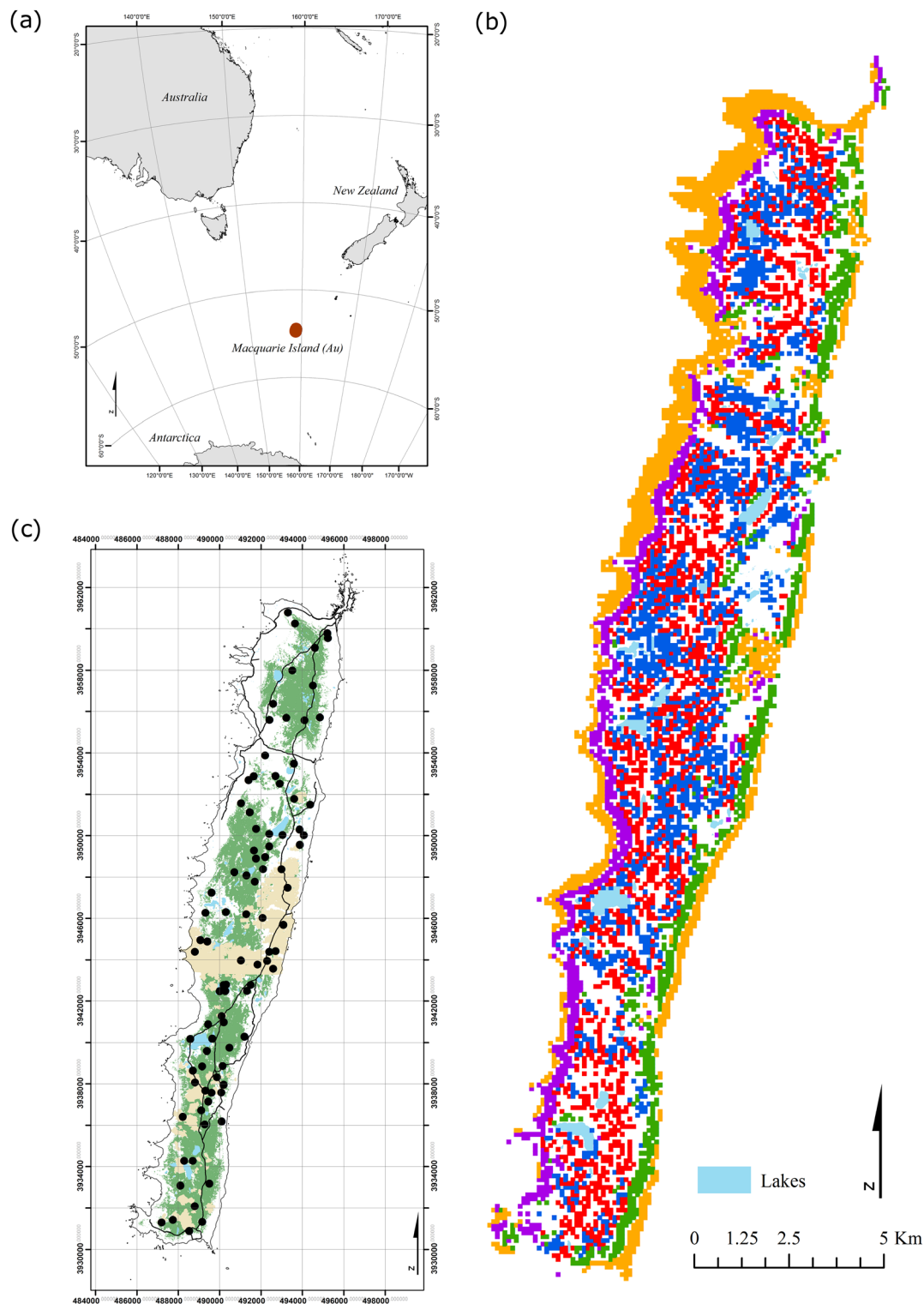


Fig. 1. Location of Macquarie Island (a); the spatial distribution of the five terrain clusters: 1 (red), associated with highest elevation and solar radiation levels with moderate wind exposure and wetness index; 2 (blue), moderate to high elevation, moderate wind exposure, amongst the highest wetness index; 3 (green), lower wind exposure, low to intermediate wetness index; 4 (purple), highest wind exposures, typically low to moderate wetness index; 5 (orange) was not surveyed as it describes hyper-saturated habitat that does not support *Azorella* populations (b); Location of survey sites over the predicted distribution of *Azorella macquariensis* (green) on the island (cream indicates no distribution model due to cloud; thin black lines indicate walking trails) (Bergstrom *et al.* 2015) (c). [Colour figure can be viewed at wileyonlinelibrary.com]

Table S1.1). Exploratory analysis was conducted to explore the potential for strong non-linear relationships between *A. macquariensis* cover and predictor variables by modelling cover using generalised additive models (GAM; family = beta, link = logit) with smoothing applied to each of the predictor variables (mgcv; Wood 2017). Cover showed some evidence of an approximately quadratic relationship with West_Dist and, therefore, West_Dist² term was included in further analysis.

For inference, we modelled proportion of *A. macquariensis* as a function of the seven previously described predictors (including West_Dist²) using a beta regression model with a logit link function (using the R package 'betareg'; Zeileis *et al.* 2016). Beta regression requires that the values of the response variable lie in the open unit interval (0,1) and, therefore, to accommodate sites with zero cover we applied the transformation $(y \times (n-1) + 0.5)/n$, where n is the sample size (following Zeileis *et al.* 2016). There was no spatial autocorrelation in the *A. macquariensis* cover model, as assessed over the ecologically relevant 22 km spatial lag distance, using global Moran's I, prior to model averaging (Bivand *et al.* 2017). Model uncertainty was addressed using multimodel inference (Cade 2015), where model averaging was applied across 42 candidate models in the top 95% confidence set (Appendix S2: Table S2.1). We

estimated effect sizes of predictors based on the model-averaged regression coefficients using the 'MuMIn' package in R (Barton & Barton 2018), after standardising estimates based on partial standard deviations (Cade 2015). This standardisation method is necessary to account for the changing multicollinear covariance structures in models that include different predictors, and enables the estimation of predictor relative importance that can be averaged across all candidate models. The ratio of the absolute value of model-averaged standardised regression coefficients, scaled relative to a maximum of 1 for the strongest predictor, was plotted to provide an estimate of variable importance (Cade 2015). The same statistical approach and terrain variables were used to assess the impact of climate on *A. macquariensis* dieback. In addition, total *A. macquariensis* cover (Cover) was included as a covariate, as well as Cover², because Cover had an approximately quadratic relationship with *A. macquariensis* dieback in the exploratory GAM. Model averaging was applied across 30 candidate dieback models in the top 95% confidence set (Appendix S2: Table S2.2). Similarly, no spatial autocorrelation occurred within the dieback model within ecologically relevant scales.

The change in *A. macquariensis* cover since 2009/2010 was examined using 20 sites that were collocated across surveys. This is the earliest and only comparable dataset

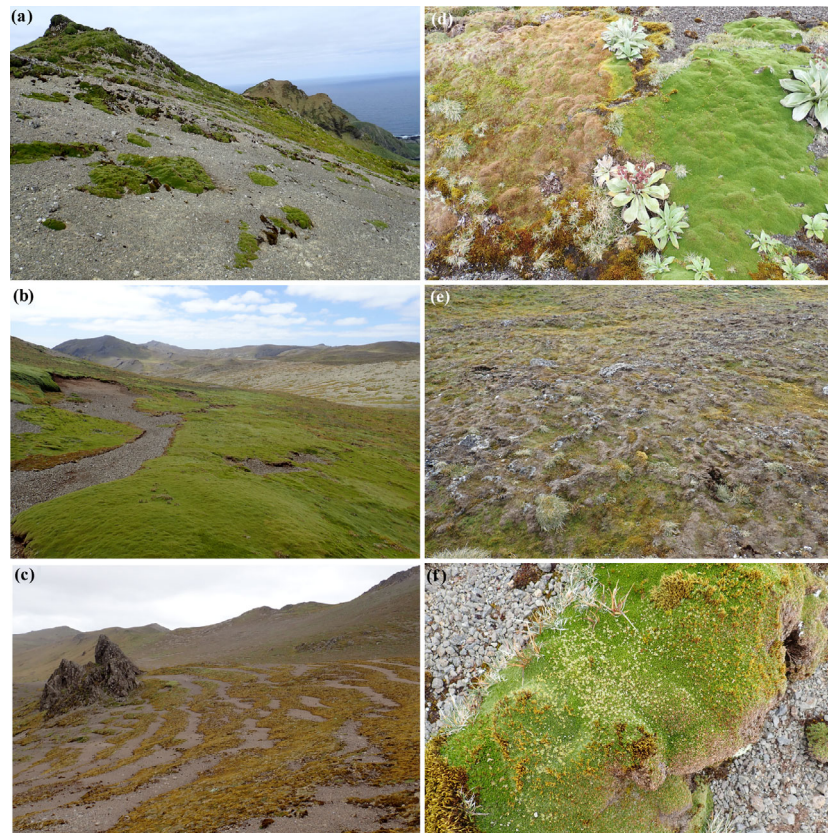


Fig. 2. Forms of *Azorella macquariensis* found on Macquarie Island, discrete cushions (a), mats (b) and terraces (c), stages and forms of observed dieback (d and e) and example of naturally occurring dieback on and around the canopy from wind scour (f). Dieback is defined as the occurrence of individual stem death within the cushion and represented by the brown to black colouration in figures d – f. [Colour figure can be viewed at wileyonlinelibrary.com]

available prior to 2016/2017. For the purpose of this comparison, the three regions of Macquarie Island determined by equal latitudinal extent were used, with sites in the northern ($n = 2$), central ($n = 14$) and southern ($n = 4$) parts of the island. Previous *A. macquariensis* dieback surveys were done at a 5×5 m scale, predominantly in the northern and southern region of the island between 2008/2009 and 2011/2012 (Bergstrom 2013, updated 2014; Bergstrom *et al.* 2015), and annually since 2009/2010 in the central region at $2 \text{ m} \times 2 \text{ m}$ scale (Whinam *et al.* 2014). Survey intensity declined between 2012 and 2015, particularly in the north that initially had three times as many sites (reduction in survey intensity in the north occurred primarily because of the complete loss of *A. macquariensis* from some historical sites), and in the south where monitoring ceased in 2012. Therefore, the full datasets of all three studies were not compared across all years because the number and spatial distribution of sites assessed changed substantially over the eight year period. To evaluate whether the full results of the comparison across periods were a possible artefact of small sample size, we included the results from the current season separated by region, north ($n = 15$), central ($n = 41$) and southern ($n = 26$) for comparison.

The presence of *A. macquariensis* seedlings was compared under different levels of *A. macquariensis* cover (m^2), *A. macquariensis* dieback (%) and fine earth fraction of growing substrate (FEF) (%) using a generalised linear model (GLM) with a binomial distribution and a logit link function. The FEF was used in the GLM as we expected the presence of *A. macquariensis* seedlings to be influenced by soil texture and more likely to occur in open areas (bare ground is negatively correlated with FEF values, $r = -0.48$), as the species is a weak competitor (Taylor 1955). The variance inflation factors (VIFs) (Barton & Barton 2018) of the seedling model were low (<2) and no spatial autocorrelation occurred over the ecologically relevant 22 km spatial lag distance (global Moran's I, Bivand *et al.* 2017). An adjusted D^2 goodness-of-fit for the seedling model was calculated using the formula: $D^2 = 1 - [(n - 1)/(n - p)] \times [1 - D^2]$, where n = number of observations, p = number of parameters and D^2 = (null deviance – residual deviance)/null deviance (Guisan & Zimmermann 2000). Hierarchical partitioning was used to estimate the individual explanatory power of each predictor variable in the seedling model using the R package 'hier.part' (Walsh & Mac Nally 2015). This provided goodness-of-fit measures for all potential models under all combinations, and calculated the increasing goodness-of-fit with each additional predictor, which was then averaged over the models to provide the individual effects (Mac Nally 2000).

To investigate the interdependence of *A. macquariensis* cover and dieback and the effect of the lag ('cover debt') between the onset of dieback and its impact on cushion cover, simple models of cover were fitted using linear and exponential spread of dieback for the northern, central and southern regions of Macquarie Island. The models took the form of cover (t_x) = cover (t_0) – dieback ($t_x - 4$), and were run under both linear and exponential spread of dieback. Current (t_0) median cover and current dieback values (m^2) were used for each region and modelled forward. Linear progression of dieback was determined between t_0 (current

median dieback, m^2) and t_{-10} (2006/2007, before the dieback event and assumed to be 0 m^2) for each region and then extrapolated forward. For the purpose of this illustration, the exponential ($y = x^2$) dieback for each region was calculated as an incremental increase of 1% of cover at t_0 . In these models, we have thus assumed (i) no cushion recovery, (ii) stem removal occurs following four years of dieback (an estimate for the progression from first infection to complete removal based on personal observation in the field, although this is likely to vary both spatially and temporally) and (iii) wind removes dead stems but does not accelerate dieback, which may potentially occur *in situ* through the loss of cushion integrity (a conservative assumption, see Hoffmann *et al.* 2019). All analyses were performed using R Studio 3.4.1 (R Core Team 2017).

RESULTS

Azorella cover

The cover of *A. macquariensis* was highly variable across sites, ranging from 0.00 ($n = 8$) to 609.67 m^2 (Table 1, Figs 3a, 4a). Where present, *A. macquariensis* cover was also highly variable within sites ($n = 82$), differing between quadrants by up to 114.9 m^2 (or 65% of the quadrant), with a coefficient of variation of over 68%. Latitude was the only significant predictor (Table 2), with cover increasing from north to south (Fig. 3a). Latitude had the largest absolute standardised estimate (1.00) and approximately three times the effect size of the next most important coefficients, Elevation (0.34) and West_Dist^2 (0.29) (Fig. 5a). There was an increase in cover with elevation and a gradual decline in cover with distance from the west coast; cover drops sharply at the eastern limit of its range on the island. Of the local terrain scale variables, Wind_Speed (0.166) had almost three times the relative effect than Solar_Rad (0.059) (Fig. 5a), but both effect sizes were small.

Azorella dieback

The extent of dieback was also highly variable across sites at which *A. macquariensis* was present, with an average of 26.9% (\pm SD 21.5%) cover affected by dieback (Table 1). Dieback was observed in 98.7% of sites surveyed and absent from only one site in the centre of the island. Three sites had $< 2\%$ dieback, $16 \leq 10\%$ dieback and 17% had levels of dieback $> 50\%$ (Fig. 4b).

Both the covariate *A. macquariensis* cover (Cover and Cover^2) and the predictor latitude significantly explained dieback (Table 2). Dieback significantly increased with decreasing latitude, to the north of the

Table 1. *Azorella macquariensis* cover and dieback descriptive statistics at the 90 field sites across Macquarie Island (total site area = 706.86 m²). Cover and dieback presented at an island-wide and regional level, regions represent three equal latitudinal extents

	N	Min. [†]	Max.	Mean (±SD)	c.v. (%)
Cover					
Total <i>Azorella</i> cover (m ²)	90	0.9	609.7	181.7 (±162.2)	88.7
Total <i>Azorella</i> cover (%)	90	0.1	86.7	25.7 (±22.8)	88.7
Northern cover (%)	19	1.3	21.2	6.68 (±6.17)	92.5
Central cover (%)	43	0.1	57.5	22.4 (±17.3)	77.1
Southern cover (%)	28	9.3	86.2	43.7 (±24.9)	57.0
Dieback					
Total <i>Azorella</i> dieback (m ²)	82	0.0	226.6	54.5 (±58.3)	107.1
<i>Azorella</i> with dieback (%)	82	0.0	86.8	26.9 (±21.5)	80.2
Northern dieback (%)	15	6.0	86.8	33.3 (±23.8)	71.4
Central dieback (%)	41	0.0	80.4	29.6 (±23.2)	78.3
Southern dieback (%)	26	0.2	58.8	18.7 (±0.2)	78.4

[†]Min excludes eight sites with no *A. macquariensis* cover ($n = 82$).

island. The relationship between dieback and cover was modal, with low dieback in areas of low cover, high dieback with intermediate cover and low dieback in areas of high cover (Table 2). This shows that the highest proportion of dieback was recorded predominantly in the centre of the island, where there was both high cover and comparatively high latitude (Fig. 3b). The model-averaged estimate of effect size shows that latitude, cover and cover² have the highest coefficient values (1.00, 0.97, 0.79, respectively) (Fig. 5b). Latitude and cover had between 7.00 and 8.83 times the effect on dieback than all other terrain variables (Fig. 5b). However, Solar_Rad, Wetness_Index and Wind_Speed had a larger effect size than West_Dist.

Seedlings were recorded at over a quarter of the sites ($n = 22$, 26.8%), and no seedlings were observed to be affected by dieback. Fine earth fraction (FEF) was the only significant predictor of the presence of *A. macquariensis* seedlings (adjusted $D^2 = 0.116$), explaining 85.86% of the independent contribution (Table 3). Fewer seedlings were observed where the fine earth fraction was higher in the top 250 mm of the soil profile.

Change in extent and distribution of dieback

At the 20 sites compared across periods, median *A. macquariensis* cover (%) declined from 40.00% (1st quartile, Q1, 17.50% – 3rd quartile, Q3, 60.63%) in 2009/2010 to 26.64% (Q1, 10.24% – Q3, 53.13%) in 2016/2017. Median cover in the north declined from 21.25% to 7.50% (Fig. 6a). In the central region, median cover declined from 20.6% to 17.50% and variation in cover was also highest in this region in both periods (Fig. 6a). In

contrast, median cover in the south across periods was comparatively similar. The median cover of the complete dataset from 2016/2017 was also highest in the south of the island compared with the other regions (and therefore not a small sample size effect) (Fig. 6a). However, the interquartile range (IQR, Q1 – Q3) in the south in the current data set was four times higher (40.4%) and the median 20.6% lower than in the subset of sites, suggesting that a sample size larger than 20 is necessary for a representative estimate of cover in this part of the island. The median cover was only slightly lower in the northern and central regions between the 20 sites and full dataset, declining by 1.5% and 8.8%, respectively.

Mean dieback across the island changed in absolute terms from $32 \pm 29\%$ (SD) in 2008/2009 (Bergstrom *et al.* 2015) to $28.2 \pm 22.4\%$ (SD) eight years later. However, the proportion cushions affected by dieback at the subset of sites declined from 40.00% in 2009/2010 (Q1 17.50% – Q3 60.63%) to 25.65% in 2016/2017 (Q1 10.24 – Q3 53.13%). The median proportion of cover affected by dieback was lower in 2016/2017 across the northern and central regions by 23.97% and 11.84%, respectively (Fig. 6b). The median proportion of the dieback present at sites was most variable in the central region of the island during both periods, with a slightly higher interquartile range (IQR) in 2016/2017 of 46.09% (Fig. 6b). In contrast, the IQR of dieback (%) in the north declined by 9.24% (Fig. 6b). The median proportion of dieback in the south remained low with a marginal increase (Fig. 6b). Dieback at the subset of sites in 2016/2017 and the full dataset was very similar in all three regions, differing least in the north (–2.4%) and most in south (+5.6%) (Fig. 6b). However, the full dataset shows higher variability in dieback in the

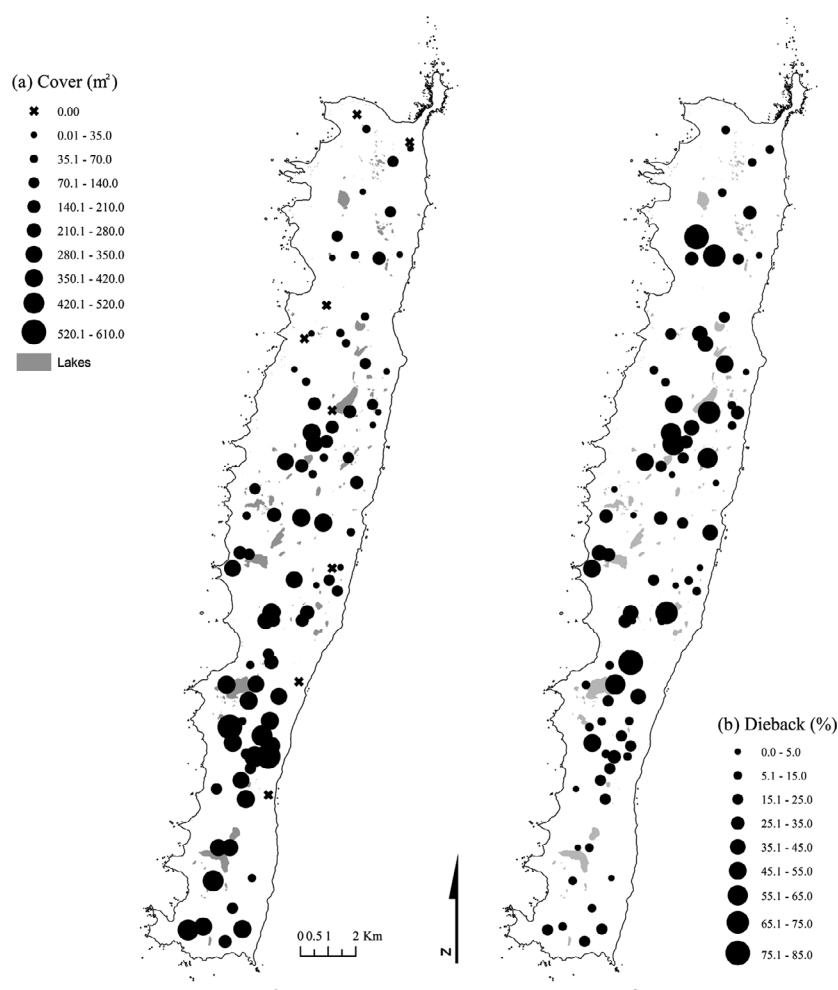


Fig. 3. Total cover of *Azorella macquariensis* (m^2) (a) and *A. macquariensis* cover affected by dieback (%) (b) at each 706.86 m^2 site 2017.

north (IQR increase by 21.1%) and south (IQR increase by 12.0%) again showing that more than 20 sites are needed to obtain a representative estimate of dieback.

The cover loss models demonstrate the implications of differences in initial cushion cover, and the rate of dieback, for the time to complete loss of the species from a landscape (Fig. 7). As might be expected, the comparatively low cover at northern sites is first to reach a point where cushion cover is equal to dieback (where cover and dieback lines intersect, Fig. 7). Under the assumption of no recovery, this is the point at which remaining cover represents extinction debt (which we term 'cover debt'), or the point at which local functional extinction occurs. Starting with current cover and dieback levels on the island, illustrative time to complete cover debt (i.e. 100% dieback cover where the dieback and cover trajectories intersect) under linear dieback progression ranges from 8 to 22 years across the island.

Complete loss of cushion cover under the exponential model ranges from 8 to 10 years (Fig. 7).

DISCUSSION

Using a stratified random design to capture the full range of microclimate conditions that *Azorella macquariensis* is exposed to on Macquarie Island, we have shown that cushion cover and condition are highly variable and that dieback is pervasive. Almost a decade after it was first observed, dieback remains a conspicuous feature of *A. macquariensis* populations across Macquarie Island. Although based on the limited evidence comparable across periods the total area affected by island-wide dieback appears to have stabilised, the location of the most active dieback has shifted southwards, from the north to central region of the island. As a result of the high variability in both cover and dieback, multiple assessment and

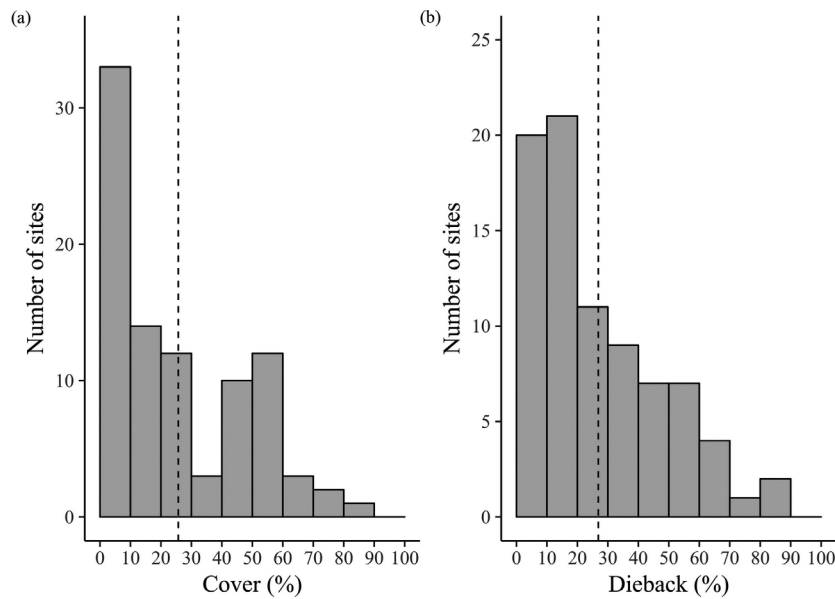


Fig. 4. Frequency distributions of (a) *Azorella macquariensis* cover (%) and (b) *A. macquariensis* dieback (%) across sites, with mean values shown by the dashed lines.

monitoring sites are needed in each region to obtain a representative estimate of the conservation status of this species.

Table 2. Relationships between terrain variables and (a) total cover of *Azorella macquariensis* (m²) and (b) proportion of *A. macquariensis* with dieback (%). Averaged beta regression models showing the estimated coefficients with standard error and Wald's z-value for predictor variables. Significant variables in bold ($P < 0.05$), ordered by effect size (see Fig. 5)

Variable	Estimated coefficient (SE)	<i>z</i>	<i>P</i>
(a) <i>Azorella</i> cover			
Intercept	-1.13 (0.10)	10.83	<0.001
Latitude [†]	-0.46 (0.10)	4.43	<0.001
Elevation	0.16 (0.11)	1.44	0.151
West_Dist	-0.04 (0.08)	0.51	0.613
West_Dist ²	-0.13 (0.12)	1.08	0.279
Wind_Speed	0.08 (0.11)	0.73	0.468
Solar_Rad	0.03 (0.07)	0.38	0.703
Wetness_Index	0.02 (0.06)	0.27	0.785
(b) <i>Azorella</i> dieback			
Intercept	-1.01 (0.10)	9.74	<0.001
Latitude [†]	0.38 (0.10)	3.71	<0.001
Cover	0.37 (0.10)	3.53	<0.001
Cover²	-0.30 (0.11)	2.83	0.005
Elevation	0.04 (0.08)	0.53	0.599
Solar_Rad	-0.04 (0.08)	0.49	0.627
Wetness_Index	-0.03 (0.07)	0.42	0.674
Wind_Speed	0.02 (0.06)	0.35	0.728
West_Dist	<0.001 (0.05)	0.00	1.000

[†]Measured as northing, that is, the inverse of latitude.

Latitude was the strongest predictor of both cushion cover and dieback, with elevation having a smaller effect in explaining variation in both. The dominant effect of these macroscale gradients may be expected in systems such as Macquarie Island, that is, that have relatively low levels of topographic complexity (elevational extent, and variation in slope and aspect) and high oceanic influence (Dobrowski 2011). Macroscale gradients are well known to form a proxy for multiple other ecological gradients, which then influence the distribution and abundance of species (Gaston 2000). Our models suggest that cushion cover and condition are driven by variables correlated with latitude but not captured by finer-scale topographic variables. On Macquarie Island, latitude is moderately correlated not only with elevation ($r = 0.31$) but also with the island's geology ($r = -0.32$). For example, vegetation communities occurring on ultramafic soils in the north have been shown to be sparse and stunted compared to vegetation on surrounding soil types (Adamson *et al.* 1993). Our results support the interpretation that cushion cover is predominantly determined by multiple covarying gradients (Bricher *et al.* 2013). In this case, the macroscale gradients that together result in increasing cover to the south of the island, where soil conditions may be better but which is also higher, cooler and likely to experience more frequent low cloud.

There was weak evidence of terrain effects on both *A. macquariensis* cover and dieback. Terrain variables represented between 3.5 and 16.6% of the relative effect size of latitude. Although small, these effects

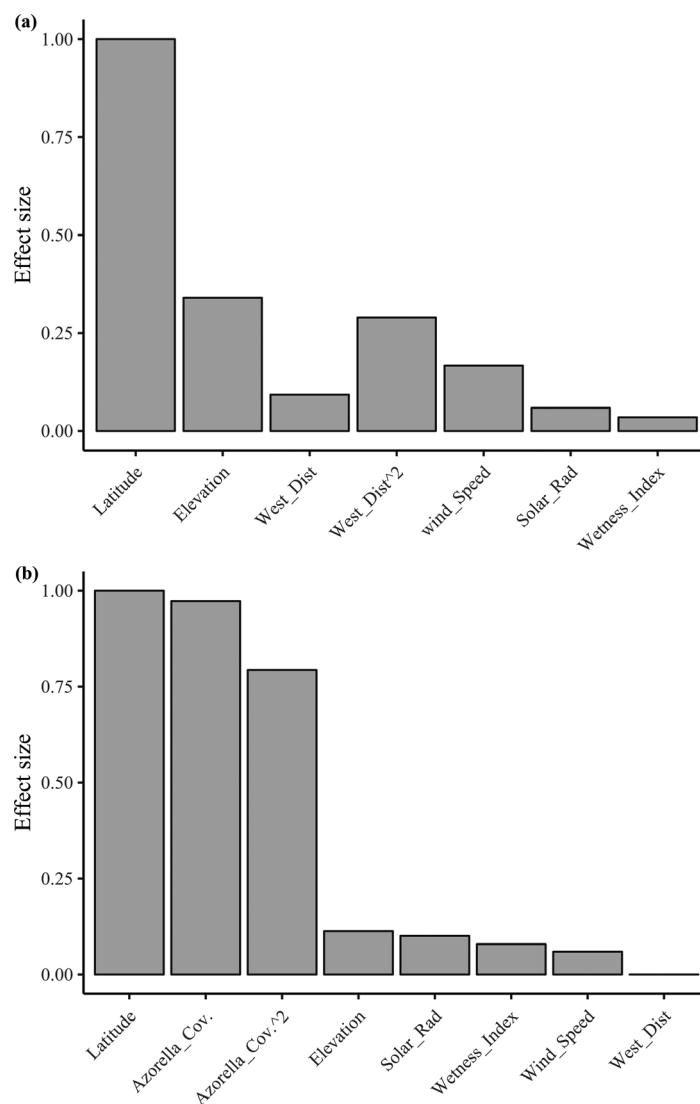


Fig. 5. Effect size of each terrain variable (ratio of the absolute value of the standardised regression coefficient) on *Azorella macquariensis* (a) cover and (b) dieback.

Table 3. The relationship between *Azorella macquariensis* seedling frequency and *Azorella* cover, dieback and fine earth fraction within the top 250 mm of the soil profile. Hierarchical partitioning showing the independent contribution of each variable (I). Significant variable for both tests in bold ($P < 0.05$). GLM dispersion parameter for binomial family taken to be 1, null deviance 95.375 on 81 d.f., and residual deviance 82.203 on 78 d.f.

Variable	Generalised linear model				Hierarchical partitioning Independent contribution (%)
	Estimated coefficient	SE	z	P	
Intercept	0.13	0.64	0.20	0.841	
<i>Azorella</i> cover (m ²)	<0.01	<0.01	−0.47	0.642	2.65
<i>Azorella</i> dieback (%)	0.02	0.01	1.35	0.178	11.49
Fine earth fraction (%)	−0.04	0.01	−2.94	0.003	85.86

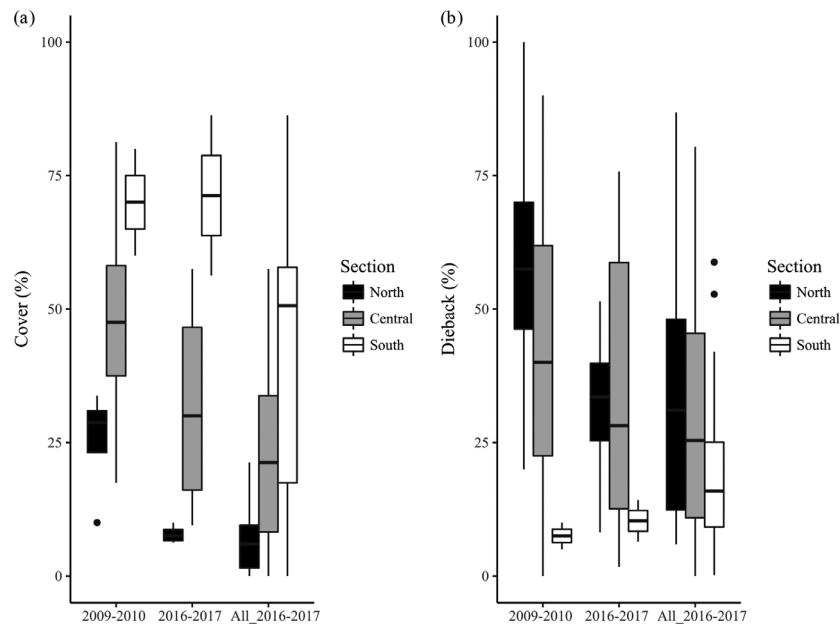


Fig. 6. Comparison of *Azorella macquariensis* (a) cover (%) and (b) dieback (%) at 20 collocated sites in the southern ($n = 2$), central ($n = 14$), and northern ($n = 4$) regions of Macquarie Island, between 2009/2010 and 2016/2017 (median, upper and lower quartiles, and range). For comparison, the full data from the 2016/2017 season are shown (All_2016–2017), also separated into southern ($n = 26$ sites), central ($n = 41$) and northern ($n = 15$) parts of the island.

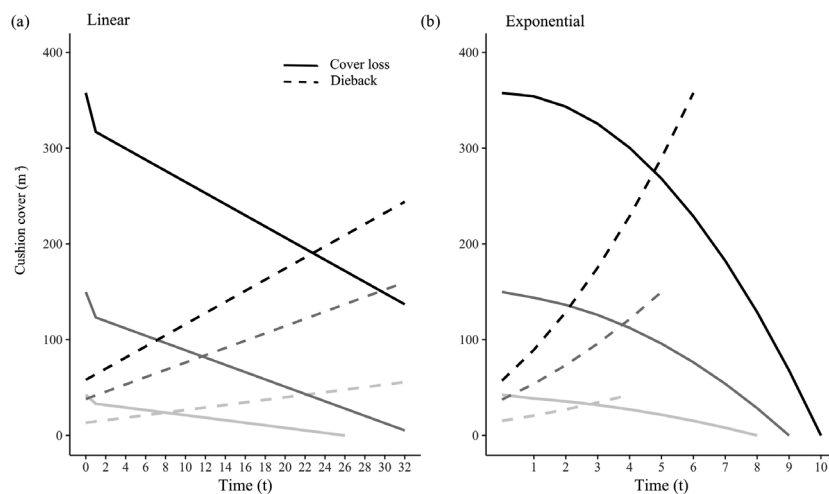


Fig. 7. *Azorella macquariensis* cover loss models showing the illustrative rate of cushion cover (solid lines) loss under two dieback (dashed lines) rates of spread, linear (a) and exponential (b). Cover and dieback are initiated (time 0) at the 2016/2017 median site values for the north (light grey), central (medium grey) and southern (black) regions of Macquarie Island. Each time step represents 1 year.

were most pronounced for *A. macquariensis* cover, which increased with wind speed and solar radiation, supporting the findings of a species distribution model (SDM) that incorporated variables from satellite imagery (Bricher *et al.* 2013). The suggestion that terrain effects operating at scales finer than macro-scale gradients may be important provides impetus for the value of empirical microclimate information

to further explore these effects. Topographic wetness index, a surrogate for soil moisture, was least important in the cover model, which supports current physiological understanding of the species that suggests that *A. macquariensis* is ombrotrophic, that is, largely dependent on atmospheric water (Bergstrom *et al.* 2015). The elevation and terrain effects suggest that dieback was more likely prevalent at sites with

higher elevation, lower solar radiation (steep slopes at lower elevations), dry soils and greater wind exposure. This provides some support for the hypothesis that *A. macquariensis* dieback will be most prevalent in areas that are traditionally considered more water-stressed, and concurs with the drought-sensitivity demonstrated for its sister species *A. selago* (le Roux *et al.* 2005). Given the strong positive relationship between *A. macquariensis* dieback and cover and negative relationship between dieback and latitude, these insights provide useful information about the likely location of future dieback. Southern populations with comparatively low elevation, and higher solar radiation, appear most promising for sustaining healthy populations should current climate trends continue.

The role of the pathogen in the viability of such refugia will also have to be considered by not only considering fine-scale empirical data on abiotic conditions but also better understanding the pathogen/s involved in the dieback. To date the pathogen(s) responsible for dieback has not been identified, although a wide range of potential fungal, bacterial and oomycetes, including the pathogenic *Rosellinia* sp. (Xylariaceae) were identified in association with *A. macquariensis* (Bergstrom *et al.* 2015). Despite the unknown identity of the pathogen(s), under the current warmer and wetter winters on Macquarie Island (Adams 2009; Bergstrom *et al.* 2015), the milder conditions may facilitate disease spread (see Harvell *et al.* 2002). For example, climate modelling of a pathogen currently of significant concern in Australia, *Phytophthora cinnamomi* Rands (Oomyceta), found that this species is likely to increase its active range into alpine zones where the pathogen was present, but previously latent due to harsh winters (Burgess *et al.* 2017). Prior to the island-wide *A. macquariensis* dieback event, single isolated occurrences of brown dieback patches with yellow chlorosis lines were recorded in the 1980s and 1990s (Whinam *et al.* 2014; Bergstrom *et al.* 2015), suggesting that pathogen/s were present but latent within the system. The change in secondary biotic interactions under altered climates has been shown to often be more important in determining the decline or extinction of a species, than the direct impact of change in local climate (Cahill *et al.* 2013; Ockendon *et al.* 2014), and this could be the case for *A. macquariensis* (Hoffmann *et al.* 2019).

Although limited comparable data are available to evaluate island-wide changes in dieback since its initiation, evidence from the subset of sites that are comparable show that high cushion dieback is now concentrated in the central region of the island, south of where the dieback event was first recorded a decade ago. Previous assessments of dieback found increases of 20 and 40% over a three-year period at

different sites (Whinam *et al.* 2014; Bergstrom *et al.* 2015), which are higher than the island-wide dieback we found. Given the high level of island-wide variability in cover and dieback, and the different methods used in each period, this comparison has to be treated with caution. Nonetheless, the consequence of sustained island-wide dieback is that there has been a loss of cushion cover, particularly in the northern and central regions, resulting in the complete loss of the species at some northern historical monitoring sites (authors DMB, JW, personal observation).

Levels of variation in the extent of dieback at individual sites in both the centre and south of the island are high. This implies that dieback may still be reaching its full potential and that these regions, particularly the island's central fellfield, could still undergo a reduction in cover similar to that which has occurred in the north. The illustrative cover loss models under linear and exponential progression of dieback demonstrate the effect of 'cover debt' on the island, that is, they clearly show how current cover as a proxy for population size overestimates the conservation status of the species. However, dieback cover on its own is also not a reliable proxy for conservation status because it is dependent on current cushion cover – evident from the different trajectories between regions of the island. Percentage dieback on its own is not adequate because this percentage could remain relatively constant, masking a shifting baseline of total cover loss. Collecting both *A. macquariensis* cover and dieback data are therefore essential because projections for future *A. macquariensis* differ substantially depending on the starting cover, historical rates of loss and rate of spread of dieback. Further data of the type we present here will enable evidence-based, predictive models of changes in the conservation status of the species.

Prospects

Azorella macquariensis grows slowly (Taylor 1955; Bergstrom *et al.* 1997), and is thought to produce comparatively low levels of seed (Orchard 1989; Shaw 2005). Little is known about the recruitment capacity of *A. macquariensis*, and to date, germination trials for *ex situ* management have been unsuccessful (Bergstrom *et al.* 2015, L. Perrins Royal Tasmanian Botanical Gardens, personal communication 2018). Similarly, *in situ* and *ex situ* germination studies for the closely related species *A. selago* have been unsuccessful (Dorne 1974; Frénot & Gloaguen 1994). In the field, *A. selago* has been shown to have low recruitment, a short dispersal distance, and to facilitate the survival of its own seedlings (Hausmann *et al.* 2010). Yet current populations of this species

elsewhere in the sub-Antarctic apparently remain in good condition (P.C. le Roux personal communication 2018). Consequently, while the presence of *A. macquariensis* seedlings is encouraging and demonstrates that the species has the capacity to regenerate in areas of dieback, its ecology suggests that any recovery is likely to be slow and patchy.

The spatial baseline of variation in *A. macquariensis* cover and condition (dieback) that we provide here will enable effective monitoring to detect future changes in the population extent and structure of this threatened, endemic species on Macquarie Island. We have shown that it is essential to measure both cover and dieback at spatially explicit sites (including information on sample grain and extent) in future assessment and monitoring exercises. Further knowledge of fine-scale habitat conditions and pathogen identity and ecology is key to identifying potential refuges for the species on the island. The areas of greatest conservation value for the species remain in the south of the island, where the highest cover and lowest dieback currently occur. Well-designed, regular monitoring of the cover and dieback of *A. macquariensis* will form an essential component of conservation management of this World Heritage site during a time of changing weather patterns.

ACKNOWLEDGEMENTS

We thank John Burgess, Rowena Hannaford, Dr Alex Fergus and the 69th Macquarie Island Australian Antarctic Program team who provided assistance during field work. Historical site data (2 m × 2 m) provided by the Department of Primary Industries, Parks, Water and Environment. We thank P.C. le Roux and anonymous reviewers for their comments on the manuscript. This research was funded by the Australian Government under an Australian Antarctic Science Program Grant no. 4312 and supported by an Australian Government Research Training Program (RTP) Scholarship and The Holsworth Wildlife Research Endowment and The Ecological Society of Australia.

REFERENCES

- Adams N. (2009) Climate trends at Macquarie Island and expectations of future climate change in the sub-Antarctic. *Pap. Proc. R. Soc. Tasman.* **143**, 1–8.
- Adamson D., Whetton P. & Selkirk P. M. (1988) An analysis of air temperature records for Macquarie Island: decadal warming, ENSO cooling and southern hemisphere circulation patterns. *Pap. Proc. R. Soc. Tasman.* **122**, 107–12.
- Adamson D. A., Selkirk J. M. & Seppelt R. D. (1993) Serpentine, harzburgite and vegetation on subantarctic Macquarie Island. *Arct. Alp. Res.* **25**, 216–19.
- Allen C. D., Macalady A. K., Chenchouni H. *et al.* (2010) A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *For. Ecol. Manage.* **259**, 660–84.
- Barton K. & Barton M. K. (2018) MuMIn: Multi-Model Inference. Version: 1.40.4. CRAN. Available from URL: <https://CRAN.R-project.org/package=MuMIn>.
- Bergstrom D. M. (2013, updated 2014) Macquarie Is. Azorella dieback 5 m x 5 m quadrats 2008–2012. (ed A. A. D. Centre, Australian Antarctic Data Centre. <http://doi.org/10.4225/15/50FF1931B92C1>)
- Bergstrom D. M., Selkirk P. M., Keenan H. M. & Wilson M. E. (1997) Reproductive behaviour of ten flowering plant species on subantarctic Macquarie Island. *Opera Bot.* **132**, 109–20.
- Bergstrom D. M., Bricher P. K., Raymond B. *et al.* (2015) Rapid collapse of a sub-Antarctic alpine ecosystem: the role of climate and pathogens. *J. Appl. Ecol.* **52**, 774–83.
- Bivand R., Altman M., Anselin L. *et al.* (2017) Package ‘spdep’: Spatial Dependence: Weighting Schemes, Statistics and Models. Version 0.7-4. CRAN. Available from URL: <https://CRAN.R-project.org/package=spdep>.
- Bland L. M., Rowland J. A., Regan T. J. *et al.* (2018) Developing a standardized definition of ecosystem collapse for risk assessment. *Front. Ecol. Environ.* **16**, 29–36.
- Breshears D. D., Cobb N. S., Rich P. M. *et al.* (2005) Regional vegetation die-off in response to global-change-type drought. *Proc. Natl Acad. Sci. USA* **102**, 15144–8.
- Bricher P. K., Lucier A., Shaw J., Terauds A. & Bergstrom D. M. (2013) Mapping sub-antarctic cushion plants using random forests to combine very high resolution satellite imagery and terrain modelling. *PLoS ONE* **8**, 1–15.
- Brolsma H. (2008) Macquarie Island AIRSAR DEM (Digital Elevation Model). Available from URL: <http://data.aad.gov.au/aadc/metadata/>.
- Burgess T. I., Scott J. K., McDougall K. L. *et al.* (2017) Current and projected global distribution of *Phytophthora cinnamomi*, one of the world’s worst plant pathogens. *Global Change Biol.* **23**, 1661–74.
- Cade B. S. (2015) Model averaging and muddled multimodel inferences. *Ecology* **96**, 2370–82.
- Cahill A. E., Aiello-Lammens M. E., Fisher-Reid M. C. *et al.* (2013) How does climate change cause extinction? *Proc. R. Soc. B* **280**, 20121890.
- Carnicer J., Coll M., Ninyerola M. *et al.* (2011) Widespread crown condition decline, food web disruption, and amplified tree mortality with increased climate change-type drought. *Proc. Natl Acad. Sci. USA* **108**, 1474–8.
- Cerfonteyn M. E., Le Roux P. C., Van Vuuren B. J. & Born C. (2011) Cryptic spatial aggregation of the cushion plant *Azorella selago* (Apiaceae) revealed by a multilocus molecular approach suggests frequent intraspecific facilitation under sub-Antarctic conditions. *Am. J. Bot.* **98**, 909–14.
- Chen I.-C., Hill J. K., Ohlemüller R., Roy D. B. & Thomas C. D. (2011) Rapid range shifts of species associated with high levels of climate warming. *Science* **333**, 1024–6.
- Chown S. L., le Roux P. C., Ramaswila T. *et al.* (2013) Climate change and elevational diversity capacity: do weedy species take up the slack? *Biol. Lett.* **9**, 20120806.
- Dobrowski S. Z. (2011) A climatic basis for microrefugia: the influence of terrain on climate. *Global Change Biol.* **17**, 1022–35.
- Dorne A.-J. (1974) Analysis of the germination under laboratory and field conditions of seeds collected in the Kerguelen Archipelago. In: *Adaptations Within Antarctic*

- Ecosystems - Proceedings of the Third SCAR Symposium on Antarctic Biology* (ed. G. A. Llano) pp. 1003–13. Smithsonian Institution, Houston, TX, Washington, D.C.
- Duke N. C., Kovacs J. M., Griffiths A. D. *et al.* (2017) Large-scale dieback of mangroves in Australia's Gulf of Carpentaria: a severe ecosystem response, coincidental with an unusually extreme weather event. *Mar. Freshwat. Res.* **68**, 1816–29.
- Field C. B., Barros V. R., Mach K. J. *et al.* (2014) Technical summary. In: *Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part A: Global and Sectoral Aspects. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* (eds C. B. Field, V. R. Barros & D. J. Dokken, *et al.*) pp. 35–94. Cambridge University Press, Cambridge and New York, NY, USA.
- Fitzgerald N. B. & Kirkpatrick J. B. (2017) Wind distortion in alpine and subantarctic plants is constant among life forms but does not necessarily reflect prevailing wind direction. *Arct. Antarct. Alp. Res.* **49**, 521–35.
- Frénét Y. & Gloaguen J. C. (1994) Reproductive-performance of native and alien colonizing phanerogams on a glacier foreland, Iles Kerguelen. *Polar Biol.* **14**, 473–81.
- Gaston K. J. (2000) Global patterns in biodiversity. *Nature* **405**, 220–7.
- Guisan A. & Zimmermann N. E. (2000) Predictive habitat distribution models in ecology. *Ecol. Model.* **135**, 147–86.
- Harris R. M. B., Beaumont L. J., Vance T. R. *et al.* (2018) Biological responses to the press and pulse of climate trends and extreme events. *Nat. Clim. Change* **8**, 579–87.
- Harvell C. D., Mitchell C. E., Ward J. R. *et al.* (2002) Climate warming and disease risks for terrestrial and marine biota. *Science* **296**, 2158–62.
- Hausmann N. S., McGeoch M. A. & Boelhouwers J. C. (2010) Contrasting nurse plants and nurse rocks: the spatial distribution of seedlings of two sub-Antarctic species. *Acta Oecol.* **36**, 299–305.
- Hoffmann A. A., Rymer P. D., Byrne M. *et al.* (2019) Impacts of recent climate change on terrestrial flora and fauna: Some emerging Australian examples. *Austral Ecol.* **44**, 3–27.
- Mac Nally R. (2000) Regression and model-building in conservation biology, biogeography and ecology: the distinction between—and reconciliation of—'predictive' and 'explanatory' models. *Biodivers. Conserv.* **9**, 655–71.
- Maclean I. M. D., Hopkins J. J., Bennie J., Lawson C. R. & Wilson R. J. (2015) Microclimates buffer the responses of plant communities to climate change. *Global Ecol. Biogeogr.* **24**, 1340–50.
- Morrison L. W. (2016) Observer error in vegetation surveys: a review. *J. Plant Ecol.* **9**, 367–79.
- Mortimer E., McGeoch M. A., Daniels S. R. & Van Vuuren B. J. (2008) Growth form and population genetic structure of *Azorella selago* on sub-Antarctic Marion Island. *Antarct. Sci.* **20**, 381–90.
- Ockendon N., Baker D. J., Carr J. A. *et al.* (2014) Mechanisms underpinning climatic impacts on natural populations: altered species interactions are more important than direct effects. *Global Change Biol.* **20**, 2221–9.
- Orchard A. E. (1989) *Azorella* Lamarck (Apiaceae) on Heard and Macquarie Islands, with description of a new species, *A. macquariensis*. *Muelleria* **7**, 15–20.
- Parnesan C. & Yohe G. (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature* **421**, 37–42.
- Pendlebury S. F. & Barnes-Keogh I. P. (2007) Climate and climate change in the sub-Antarctic. *Pap. Proc. R. Soc. Tasman.* **141**, 67–82.
- Phiri E. E., McGeoch M. A. & Chown S. L. (2015) The abundance structure of *Azorella selago* Hook. f. on sub-Antarctic Marion Island: testing the peak and tail hypothesis. *Polar Biol.* **38**, 1881–90.
- R Core Team. (2017) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna.
- Rolland V., Bergstrom D. M., Lenne T. *et al.* (2015) Easy come, easy go: capillary forces enable rapid refilling of embolized primary xylem vessels. *Plant Physiol.* **168**, 1636–47.
- le Roux P. C. & McGeoch M. A. (2008) Rapid range expansion and community reorganization in response to warming. *Global Change Biol.* **14**, 2950–62.
- le Roux P. C. & McGeoch M. A. (2010) Interaction intensity and importance along two stress gradients: adding shape to the stress-gradient hypothesis. *Oecologia* **162**, 733–45.
- le Roux P. C., McGeoch M. A., Nyakatia M. J. & Chown S. L. (2005) Effects of a short-term climate change experiment on a sub-Antarctic keystone plant species. *Global Change Biol.* **11**, 1628–39.
- Selkirk P. M. (2012) Plateau vegetation on sub-antarctic macquarie Island. *Pap. Proc. R. Soc. Tasman.* **146**, 71–9.
- Selkirk P. M., Seppelt R. D. & Selkirk D. R. (1990) *Subantarctic Macquarie Island: Environment and Biology*. Cambridge Press University Press, Cambridge.
- Shaw J. (2005) *The Reproductive Ecology of Vascular Plants on Subantarctic Macquarie Island (Unpublished Doctoral Dissertation)*. University of Tasmania, Hobart.
- Sonter R. O., Semple W. S. & Lawrie J. W. (2000) Soils, vegetation and land use. In: *Soils: Their Properties and Management* (eds P. E. Charman & B. W. Murphy) pp. 271–86. Oxford University Press, Melbourne.
- Taylor B. W. (1955) The flora, vegetation and soils of Macquarie Island. In: *ANARE Reports, Series B*, **11**, 1–192. Australian Antarctic Division, Melbourne.
- Tweedie C. E. & Bergstrom D. M. (2000) A climate change scenario for surface air temperature at subantarctic Macquarie Island (ed.). In: *Antarctic Ecosystems: Models for Wider Understanding* (eds W. Davison, C. Howard-Jones & P. Broady) pp. 272–81. Canterbury University Press, Canterbury.
- Verbala D. (2008) The greening and browning of Alaska based on 1982–2003 satellite data. *Global Ecol. Biogeogr.* **17**, 547–55.
- Walsh C. & Mac Nally R. (2015) Package 'hier.part': Hierarchical Partitioning. Version 1.0–4. p. Variance partition of a multivariate data set. CRAN. Available from URL: <https://CRAN.R-project.org/package=hier.part>.
- Whinam J., Abdul-Rahman J. A., Visoiu M., di Folco M. B. F. & Kirkpatrick J. B. (2014) Spatial and temporal variation in damage and dieback in a threatened subantarctic cushion species. *Aust. J. Bot.* **62**, 10–21.
- Wintle B. C., Fidler F., Vesk P. A. & Moore J. L. (2013) Improving visual estimation through active feedback. *Methods Ecol. Evol.* **4**, 53–62.
- Wood S. N. (2017) *Generalized Additive Models: An Introduction With R*. Chapman and Hall/CRC, New York.

Zeileis A., Cribari-Neto F., Gruen B. *et al.* (2016) betareg: Beta Regression. Version 3.1-0. Available from URL: <https://CRAN.R-project.org/package=betareg>

SUPPORTING INFORMATION

Additional supporting information may/can be found online in the supporting information tab for this article.

Appendix S1. Extended methods of the terrain class model (TCM) and subsequent stratified random site selection, to ensure the full range of microclimate potentially experienced by *Azorella macquariensis* was sampled.

Appendix S2. *Azorella macquariensis* cover and die-back candidate models used in the multimodel inference approach to estimate effect sizes of predictor variables.

Published as:

APPENDIX S1.

TERRAIN CLASS MODEL AND SITE SELECTION

Identifying terrain classes

A terrain class model (TCM) was developed to stratify the selection of sampled field sites to represent the breadth of microclimate conditions to which *Azorella macquariensis* is exposed. Terrain classes, i.e. discrete areas within the landscape that share similar terrain structure, were identified using a fuzzy c-means clustering (*cluster* package in R) on terrain variables, to assign cluster membership to each site based on the terrain characteristics of the site. Terrain variables were calculated as in Bricher *et al.* (2013), using a 5m x 5m resolution Digital Elevation Model (DEM) of Macquarie Island (Brolsma 2008). Because the large field sites (706.86 m²) were selected on ground with likely lower precision than the resolution of the DEM, the DEM derived variables (5m x 5m) were aggregated to 100m x 100m, and all further analysis for the TCM was conducted on these aggregated data. Variables used in the TCM included those that capture different mechanisms through which terrain variation might affect microclimate variation conditions: elevation; slope; surface curvature; topographic wetness index (Wetness_Index); solar radiation (Solar_Rad); and topographically-deflected wind speed (Wind_Speed) (Table S1.1.). Slope was highly correlated with Solar_Rad ($r = 0.74$) and was therefore excluded from the TCM. The maximum correlation between variables was between Wetness_Index and Solar_Rad ($r = 0.511$; Fig. S1.1). The optimum number of cluster centres was determined by comparison of three different metrics: (i) Xie-Beni Index (Fig. S1.2), which measures the overall compactness and separation of clusters (Xie and Beni 1991); (ii) cluster stability (Fig. S1.3), which is the pairwise correlation between cluster solutions seeded with different initial cluster centres (similar to method of Mahlstein and Knutti 2010); and (iii) the number of components in a Principle Components Analysis (PCA) explaining $\geq 95\%$ of the variation (Table S1.2). Based on these three indices a five-cluster solution was confirmed as the optimal fuzzy cluster solutions for these data.

Broadly, the characteristics of each cluster can be described as:

- Cluster 1 (red) is associated with the highest elevation sites, which also receive the highest amount of solar radiation. These cells are intermediate in terms of wind speed and wetness index.
- Cluster 2 (blue) is associated with cells that are at a slightly lower elevation than those in cluster 1. Cluster 2 cells are amongst the wettest areas, but intermediate in wind exposure.
- Cluster 3 (green) is associated with cells that are the least exposed to wind. These areas typically have a low to intermediate wetness index.
- Cluster 4 (purple) is associated with cells that are highly wind exposed, and are amongst the driest areas on the island.
- Cluster 5 (orange) is associated with cells that are on the coastal margins of the island, are wet, and have intermediate exposure to wind and solar radiation.

Table S1.1. Topographic variables used in the terrain class model (TCM) and/or beta regression (BR) models for *Azorella macquariensis* cover and dieback on Macquarie Island (MI).

Variable	Justification	TCM	BR
Latitude (measured by Northing) (m)	Macquarie Island is a long narrow island, approximately north-south in orientation. Macro-scale gradients, such as latitude, often form proxies for other ecological gradients that effect the distribution and abundance of species (Gaston 2000). Southern <i>A. macquariensis</i> populations have been observed to have high cover, often occurring in mat form (Bergstrom <i>et al.</i> 2015), suggesting a macroscale gradient on the island. While there is a number of potential ecological variables that latitude could be correlated with, it is possible that latitude may provide a surrogate for climatic conditions. The southern plateau is regularly observed to be shrouded in cloud (Selkirk <i>et al.</i> 1990), which potentially increases in relative humidity and decreases in temperature as the latitude increases (towards the south).	✗	✓
Elevation (m)	The vegetation of MI has a strong relationship with elevation, with <i>A. macquariensis</i> at highest density at >200m asl (Bricher <i>et al.</i> 2013). Elevation also provides a proxy for temperature, which has a lapse rate of 0.8°C per 100m on the island (Tweedie and Bergstrom 2000).	✓	✓
Distance to west coast (West_Dist) (m)	The prevailing and strong winds are westerly to north-westerly on Macquarie Island (Fitzgerald and Kirkpatrick 2017), which brings warmer and wetter fronts (Adams 2009). Sister species <i>A. selago</i> is susceptible to drought that causes stem senescence, as a likely function of both humidity and wind (le Roux <i>et al.</i> 2005). <i>A. macquariensis</i> is susceptible to abrasion from cold, dry winds from the southwest (Fitzgerald and Kirkpatrick 2017). The importance of humidity to <i>A. macquariensis</i> , and the contribution of wind directionality to relative humidity, suggests that distance to west coast will be more ecologically important than distance to the nearest coastline.	✗	✓

Topographic wetness index (Wetness_Index) (no units)	The wetness index provides a different proxy for soil water availability, determined by the position of the site within the catchment (Beven and Kirkby 1979; Bricher <i>et al.</i> 2013). For example, those sites which are located on ridgelines are generally drier than those located in valley bottoms in the base of the catchment.	✓	✓
Topographically-deflected wind speed (Wind_Speed) (km.hr⁻¹)	Measure of exposure to varying wind-speeds, which may provide a proxy for water-loss through increased evapotranspiration (Bonan 2008). Wind speed is calculated from the slope, curvature and slope based on the average prevailing wind of 35.1 km -hr ⁻¹ from the northwest to west (Bricher <i>et al.</i> 2013).	✓	✓
Solar radiation (Solar_Rad) (Wm⁻²)	Solar radiation directly facilitates plant growth through the provision of light energy for photosynthesis (Bonan 2008) and indirectly through affecting heating of air and surfaces (Fu and Rich 2002), wind speed and snow melt (Bonan 2008). Solar irradiation levels are an important factor in microsite selection in a related species, <i>A. compacta</i> (Kleier <i>et al.</i> 2015). Solar radiation was calculated over a year using the solar radiation function in ArcGIS 9.3 (Bricher <i>et al.</i> 2013)	✓	✗
Curvature (no units)	Landform curvature is important for calculating the flow paths of water in the landscape, influencing flow convergence and divergence (Zevenbergen and Thorne 1987). In absence of localised precipitation across the island, it provides a proxy for water availability.	✓	✗

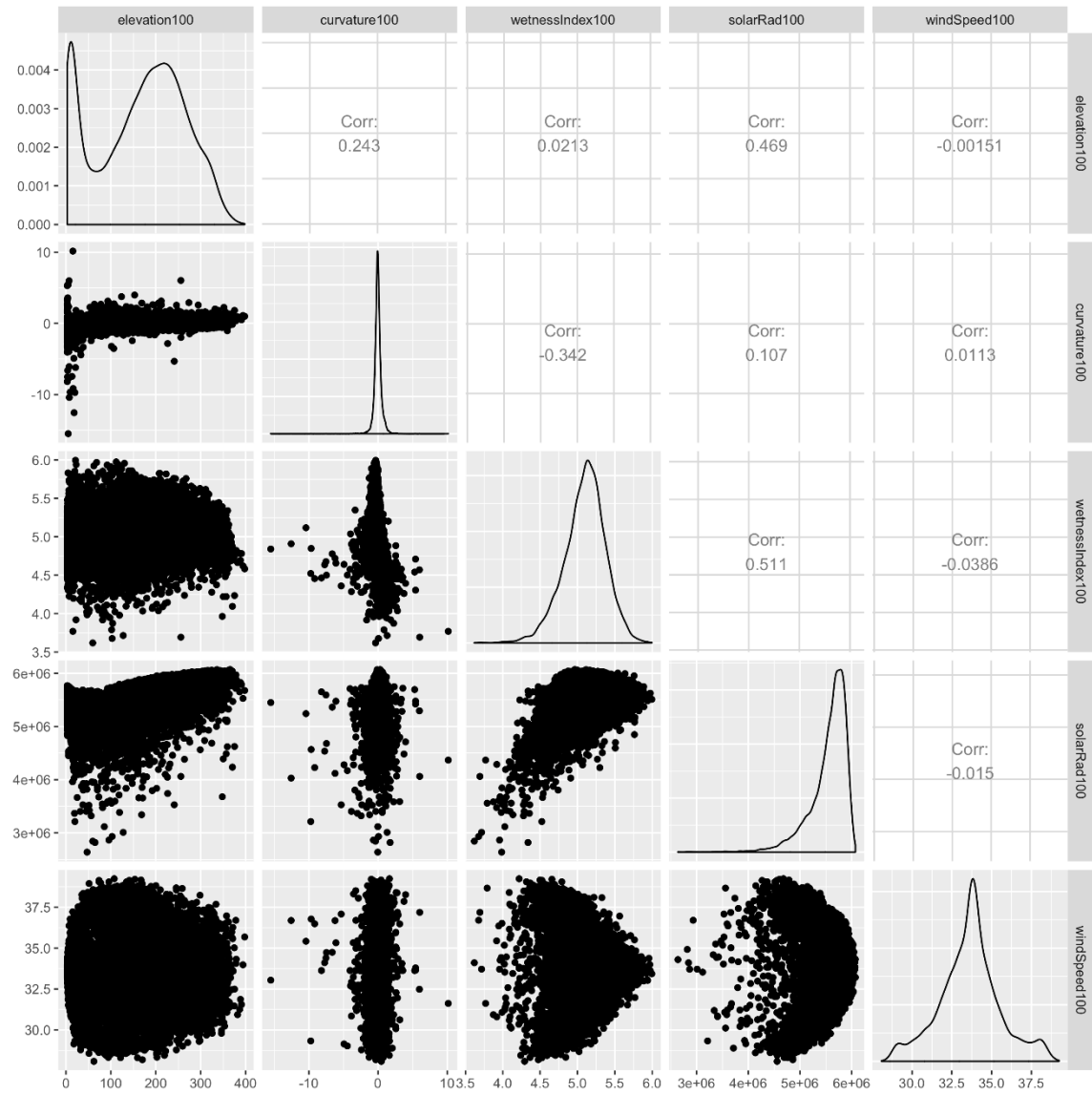


Figure S1.1. Pair-wise correlations for five terrain variables at a spatial resolution of 100 m x 100 m (mean across all sub-cells).

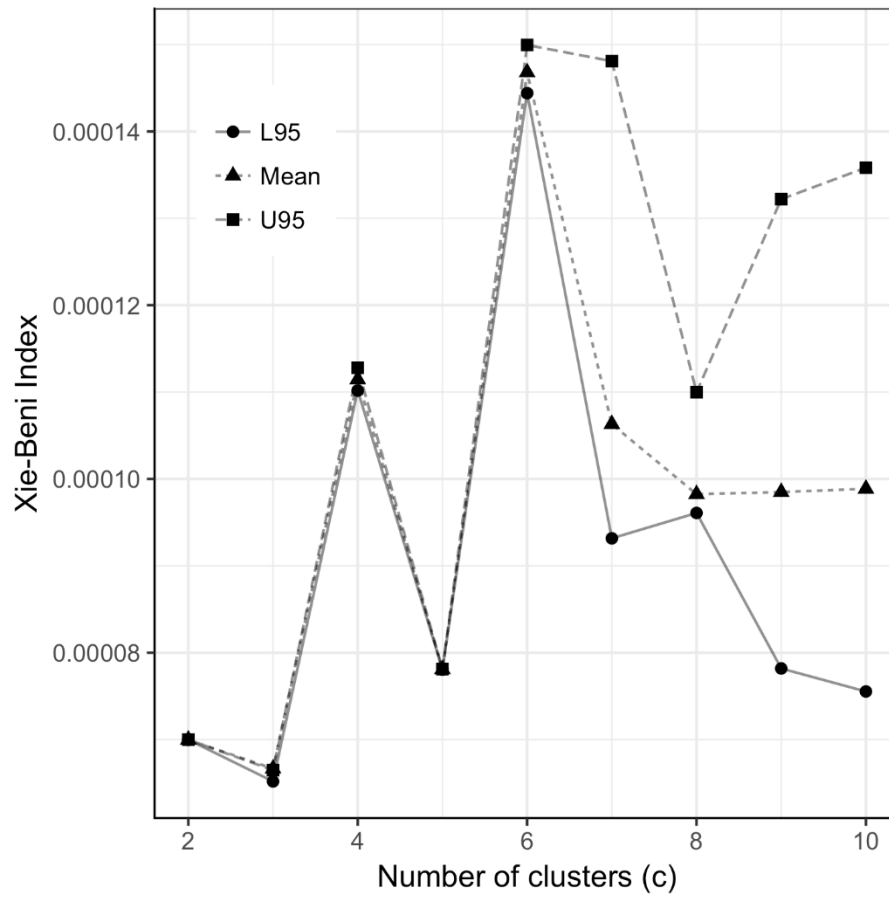


Figure S1.2. Xie-Beni Index for cluster solutions 2-10 suggesting two, three or five clusters may be optimal.

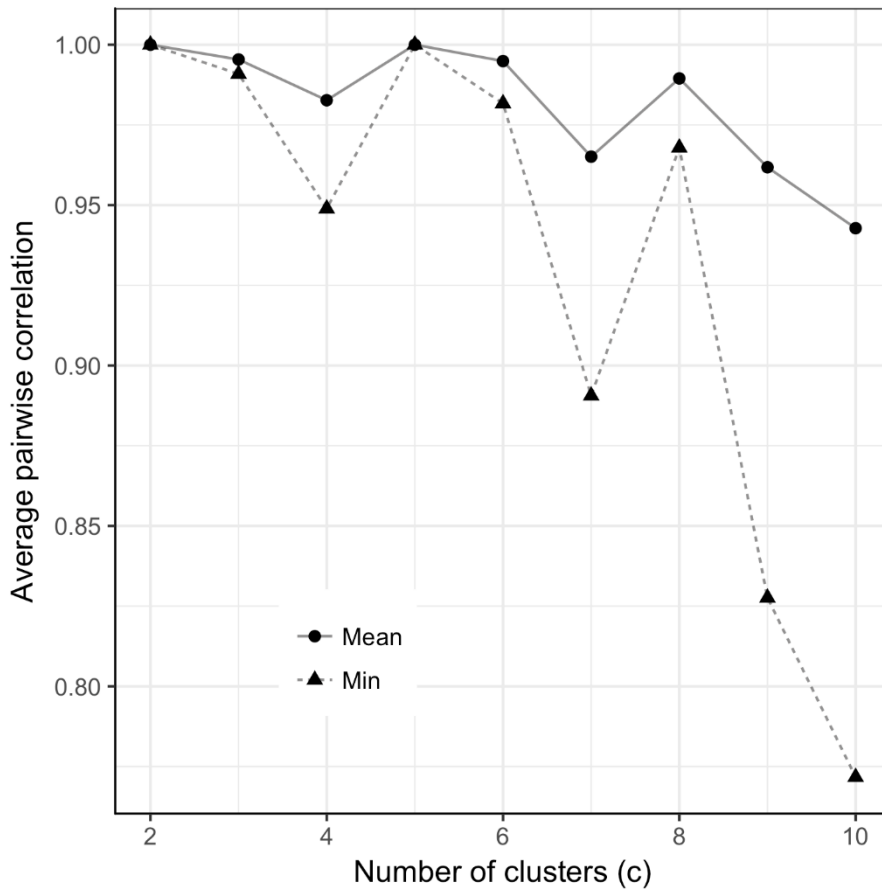


Figure S1.3. Average pairwise correlation between cluster solutions suggest that two, three or five clusters may be optimal.

Table S1.2. Principle Component Analysis (PCA) applied to these data showed that four or more components were required to explain $\geq 95\%$ of the variation in these data.

	PC1	PC2	PC3	PC4	PC5
SD	1.31	1.19	1	0.78	0.53
Proportion of variance	0.34	0.28	0.20	0.12	0.18
Cumulative proportion of variance	0.34	0.62	0.82	0.95	0.1

Stratified random site selection

To stratify the putative microclimate we chose not to use a hard clustering approach (i.e. assigning a cell to the cluster with the highest membership association) because the membership associations suggest that many cells exist on the boundary between two or more clusters. These associations could lead to an overly confident representation of the mesoclimate classifications, where noise in the data (DEM error $\pm 5\text{m}$) could result in many cells shifting between cluster assignments. Therefore cells were only retained for field site selection if the highest cluster membership association was at least double that of the second highest cluster centre membership association (Fig S1.4). This maximised the likelihood of sampling the full range of microclimate conditions across the island and provided good contrast in the mesoclimate conditions experienced at the sites that were selected for surveys (Figs. S1.4. and S1.5.). Cluster 5 was removed from the site selection because it contains habitat unsuitable for *A. macquariensis*, primarily tarns and hyper-saturated lowland featherbeds (bogs) (Taylor 1955).

Survey sites were then selected by randomly sampling the retained cells from across each of the eight geographic blocks (clustered on latitude and longitude), ensuring that a minimum of two cells from each of four clusters are selected per geographic block (Figs. S1.6. and S1.7.). This was done to ensure that terrain clusters were represented across the geographic extent of the island. If randomly generated sites were located in the same terrain cluster and within 100 m of historical monitoring sites established by Whinam *et al.* (2014), Bergstrom *et al.* (2015) or Bricher *et al.* (2013), then the sites were collocated.

Once field site selection had been completed, the 70 realised site locations met the following conditions: (i) within 100 m of the randomly generated point, (ii) remained within the cluster cell, (iii) *Azorella* was present ($>0\%$ cover) at 62 sites and an additional eight sites had no *A. macquariensis* (absences), and (iv) the site could be safely accessed. An additional 20 sites, to bring the total number of sites to 90, were established to increase spatial representation in areas of core *Azorella* habitat and were primarily collocated with historical sites. The position of sampled sites thus represented the range of micro-topography experienced by *Azorella macquariensis* on Macquarie Island, and consequently the putative range of microclimates that exist on the island within those areas that *Azorella* is known to occupy (Fig. S1.8.).

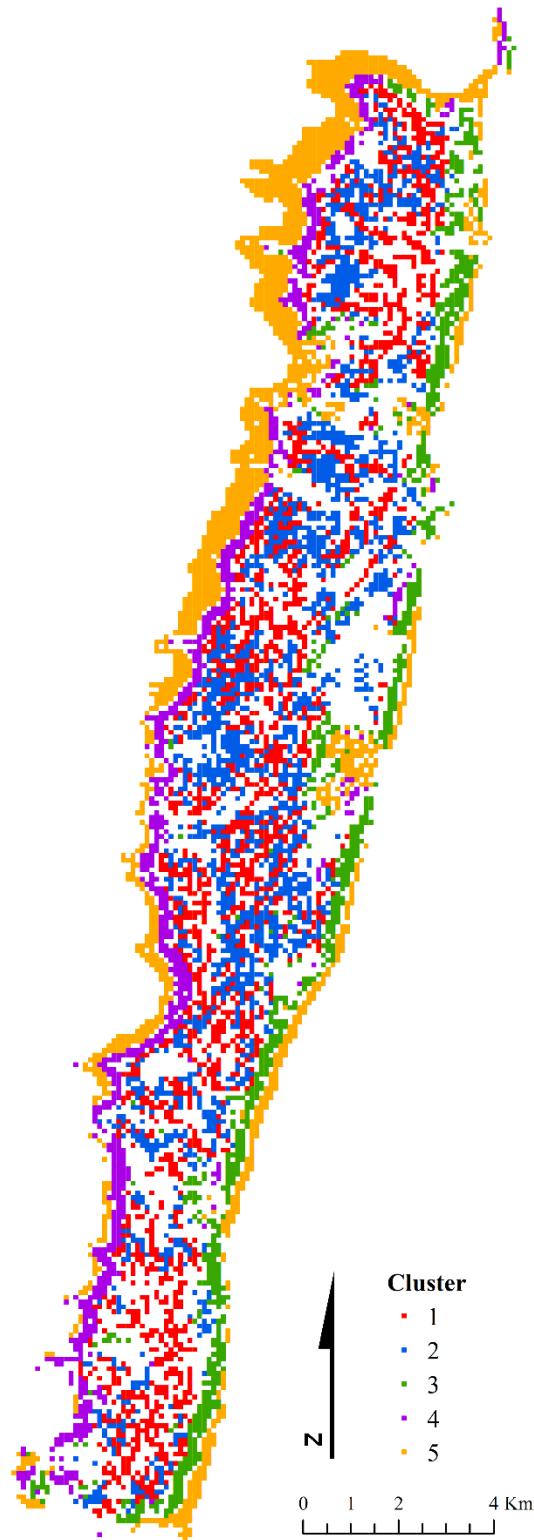


Figure S1.4. The distribution of cluster solutions across Macquarie Island when cells with a cluster membership association of at least double that of the second highest cluster membership association are retained.

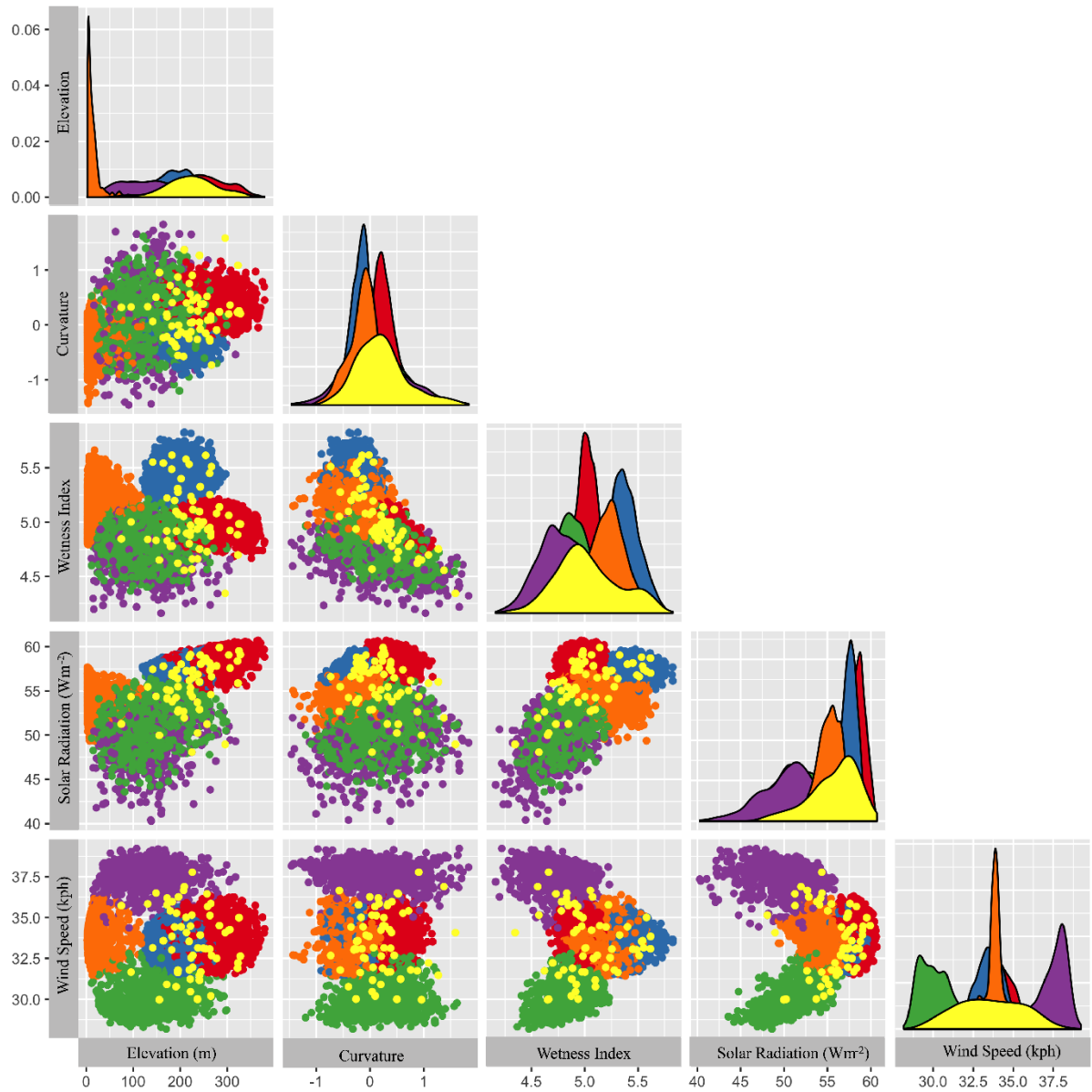


Figure S1.5. The pair-wise parameter space occupied by each of the five clusters after the removal of cells with a cluster membership association of less than double that of the second highest cluster membership association are retained. Overlaid in yellow is the distribution of survey sites selected by a stratified random sampling from both geographic and environmental space (solar radiation adjusted for presentation $\times 10^5$)

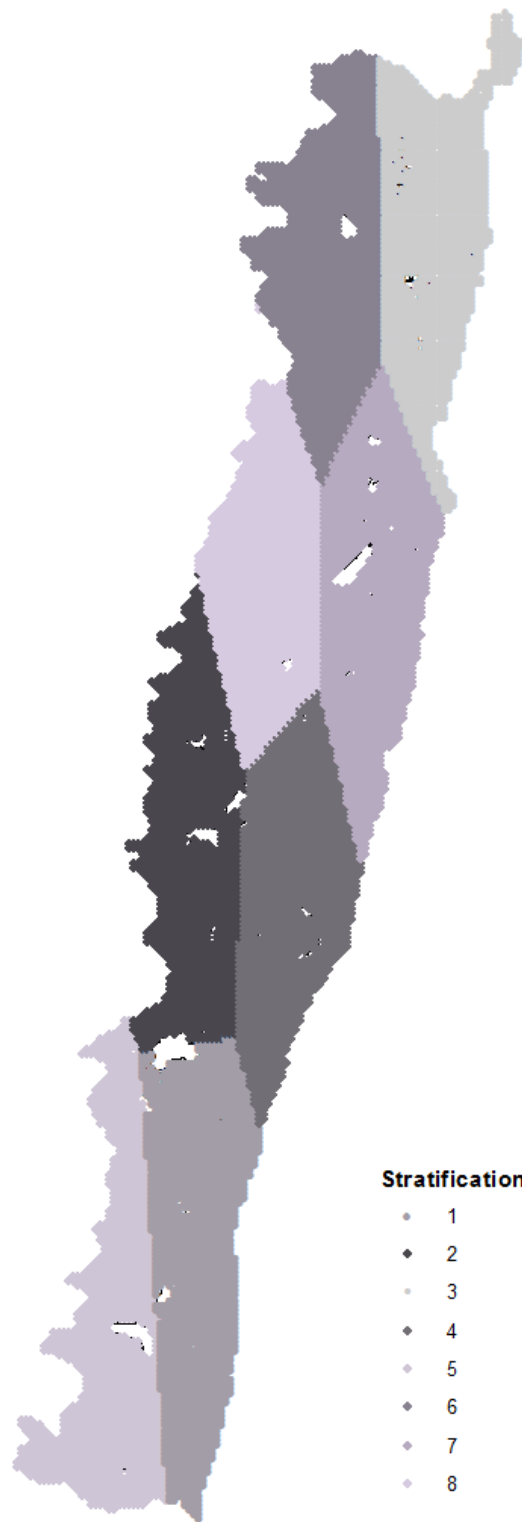


Figure S1.6. Blocking of the island for geographic component of the stratified sampling. Blocking was achieved using k-means clustering on latitude and longitude coordinates with $k = 8$.

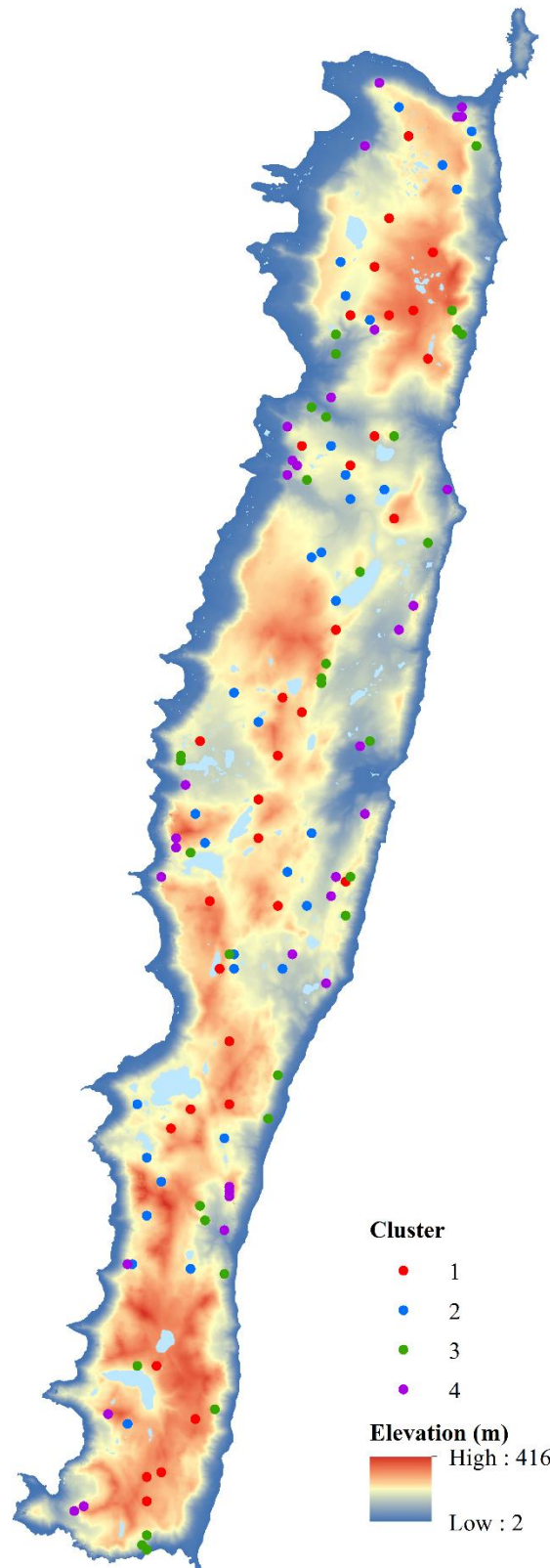


Figure S1.7. Site selection results, based on stratified random sampling by terrain classes and geographic blocks across Macquarie Island.

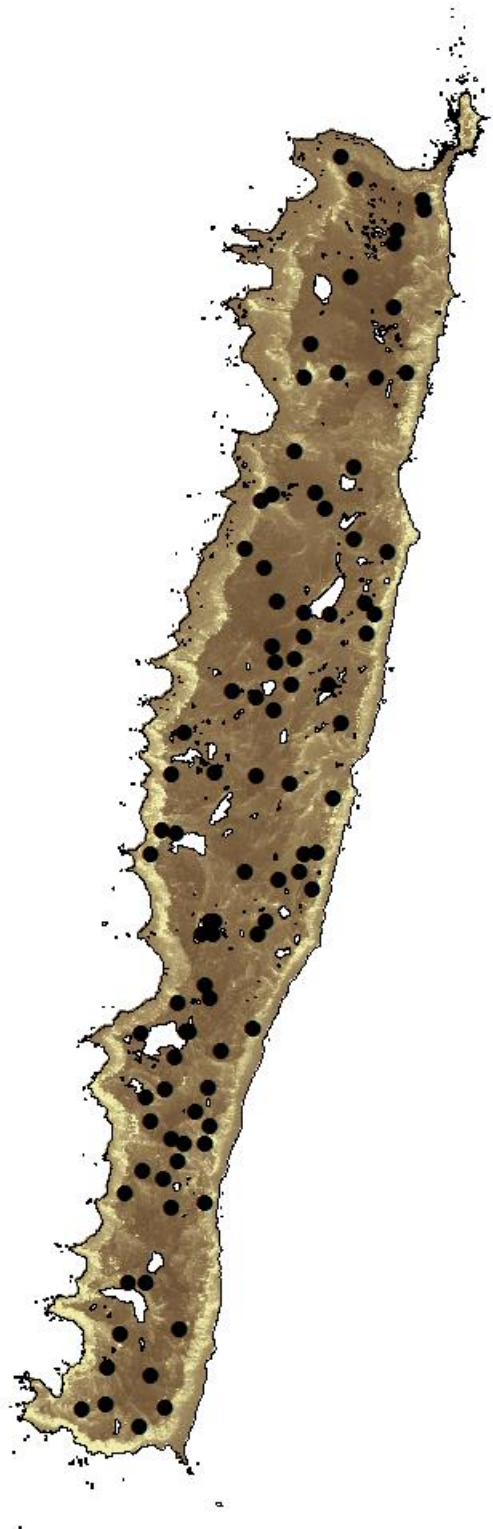


Figure S1.8. Sites established in the field across the putative microclimate on Macquarie Island.

REFERENCES

- Adams N. (2009) Climate trends at Macquarie Island and expectations of future climate change in the sub-Antarctic. *Pap. Proc. R. Soc. Tasman.* **143**, 1-8.
- Bergstrom D. M., Bricher P. K., Raymond B., *et al.* (2015) Rapid collapse of a sub-Antarctic alpine ecosystem: the role of climate and pathogens. *J. Appl. Ecol.* **52**, 774-83.
- Beven K. J. & Kirkby M. J. (1979) A physically based, variable contributing area model of basin hydrology. *Hydrological Sciences Bulletin* **24**, 43-69.
- Bonan G. B. (2008) *Ecological climatology : concepts and applications*. Cambridge : Cambridge University Press, Cambridge.
- Bricher P. K., Lucieer A., Shaw J., Terauds A. & Bergstrom D. M. (2013) Mapping Sub-Antarctic Cushion Plants Using Random Forests to Combine Very High Resolution Satellite Imagery and Terrain Modelling. *PLOS ONE* **8**, 1-15.
- Brolsma H. (2008) Macquarie Island AIRSAR DEM (Digital Elevation Model). <http://data.aad.gov.au/aadc/metadata/>.
- Fitzgerald N. B. & Kirkpatrick J. B. (2017) Wind distortion in alpine and subantarctic plants is constant among life forms but does not necessarily reflect prevailing wind direction. *Arct. Antarct. Alp. Res.* **49**, 521-35.
- Fu P. D. & Rich P. M. (2002) A geometric solar radiation model with applications in agriculture and forestry. *Comput. Electron. Agric.* **37**, 25-35.
- Kleier C., Trenary T., Graham E. A., Stenzel W. & Rundel P. W. (2015) Size class structure, growth rates, and orientation of the central Andean cushion *Azorella compacta*. *Peerj* **3**, 1-14.
- le Roux P. C., McGeoch M. A., Nyakatya M. J. & Chown S. L. (2005) Effects of a short-term climate change experiment on a sub-Antarctic keystone plant species. *Global Change Biol.* **11**, 1628-39.
- Mahlstein I. & Knutti R. (2010) Regional climate change patterns identified by cluster analysis. *Climate Dynamics* **35**, 587-600.
- Taylor B. W. (1955) The flora, vegetation and soils of Macquarie Island. In: *ANARE Reports, Series B*, 11, 1-192. Australian Antarctic Division, Melbourne.
- Tweedie C. E. & Bergstrom D. M. (2000) A climate change scenario for surface air temperature at subantarctic Macquarie Island (ed.). In: *Antarctic Ecosystems: Models for Wider Understanding* (eds W. Davison, C. Howard-Jones and P. Broady) pp. 272-81. Canterbury University Press, Canterbury.

- Whinam J., Abdul-Rahman J. A., Visoiu M., di Folco M. B. F. & Kirkpatrick J. B. (2014) Spatial and temporal variation in damage and dieback in a threatened subantarctic cushion species. *Aust. J. Bot.* **62**, 10-21.
- Xie X. L. L. & Beni G. (1991) A validity measure for fuzzy clustering. *Ieee Transactions on Pattern Analysis and Machine Intelligence* **13**, 841-47.
- Zevenbergen L. W. & Thorne C. R. (1987) Quantitative analysis of land surface topography. *Earth Surface Processes and Landforms* **12**, 47-56.

APPENDIX S2

Table S2.1. *Azorella macquariensis* cover candidate models used in the multimodel inference approach to estimate effect sizes of predictor variables. Term codes: Elevation (1), Latitude (2), Solar_Rad (3), West_Dist (4), West_Dist^2 (5), Wetness_Index (6), Wind_Speed (7).

Component models	df	Log likelihood	AICc	delta	weight
1257	6	57.77	-102.52	0	0.12
125	5	56.17	-101.63	0.89	0.07
124	5	55.77	-100.82	1.7	0.05
12457	7	58.06	-100.75	1.77	0.05
1245	6	56.74	-100.48	2.04	0.04
12	4	54.43	-100.39	2.13	0.04
12567	7	57.86	-100.36	2.16	0.04
12357	7	57.84	-100.32	2.2	0.04
2357	6	56.63	-100.26	2.26	0.04
1235	6	56.44	-99.88	2.65	0.03
235	5	55.27	-99.82	2.7	0.03
1256	6	56.39	-99.78	2.74	0.03
1246	6	56.37	-99.73	2.79	0.03
1247	6	56.35	-99.68	2.84	0.03
127	5	55.15	-99.58	2.94	0.03
257	5	55.12	-99.53	2.99	0.03
126	5	55.01	-99.3	3.22	0.02
12456	7	57.05	-98.73	3.79	0.02
1234	6	55.86	-98.7	3.82	0.02
124567	8	58.2	-98.62	3.9	0.02
123	5	54.6	-98.49	4.03	0.02
12345	7	56.92	-98.47	4.05	0.02
123457	8	58.1	-98.43	4.09	0.02
12467	7	56.88	-98.4	4.12	0.01
1267	6	55.66	-98.31	4.21	0.01
23457	7	56.83	-98.29	4.23	0.01
2345	6	55.64	-98.26	4.26	0.01

123567	8	57.9	-98.03	4.49	0.01
23567	7	56.65	-97.94	4.58	0.01
2457	6	55.42	-97.82	4.7	0.01
12356	7	56.56	-97.75	4.77	0.01
2356	6	55.27	-97.52	5	0.01
25	4	52.99	-97.51	5.01	0.01
1237	6	55.21	-97.4	5.12	0.01
12346	7	56.38	-97.4	5.13	0.01
12347	7	56.37	-97.37	5.15	0.01
2567	6	55.12	-97.24	5.28	0.01
1236	6	55.06	-97.1	5.42	0.01
234	5	53.91	-97.1	5.42	0.01
23	4	52.57	-96.67	5.85	0.01
123456	8	57.12	-96.46	6.06	0.01
245	5	53.57	-96.42	6.1	0.01

Term code	2	1	5	7	4	3	6
Importance:	1	0.81	0.69	0.5	0.37	0.33	0.26
N containing models	42	29	26	19	19	21	16

Table S2.2. *Azorella macquariensis* dieback candidate models used in the multimodel inference approach to estimate effect sizes of predictor variables. Term codes: Cover (1), Cover^2 (2), Elevation (3), Latitude (4), Solar_Rad (5), West_Dist (6), Wetness_Index (7), Wind_Speed (8).

Component models	df	Log likelihood	AICc	delta	weight
124	5	39.08	-67.37	0	0.15
1247	6	39.67	-66.22	1.15	0.09
1234	6	39.57	-66.03	1.34	0.08
1245	6	39.44	-65.75	1.62	0.07
12345	7	40.61	-65.71	1.66	0.07
1248	6	39.28	-65.44	1.93	0.06
1246	6	39.08	-65.05	2.32	0.05
12347	7	40	-64.49	2.88	0.04
123458	8	41.18	-64.39	2.98	0.03
12478	7	39.92	-64.33	3.04	0.03
12457	7	39.9	-64.28	3.09	0.03
12348	7	39.86	-64.21	3.16	0.03
12458	7	39.71	-63.9	3.47	0.03
12467	7	39.67	-63.82	3.55	0.03
12346	7	39.58	-63.64	3.73	0.02
123457	8	40.76	-63.55	3.82	0.02
12456	7	39.45	-63.39	3.98	0.02
123456	8	40.61	-63.25	4.12	0.02
12468	7	39.28	-63.04	4.33	0.02
123478	8	40.33	-62.69	4.68	0.01
124578	8	40.21	-62.44	4.93	0.01
1234578	9	41.33	-62.16	5.21	0.01
123467	8	40.01	-62.05	5.33	0.01
1234568	9	41.2	-61.89	5.48	0.01
124678	8	39.93	-61.88	5.49	0.01
124567	8	39.9	-61.83	5.54	0.01
123468	8	39.88	-61.8	5.57	0.01
124568	8	39.71	-61.45	5.92	0.01

1234567	9		40.76	-61.02	6.35	0.01		
14	4		34.5	-60.49	6.88	0		
<hr/>								
Term Code:	1	4	2	3	5	7	8	6
Importance:	1	1	1	0.38	0.35	0.32	0.28	0.22
N containing								
models	30	30	29	14	14	13	13	13
<hr/>								

Chapter 2

Fine-scale variability and drivers of dieback in a keystone cushion plant on sub-Antarctic Macquarie Island

Introduction

Anthropogenic climate change is one of the greatest challenges facing conservation managers. In addition to the direct impacts of climate change on plants and animals, emerging diseases and pathogens are anticipated to become an increasing threat as a consequence (Harvell et al. 2002; Hoberg and Brooks 2015). Species have both a variable susceptibility and response to different pathogens under changing climates (Rohr et al. 2011; Chakraborty 2013). Despite this, crop pathogens have moved on average 2.7 ± 0.8 km yr⁻¹ poleward since 1960, increasing their global footprint and threatening future food security (Bebber et al. 2013). The emergence of novel pathogens under climate change suggests that plants are maladapted to the new threat, leaving them unable to use evolved strategies to resist disease (Stenlid and Oliva 2016). Landscape-scale plant mortalities have often been associated with warmer, wetter conditions, and less extreme minimum temperatures and higher humidity are increasing the prevalence of plant diseases in both agricultural and natural systems (Harvell et al. 2002; Anderson et al. 2004; Garrett et al. 2016). One such example of extensive pathogen spread is *Dothistroma septosporum* needle blight of pines. It occurs in forestry and natural systems, across both hemispheres in response to a higher frequency of warm rain events (Woods et al. 2005). Another example is *Xylella fastidiosa*, a plant pathogen with a broad host range from the Americas that is predicted to expand further through Europe, and potentially globally, under future climate conditions (Sicard et al. 2018). The negative consequences of this increasing pathogen footprint are likely to be severe for biodiversity (Harvell et al. 2002) and ecosystem services (Fisher et al. 2012; Boyd et al. 2013).

Higher elevation and latitude sites are particularly susceptible to novel pathogens as historically cold climates become warmer, with less extreme cold events (Pauchard et al. 2016). The increasingly mild winter conditions and lack of extreme cold events allow for higher pathogen survival in several plant species (Harvell et al. 2002). In these regions, cold-adapted species may be increasingly susceptible to disease under higher temperatures and changing disease communities (Cohen et al. 2019). For example, the root-rot fungus *Phytophthora cinnamomi* is predicted to expand into the Australian alpine region with the reduction of extreme cold events (Burgess et al. 2017). The ongoing island-wide dieback of the dominant alpine species *Azorella macquariensis* Orchard (Apiaceae, Macquarie cushions) on sub-Antarctic Macquarie Island (Whinam et al. 2014; Bergstrom et al. 2015) is the first occurrence of landscape-scale dieback in the sub-Antarctic. Despite no causal disease being identified, a number of fungal,

bacterial and oomycete taxa have been identified in association with *A. macquariensis*, including some pathogenic taxa (Bergstrom et al. 2015).

The trigger for *A. macquariensis* dieback was hypothesised to be a reduction in plant available water over 17 summer growing seasons that facilitated a secondary pathogenic infection of weakened plants (Bergstrom et al. 2015). However, the relationship between climate conditions, pathogens and cushion plant decline remains poorly understood, and the pathogens responsible have not been identified. It is also unclear whether ongoing dieback is driven by conditions that (i) continue to place the plant under water stress (low plant available water) during the summer growing season, (ii) are increasingly conducive to pathogens during winter, which coincides with *A. macquariensis* dormancy, or (iii) a combination of both factors. Despite *A. macquariensis* being physiologically adapted to the small daily fluctuations of stable oceanic island weather (Rolland et al. 2015), similar to the closely related *A. selago* (le Roux et al. 2005) it is not well adapted to the increased evapotranspiration rates on the island and increased variability in rainfall (Bergstrom et al. 2015). If water stress alone is driving dieback, this suggests that the highest proportion of dieback would be located in areas of highest abiotic ‘stress’ on the island. Topographic modelling of *A. macquariensis* dieback found latitude (N-S location on island) to be a significant predictor of plant condition, while other macro-variables (elevation, distance to west coast) and topographically-derived variables (topographically deflected wind speed and topographic wetness index) that are likely to affect evapotranspiration rates were unrelated to plant condition (Dickson et al. 2019). Therefore, while the comparatively coarse topographic modelling allowed some topographically derived variables to be ruled out as likely drivers of this decline in plant condition, the mechanisms responsible for the highly spatially variable *A. macquariensis* dieback remain poorly understood.

Plant distribution and condition responds to fine-scale climate variation (Körner and Hiltbrunner 2018). Furthermore, species’ can vary their phenotypical response to seasonal variation (Körner and Hiltbrunner 2018). Therefore, to effectively detect, quantify and monitor change in *A. macquariensis* and the associated fellfield ecosystem, it is necessary to characterise the fine-scale spatial variability in the system (see Bland et al. 2018; Sato and Lindenmayer 2018). Previously, *A. macquariensis* condition has been assessed using three approaches: a binary presence-absence of dieback (Bergstrom et al. 2015; Dickson et al. 2019); three broad condition classes (healthy, brown, black; Bergstrom 2013, updated 2014); or alternately four classes (healthy versus the damage classes: yellow, speck, and grey; Whinam

et al. 2014). The condition classes used previously did not consistently record percentage cover or identify the stage or type of dieback. For example, Whinam et al. (2014) makes no distinction between naturally occurring wind-scour dieback and the necrosis following the chlorosis line. However, the ability to understand the progression and rate of spread of pathogen driven dieback across the island is limited by the joint class. Separating *A. macquariensis* into finer-scale condition classes, with detailed descriptions of each, would allow better quantification of the spatial distribution and variation in cushion condition. It would also enable a better understanding of the island-wide progression of dieback through the development of condition classes that identify the stage of dieback, and establish replicable monitoring of populations thereafter.

The fine-scale response of plants to climate (Körner and Hiltbrunner 2018) means that it is also important to use relational and abiotic data at relevant spatial and temporal scales to identify relationships between plant vitality and the environment (Graae et al. 2012). This is particularly relevant for alpine systems, where the low-growing flora are strongly influenced by soil and near-ground temperatures, in contrast to the surrounding free-air macro-climate as generally measured by local weather stations (Körner and Hiltbrunner 2018; Lembrechts et al. 2019). Macquarie Island is characterised by a tree-less alpine plateau (>200 m above sea level, asl), where the low-growing (< 450 mm high) *A. macquariensis* is the dominant vascular species (Taylor 1955). The highly variable cushion is dormant during the colder winter period (April – September) and its leaves senesce (Taylor 1955), and this may reduce the effects of small scale winter climate variation. However, the increasingly wet winter climate may benefit pathogens increasing the extent of cushion dieback. Therefore, accurate seasonal microclimate measurements on Macquarie Island, at a scale representative of cushion conditions, are needed if the drivers of cushion condition are to be teased apart.

To better understand dieback progression at a landscape scale, I test if there is a relationship between plant location on the island and cushion condition using a standardised quantification of cushion condition classes and subclasses, along with *in-situ* microclimate measurements. The support for two hypotheses that may also operate additively or synergistically, is then examined. Dieback severity is predicted either by (i) stress caused by above-ground microclimate conditions (water-stress hypothesis) or (ii) pathogen activity (pathogen hypothesis). If microclimate stress drives condition, *A. macquariensis* dieback is expected to increase vapour pressure deficit (VPD) and exposure to drying winds (Bergstrom et al. 2015) or potentially with high fine gravel content (if related to soil water holding capacity) (Whinam

et al. 2014). Alternatively, if dieback severity is predicted by pathogen activity then dieback is expected to be high at sites with fewer, less extreme cold days (Burgess et al. 2017) and high humidity (Huber and Gillespie 1992). Building on the coarse-scale climate and cushion condition approach taken in Chapter 1, this chapter uses microclimate and fine-scale cushion condition classes to further tease apart the drivers of dieback. The implication of the results are discussed in the context of the future persistence and management of this critically endangered keystone species under projected climate change.

Materials and methods

Study system

The World Heritage listed Macquarie Island (54°30'S, 158°55'E) is an oceanic sub-Antarctic island of 123.9 km² (~c. 34 km long, c. 5 km wide) (Fig. 1). The island is surrounded by steep escarpments, which rise to an undulating alpine plateau, extending between 200 and 433 m above sea level (asl) (Selkirk et al. 1990). Historically the local climate has been very stable, primarily cool (av. 4.8°C), misty (RH, 89 %, rainfall 895 mm annum⁻¹) and windy (9.3 ms⁻¹) (Selkirk et al. 1990). However, there has been a significant change in the regional climate during the past 40 years (Bergstrom et al. 2015), represented as an increase in sunshine hours, increase in average wind speeds (Bergstrom et al. 2015), and more frequent, extreme cyclonic events (Adams 2009). The average temperature increased to the late 1980s (Adamson et al. 1988) when the mean warming temperatures plateaued (Pendlebury and Barnes-Keoghan 2007). Despite a substantial increase in annual rainfall to 1080 mm year⁻¹, the rainfall primarily occurs as more intense events in winter and is now more episodic (Bergstrom et al. 2015). These conditions have resulted in a significant increase in the evapotranspiration rate and a decadal reduction in plant available water during the summer growing season from 1990 to 2008 (Bergstrom et al. 2015).

The perennial semi-deciduous endemic *Azorella macquariensis* is the dominant vascular species on the island plateau and is found in three habitats, east-facing slopes, fellfield and polar deserts, and sub-dominant in mid-elevation short-grasslands (Selkirk 2012; Bricher et al. 2013). The species ranges in form from discrete cushions through to extensive mats and is a major component of the iconic terraces on the island (Orchard 1989). *A. macquariensis* undergoes winter dormancy (~April – September), with senesced leaves held within the canopy

to decompose, before new leaves are produced for the summer growing season (October – March) (Taylor 1955). The cushion's winter dormancy suggesting that the increased winter rainfall is of little value for growth. Within the top 2-5 cm of canopy, a compact layer of bryophytes and decomposing leaves occur, which is utilised by fine adventitious roots as a source of moisture and nutrients (Bergstrom et al. 2015). Genetic differentiation exists between populations and although there is no evidence of spatial genetic structure, *A. macquariensis* has higher genetic diversity than very closely related species *A. selago* on Marion Island (Chau et al. 2019). *Azorella macquariensis* is considered a landscape engineer and keystone species, because it concentrates water and carbon within its canopy, facilitates more diverse microarthropod communities (Bergstrom et al. 2015) and similar to other *Azorella* species, facilitates other vascular flora species in high exposure, high elevation areas (Badano et al. 2006; le Roux and McGeoch 2010).

Field survey

Sixty-two sites were established and surveyed between December 2016 and February 2017 across the extent of the Macquarie Island plateau (Fig. 1). The survey coinciding with the active summer growing season of *A. macquariensis*. The site locations were determined using a random stratified survey design using four terrain classes and eight geographic units to ensure the diversity of microclimates were surveyed across the island (method described in detail in Dickson et al. 2019). All sites contained *A. macquariensis*. Within each 706.86 m² (15 m radius) site, six plots were stratified across representative cover and condition of *A. macquariensis*. Each plot consisted of two immediately adjacent 1 x 1m quadrats, which were photographed from directly above for image analysis.

Microclimate and terrain variables

Macquarie Island only has one permanent weather station, taking measurements at 1.5 m above the ground, which is considered unrepresentative of the alpine plateau because it is located at sea level on the northern most part of the island (Fitzgerald and Kirkpatrick 2017). However, accurate microclimate measurements can be achieved by deploying a fine-scale network of temperature data-loggers over adequate timeframes to take into account influences from terrain and habitat complexity (see Ashcroft and Gollan 2012; Graae et al. 2012; Körner and Hiltbrunner 2018). Therefore, to quantify microclimate at an appropriate scale within this system, data loggers (DS1923 Hygrochon Temperature & Humidity iButtons, Maxim) were deployed at each site between 15/12/2016 and 27/02/2017 and collected between 24/11/2017

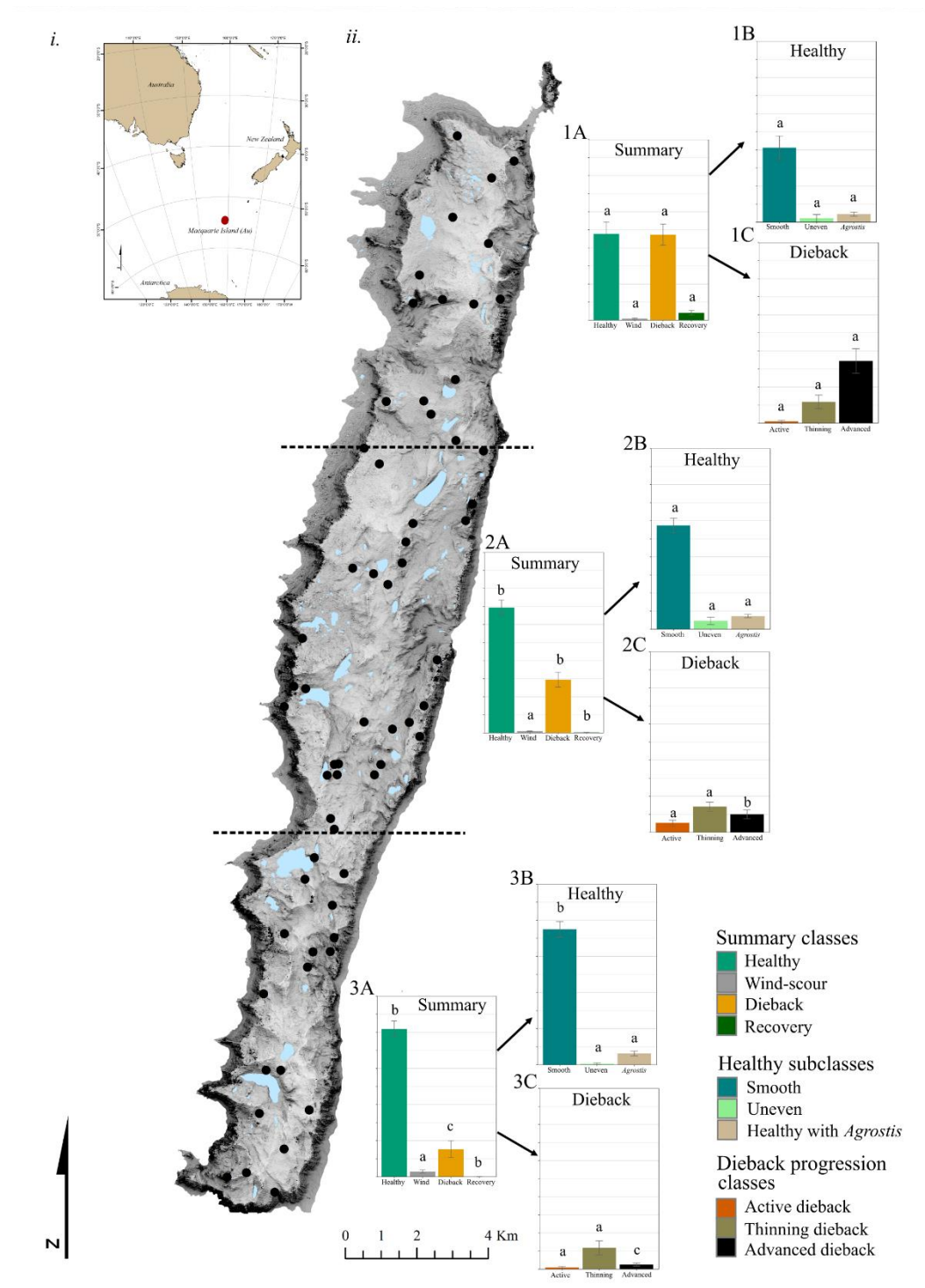


Fig. 1. Location of Macquarie Island (i) and survey sites on the island (ii, black circles), with the island divided into three equal latitudinal regions, North (1A-C), Central (2A-C) and South (3A-C). Proportion of *Azorella macquariensis* (with standard error bars) within the classes (Healthy, Wind-scour, Dieback, and Recovery) in each region (1A, 2A, 3A). Subsequently, the proportion of *A. macquariensis* within each Healthy subclass (Smooth, Uneven and *Agrostis*) in each region (1B, 2B, 3B) and the proportion of *A. macquariensis* within each Dieback progression class (Active, Thinning and Advanced) in each region (1C, 2C, 3C) is presented individually. Classes and subclasses that are significantly different across regions (i.e. 1-3, north, central and south) are indicated on the figure by a different letter, the same scale is used across classes and subclasses (0 – 100 %, 10 % increments).

and 02/01/2018. The loggers were secured in a free-hanging plastic fob and hung in an upturned light grey PVC container (50 mm diameter). Three slits were cut into each side of the container to improve cross ventilation, while still providing shelter from direct solar radiation and precipitation. The container was fixed 40 mm above the ground, to replicate the approximate height of *A. macquariensis*. Where possible the data logger was located on bare ground, to ensure that the microclimate measured was that experienced by the cushion, not the microclimate created by the cushion or other vascular vegetation. Data loggers recorded air temperature (°C) and relative humidity (%) at high resolution, every four hours (0300, 0700, 1100, 1500, 1900, 2100), acknowledging that cushions exposed to direct sunlight are likely to experience higher temperatures (Bonan 2008).

Microclimate variables were calculated from the data logger data. Variables were chosen for analysis that are known to affect plant and pathogen stress and growth, including temperature and humidity extremes, vapour pressure deficit (Bergstrom et al. 2015) and number of freezing days (Burgess et al. 2017) (Table 1). Each variable was calculated separately for the summer growing (October – March) and winter (April – September) seasons.

Soil pits were dug to 250 mm (approximate *A. macquariensis* root zone) at each site to characterize soil texture and gravel proportions, as potential determinants of *A. macquariensis* cover and condition. A visual estimate of the proportion of four classes of gravel was taken: coarse gravel (60 – 20 mm), medium gravel (20 – 6 mm), fine gravel (6 – 2 mm) and fine earth fraction (< 2 mm) (Sonter et al. 2000).

Additional terrain variables that were likely to affect plant stress or growth were derived from the 5 x 5m Macquarie Island DEM (Brolsma 2008), including northwest and southwest wind shelter (Table 1). Terrain variables were derived using SAGA (Conrad et al. 2015) and the RSAGA package (Brenning et al. 2018).










Condition classes








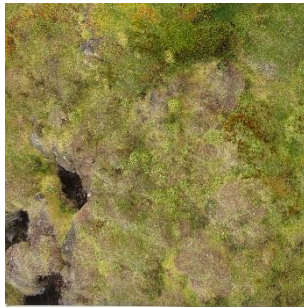
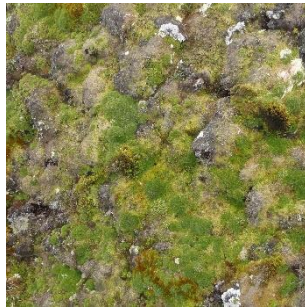
Four *Azorella macquariensis* condition classes and eight subclasses were described (Table 2): (1) ‘healthy’ (subclasses: ‘smooth’, ‘uneven’, ‘*Agrostis*’); (2) ‘wind-scour’; (3) ‘dieback’ (subclasses: ‘brown’, ‘olive’, ‘black’, ‘ablated’, ‘dieback with *Agrostis*’); and (4) ‘recovery’. Three dieback progression classes were defined as: ‘active’ dieback (‘brown’), ‘thinning’ dieback (‘olive’ + ‘dieback with *Agrostis*’) and ‘advanced’ dieback (‘black’ + ‘ablated’) (Table 2). Most individual cushions contain more than one condition class, subclass or progression










Table 1. Microclimate and terrain variables used in *Azorella macquariensis* condition and microclimate models for Macquarie Island. All microclimate variables were calculated from site data loggers for both the summer growing (October – March) and winter (April – September) seasons.




Variable	Abbreviation	Description
Extreme cold	Cold _{ext}	Mean daily temperature 5 th percentile.
Extreme hot	Hot _{ext}	Mean daily temperature 95 th percentile.
Extreme dry	Dry _{ext}	Mean daily relative humidity 5 th percentile.
Extreme humidity	Humidity _{ext}	Mean daily relative humidity 95 th percentile.
Vapour pressure deficit	VPD	Daily site temperature and relative humidity readings were used to calculate VPD (Pa), following Allen et al. (1998).
Freezing days	Freezing _{ext}	Number of days with temperatures below 0°C.
Northwest wind shelter	Wind_Shelter _{nw}	Shelter from the strong northwest (310°, ±80°) wind. The northwest wind is the direction of the strongest gusts and predominant wind direction on the island (Adams 2009).
Southwest wind shelter	Wind_Shelter _{sw}	Shelter from the cold southwest (225°, ±80°) wind. Wind-scour occurs on the southwest cushion face at the intersection of colder and more biologically abrasive southwest winds (Fitzgerald and Kirkpatrick 2017).
Fine gravel content	Fine_Gravel	Proportion of fine gravel (6 – 2 mm), as an indication of water holding capacity.

Table 2. Description of *Azorella macquariensis* condition classes and subclasses.

Classes and subclasses	Description	Example 1.	Example 2.	Example 3.
Healthy subclasses				
Smooth	Smooth green predominantly firm canopy. <i>Epiphyte cover is not included.</i>			
Uneven	Highly uneven, with firm green canopy. <i>Epiphyte cover is not included.</i>			
<i>Agrostis</i>	<i>Agrostis magellanica</i> or isolated <i>Luzula crinita</i> cover growing on healthy green cushion canopy, low levels of etiolation. Estimation of cover in this class only includes the area of cushion directly covered by <i>A. magellanica</i> or <i>L. crinita</i> .			

Classes and subclasses	Description	Example 1.	Example 2.	Example 3.
Wind-scour				
Wind-scour	A well-known phenomenon that is observed throughout the range of <i>Azorella</i> species. Natural grey to black stem death occurring in small (< 20% of canopy) exposed patches, occurring on the southwest faces of the cushion throughout the year (Fitzgerald and Kirkpatrick 2017).			
Dieback subclasses				
Brown	Bright brown or yellow colouration of canopy. Indicating 1 st -year leaf/canopy/stem death/senescence, but during the typical growing season (October – March). May affect all or a proportion of leaves present per rosette. <i>Epiphyte or healthy cover not included.</i>			
Olive	Thinning of rosette density, olive green discolouration caused by the loss of healthy leaves and prevalence of liverworts near the surface of the canopy, patchiness of condition and loss of canopy turgidity/firmness. <i>Epiphyte cover not included.</i>			

Classes and subclasses	Description	Example 1.	Example 2.	Example 3.
Dieback with <i>Agrostis</i>	<i>Agrostis magellanica</i> or isolated <i>Luzula crinita</i> cover growing on cushion canopy with dieback (all dieback subclasses). Estimation of cover in this class only includes the area of cushion directly covered by <i>A. magellanica</i> or <i>L. crinita</i> .			
Black	Black canopy indicating stem death, generally progressing to loss of canopy integrity, resulting in patchy removal of top leaves from wind exposure. Indicating 2+ years post initial stem death (Whinam et al. 2014) and failure to emerge from senescence. <i>Epiphyte cover not included.</i>			
Ablated	Area formerly occupied by cushions, clearly defined by the presence of characteristic uneven peat surface, relictual cushion root mass and occasionally bowl shape. Some cushion cover can remain at the edge. Class likely to be underestimated in areas of high exposure or flooding where all traces are removed. Indicates 3+ years since infection.			

Classes and subclasses	Description	Example 1.	Example 2.	Example 3.
Recovery				
Recovery	Small very healthy (bright green) rosettes or cushions growing within or adjacent to larger dead (black) <i>A. macquariensis</i> cushions			

class, reflecting the propensity of *A. macquariensis* to host epiphytes and that pathogens often move in a line across the cushion, at between 25 and 83 mm month⁻¹ (Whinam et al. 2014).

Image analysis

Each photograph was cropped to the 1 m x 1 m quadrat and rectified to square in Adobe Photoshop CC 19.0 to remove small distortions prior to analysis. I delineated polygons for each condition subclass on each photograph in Inkscape 0.92.3 (Inkscape Project 2018) using expert knowledge. Unsupervised image analysis was not used because of the highly variable light conditions during the survey period and colour similarity amongst condition subclasses and associated vascular and non-vascular flora. Polygons of each subclass were subsequently measured using their unique RGB code in ImageJ 1.52i (Rueden et al. 2017) and calculated as a proportion of the total quadrat (1 m²). The total *A. macquariensis* cover (cover, %) was calculated as the sum of all cushion condition subclasses per plot and then divided by the number of quadrats. The proportion of each condition class per site (12 x 1 m² quadrats) was calculated as the total of the class in each plot divided by cover (%). The mean (\pm s.e., n = 12) plot data was used for all subsequent cover and dieback analyses to address the data distribution within the highly spatially variable species. The number of cushions were not counted, as discrete cushions and mats can be composed of multiple individuals (Cerfonteyn et al. 2011).

‘Healthy’ and ‘dieback’ classes were described as the sum of their individual subclasses. To test for a relationship between location and condition the island was divided into three equal latitudinal regions, northern, central, and southern.

Statistical analysis

Regional condition and microclimate

To determine whether there was a relationship between the proportion of *A. macquariensis* within each cushion condition class and broad latitudinal regions on the island a non-parametric Kruskal-Wallis one-way analysis of variance was used. The average proportion of *A. macquariensis* within each condition class (%) was described as a function of location (northern, central and southern). A posthoc Dunn's test of multiple comparisons with Holm's adjusted p-values (Dinno and Dinno 2017) was used to determine differences between regions for each condition class. The condition classes tested included the four classes, three healthy subclasses, and three dieback progression classes.

To determine if there was a significant relationship between microclimate and latitudinal regions, a one-way analysis of variance model (ANOVA) and post-hoc Tukey's Honest Significant Difference test was used. Each of the six summer microclimate variables (Table 1) were tested against the three equal latitudinal regions of the island, northern central and southern. To meet model assumptions Vapour pressure deficit (VPD, kPa) and freezing_{ext} (days with temperatures below 0°C) were log-transformed, and humidity_{ext} (95th percentile of the mean daily relative humidity) was tested using a non-parametric Kruskal-Wallis, with a Dunn's test of multiple comparisons using Holm's adjusted p-values.

Macroclimate

Latitude was hypothesised to be a proxy for macro-climate by Dickson et al. (2019), although latitude is also correlated with elevation ($r = 0.31$). Elevation has a lapse rate of $-0.71^{\circ}\text{C } 100 \text{ m}^{-1}$ on the island, which increases non-linearly (Tweedie and Bergstrom 2000). To determine if a latitudinal temperature gradient occurred independent of elevation, the relationship between temperature and the covariates latitude and elevation was modelled using a general linear model (similar to Córdova et al. (2016), i.e $\text{temp} \sim \text{lat} + \text{elev}$). Models were run for the different temperature variables that capture aspects of daily and seasonal temperature variation (i.e. the daily mean, T_mean; mean daily minimum, T_min; and mean daily maximum, T_max), and for summer (Oct – Mar) and winter (Apr – Sep). Northing was used as the measurement for latitude to be able to directly relate the rate of change of temperature in kilometres down the island.

To test for a significant change in extreme macroclimate temperature prior to and during the occurrence of *A. macquariensis* dieback, monthly summary weather data from the Macquarie Island Bureau of Meteorology weather station #300004 (Bureau of Meteorology 2019), was evaluated between 1948 to 2018. Extreme monthly temperature (°C) values assessed included: Mean number of frost days (ground temperature $\leq -1^{\circ}\text{C}$, BoM_frost), lowest monthly minimum (BoM_T.ex.min), mean monthly minimum (BoM_T.av.min), mean monthly maximum (BoM_T.av.max), and highest monthly maximum (BoM_T.ex.max). Linear regression was used to assess change in each continuous temperature variable over time for each month. To assess the BoM_frost count data over time GLMs (family = negative binomial) were run in the package 'MASS' (Ripley et al. 2019) for May – November, each month with more than 15 % of the years with counts greater than zero. Relative humidity data was not

assessed because collection instrumentation changed over the period of interest (Bergstrom et al. 2015).

Island-wide models of Dieback, Wind-scour, and Recovery condition classes

The variables used to model the relationship between *in-situ* microclimate variables and the proportion of *A. macquariensis* cover affected by dieback across Macquarie Island included, (i) variables previously suggested to stress the plants or promote pathogen virulence and extent, and (ii) relevant terrain variables from Dickson et al. (2019) (wind shelter and soil gravel content). Other potential proxies for atmospheric water, such as cloud cover and wind direction (moisture), were considered but would necessarily be topographically-derived and subject to the limitations identified in the previous Chapter. To reduce collinearity the microclimate variable choice was informed by an exploratory principal component analysis (PCA, `prcomp`, in 'stats' package). Summer (growing season) variables included in the models represented the three main axes (i) `freezingext`, representing `coldext`, (ii) `humidityext` representing `dryext` (negative relationship), and (iii) VPD representing `hotext` and affecting water availability.

The effect of microclimate on island-wide *A. macquariensis* dieback was modelled as the proportion of the Dieback (0 to 1) class as a function of (i) microclimate conditions that may affect pathogen activity, including `freezingext` and `humidityext` (%), (ii) variables that are likely to influence plant available water, including VPD (Pa), `Fine_Gravel` (%) and `Wind_Shelternw` (no units) and (iii) the covariate *A. macquariensis* cover (`Cover`, %). No strong non-linear relationships between Dieback and predictor variables were identified in preliminary analysis using Generalized Additive Models (GAM; family = beta, link = logit) with smoothing applied to each of the predictor variables (`mgcv`; Wood 2017). Consequently, no polynomial terms were included. Dieback (0,1) was modelled as a function of the six previously described predictor variables using a beta regression model with a logit link function (`betareg`; Zeileis et al. 2016). The variance inflation factors (VIFs) (Barton and Barton 2018) of the model were low (< 2.6), showing little collinearity. There was no spatial autocorrelation over the spatial lag of 22 km on a 34 km island (global Moran's I, Bivand et al. 2017).

To enable direct comparison of the direction and effect size of each predictor variable, predictor variables were standardised by subtracting the mean and dividing by the standard deviation. The response curve was plotted for each predictor variable within the surveyed range, while holding the remaining variables at the 50th percentile value, to explore the response of dieback under varying microclimate and terrain conditions. The rows of data were resampled 1000

times to produce bootstrapped 95 % confidence intervals around the mean using the `lm.boot` function from the 'simpleboot' in R. The figures were overlaid with the cushion dieback (%) recorded at each site.

To further explore the relationship between dieback and the two significant variables within the beta regression dieback model, a linear regression model was run to determine if there was a significant difference between the slopes for the levels of cover affected by dieback for cushions with $< 5\%$ dieback and those with $\geq 5\%$ dieback. The 5th percentile was used for healthy cushions, to account for erroneous records. The model was described as $\text{humidity}_{\text{ext}}$ as a function of $\text{freezing}_{\text{ext}}$ with an interaction of the binary dieback class. The $\text{humidity}_{\text{ext}}$ response lines were plotted for sites with $< 5\%$ and $\geq 5\%$ dieback and the recorded site values overlaid.

Wind-scour and recovery condition classes had a high proportion of zeros (Recovery = 69.4 %, Wind-scour = 19.4 %) and model convergence was not satisfactorily achieved using zero-inflated beta regression models. Thus, the conservative approach of modelling these data as presence/absence using GAMs was adopted, which provided the best fit for both response variables. The presence of Wind-scour was modelled as a function of the predictor variables $\text{freezing}_{\text{ext}}$ (n), $\text{Wind_Shelter}_{\text{sw}}$ (no units), Fine_Gravel (%) and the covariate Cover (%) using a GAM (family = binomial, link = cloglog) with smoothing applied to each of the predictor variables (mgcv; Wood 2017). The same method was used to assess the effect of microclimate on the presence of Recovery, using the predictor variables condition subclass Black (%), summer VPD (Pa), $\text{Wind_Shelter}_{\text{nw}}$ (0-1) and the covariate class Dieback (%). The estimated level of concurvity between individual variables (Wood 2017) was low (≤ 0.25) for Wind-scour model and low to moderate (≤ 0.58) for the Recovery model. No spatial autocorrelation occurred over distances up to 22 km (Moran's I, Bivand et al. 2017).

All analyses were performed using RStudio Desktop 1.2.1335 using R for Windows 3.6.0 (R Core Team 2019).

Results

Regional variation in microclimate

Of the six extreme (5th or 95th percentile) microclimate variables recorded during growing season assessed for inclusion within models, freezing_{ext} ($F_{2,59} = 17.13, p < 0.001$) and cold_{ext} ($F_{2,59} = 6.50, p < 0.01$) differed significantly between the three regions (Fig. 2). The number of southern freezing_{ext} days was significantly higher than the number of northern ($p < 0.001$) and central ($p < 0.001$) freezing days (Fig. 2), however, there was no significant difference between the north and centre. Similarly, cold_{ext} ($r = -0.79$ with freezing_{ext}) was lower in the south than both the centre and north of the island ($p = 0.002, p = 0.03$, respectively; Fig. 2). Mean microclimate statistics are presented in Table B1.1, Appendix B.

There was a significant temperature lapse and latitudinal gradient for T_{mean}, T_{min}, and T_{max}. All three temperature variables were significantly lower at high elevation sites for all three time periods (annual, growing season and winter senescence season) and significantly colder towards the south for all variables but annual and summer T_{max} (Table B1.2., Appendix B). The goodness-of-fit was highest in winter ($\text{adj-R}^2 = 0.87 - 0.95$) and lowest in the growing season ($\text{adj-R}^2 = 0.42 - 0.69$). The elevational temperature lapse was highest for T_{max} ($-1.14 \pm 0.19^\circ\text{C } 100 \text{ m}^{-1}$) and lowest for T_{min} ($-0.58 \pm 0.06^\circ\text{C } 100 \text{ m}^{-1}$) over the growing season (Table B1.2., Appendix B). The latitudinal temperature gradient down the full extent of the island was highest during the summer growing season ($T_{\text{mean}} = 0.49 \pm 0.15^\circ\text{C}$) and lowest during winter ($T_{\text{min}} = 0.12 \pm 0.06^\circ\text{C}$) (Table B1.2., Appendix B).

Macroclimate

There was a significant increase in the monthly mean minimum and maximum temperatures between 1948 and 2018, for five and nine of the 12 months, respectively (Table B1.3., Appendix B). The extreme monthly maximum temperature increased significantly over this period for all months except June (Table B1.3., Appendix B). Conversely, there was no significant change over the same time period for any of the extreme cold temperature variables during any month (Table B1.3., Appendix B). Across all metrics, January to May, August, and September were most likely to have experienced significant warming.

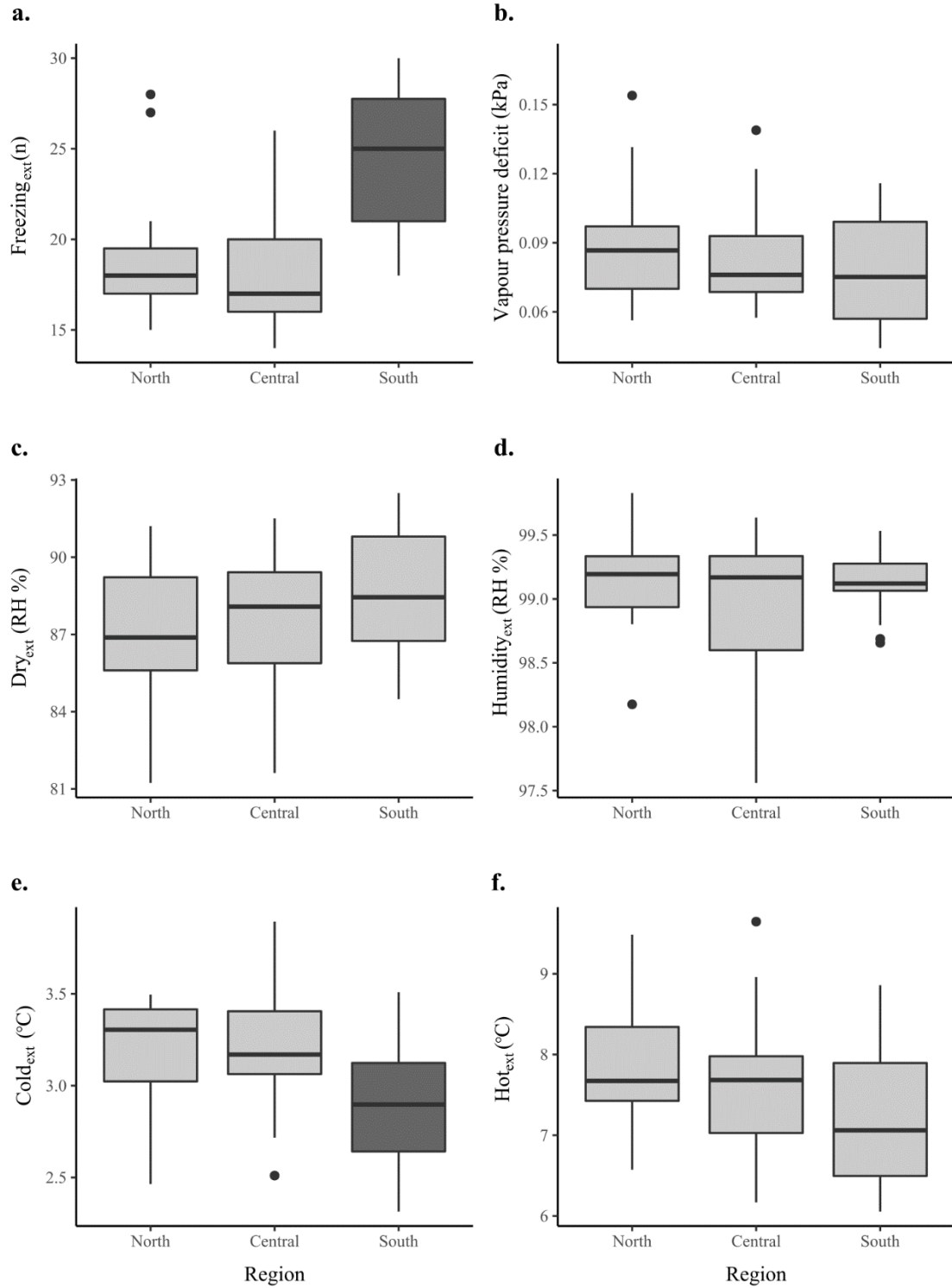


Fig. 2. Growing season (October – March) microclimate site values for three equal latitudinal regions across Macquarie Island, between December 2016 and February 2017 (Median with box representing upper and lower quartile, bars represent range). North ($n = 15$), central ($n = 29$), south ($n = 18$). Significant difference between regions denoted by different shades of grey ($p = 0.05$). Freezing_{ext} (number of days $<0^{\circ}\text{C}$), Dry_{ext} (daily average 5th percentile of relative humidity, %), Humidity_{ext} (daily average 95th percentile of relative humidity, %), Cold_{ext} (daily average 5th percentile of temperature, $^{\circ}\text{C}$) and Hot_{ext} (daily average 95th percentile of temperature, $^{\circ}\text{C}$).

Cushion condition

(1) Healthy

Approximately two-thirds (67.8 %, ± 3.19 s.e.) of the island-wide cushion cover was Healthy (Table 3, B1.4., Appendix B). The amount of Healthy cover varied significantly amongst regions ($X^2 = 14.75$, $df = 2$, $p < 0.001$), with less in the north than both the centre ($z = 2.46$, $p = 0.03$) and south ($z = -3.84$, $p < 0.001$; Fig. 1).

Of the Healthy subclasses, only Smooth varied significantly between regions ($X^2 = 15.52$, $df = 2$, $p < 0.001$), where it was higher in the south than the centre ($z = -2.59$, $p = 0.02$) and north ($z = 3.89$, $p < 0.001$; Fig. 1, Table B1.4., Appendix B). The less frequently encountered subclasses, Uneven and *Az_Agrostis*, did not significantly vary between regions ($X^2 = 1.54$, $df = 2$, $p = 0.46$; $X^2 = 4.20$, $df = 2$, $p = 0.12$, respectively) and had a comparable mean cover across all regions, ranging from 0.6 – 4.6 % and 4.5 – 7.3 %, respectively (Table B1.4., Appendix B).

(2) Wind-scour

On average, 1.5 % (± 0.30 s.e.) of the island-wide cushion cover was affected by Wind-scour (Table 3), ranging from 0.8 % (± 0.34 s.e.) in the north to 2.9 % (± 0.89 s.e.) in the south (Fig. 1). While a significant difference in the proportion of Wind-scour between regions was detected ($X^2 = 6.67$, $df = 2$, $p = 0.04$), the post-hoc test did not identify where the difference lay. The presence of Wind-scour on *A. macquariensis* was significantly predicted by lower southwest wind-shelter ($p = 0.021$) and higher cushion cover ($p = 0.002$), explaining 61.2 % of deviance (Fig. 3a., Table B1.5., Appendix B). Wind-scour was highest in the south of the island, at sites with high exposure and higher cushion cover (Fig. 3a.). The number of freezing days had no significant effect on the presence of Wind-scour, while the likelihood of presence increased slightly with higher fine gravel content (Fig. 3a.).

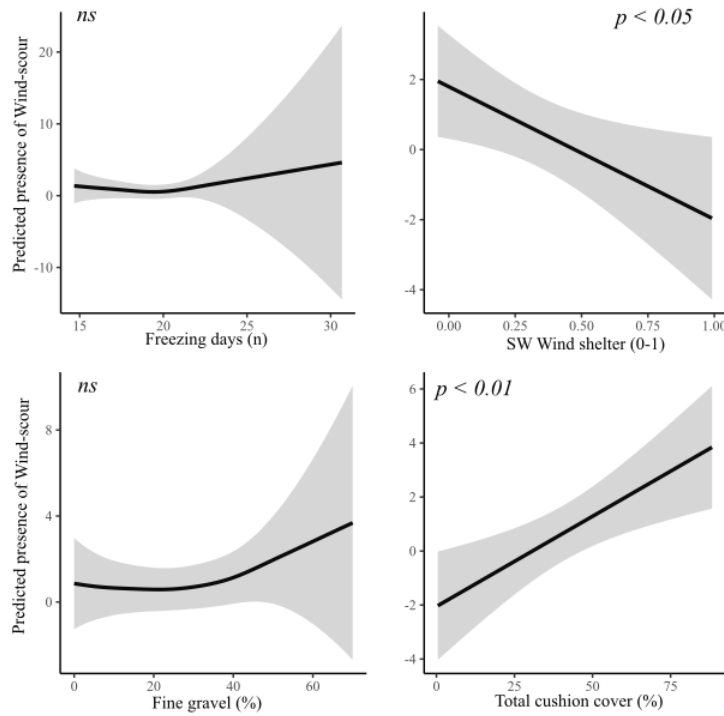
(3) Dieback

Across the island almost one third (29.66 %, ± 3.08 s.e.) of cushion cover was affected by Dieback (Table 3). It differed significantly between the regions ($X^2 = 6.67$, $df = 2$, $p = 0.04$), with more in the north than the central ($z = -2.20$, $p = 0.03$) or the south ($z = 2.29$, $p = 0.04$; centre also $>$ south, $z = 3.97$, $p < 0.001$; Fig. 1). Dieback was 32 % higher in the north (47.3 % ± 5.84) than in the south (15.2 % ± 4.62 ; Table 3).

Table 3. Total cover of *Azorella macquariensis* and the proportion (%) of each condition class (Healthy, Wind-scour, Dieback and Recovery) and dieback progression subclasses (Active, Thinning, Advanced) averaged across six plots at 62 sites across Macquarie Island.

Condition class	N	Min.	Max.	Mean (\pm s.e.)
Healthy (%)	62	6.0	100.0	67.76 (\pm 3.19)
Wind-scour (%)	62	0	13.4	1.5 (\pm 0.30)
Dieback (%)	62	0	86.9	29.7 (\pm 3.08)
<i>Active Dieback (%)</i>	62	0	26.9	3.0 (\pm 0.77)
<i>Thinning Dieback (%)</i>	62	0	54.3	13.0 (\pm 1.83)
<i>Advanced Dieback (%)</i>	62	0	85.6	13.7 (\pm 2.50)
Recovery (%)	62	0	15.3	1.1 (\pm 0.38)
Island-wide <i>A. macquariensis</i> cover (%)	62	0.5	88.3	41.7 (\pm 2.73)

(a.) Wind-scour presence



(b.) Recovery presence

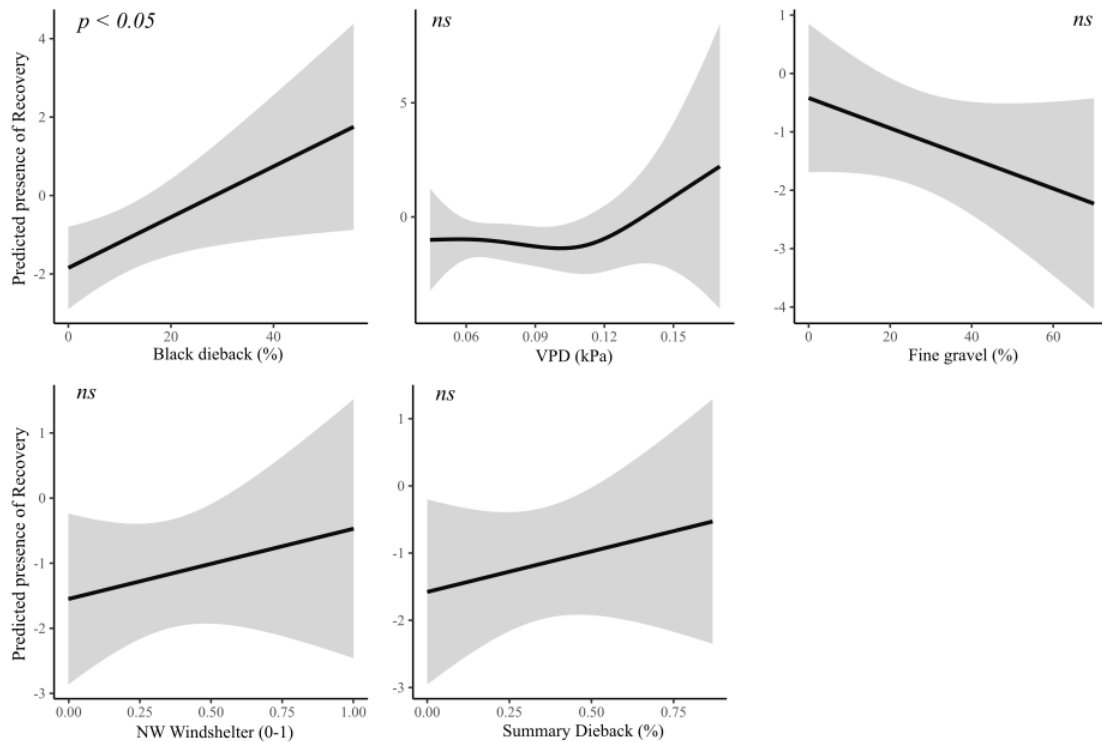


Fig. 3. Modelled occurrence of (a.) wind-scour on *Azorella macquariensis* against freezing days (growing season days $<0^{\circ}\text{C}$, n), southwest wind shelter (0-1), fine gravel (%) and total cushion cover (%) and; (b.) *A. macquariensis* recovery against ‘black’ dieback subclass, VPD (average daily growing season vapour pressure deficit, kPa), fine gravel (%), northwest wind shelter (0-1), and dieback class (%) (generalised additive models with 95 % confidence intervals). Growing season defined as October to March, inclusive.

The amount of *A. macquariensis* affected by Dieback (%) was predicted by humidity_{ext} and freezing_{ext} (Pseudo-R² = 0.27, Fig. 4, Table B1.6., Appendix B). Dieback was higher in sites with fewer freezing_{ext} days and higher humidity_{ext} (Fig. 4. and Fig. B1.1., Appendix B). Variables related to water-stress (NW wind shelter, fine gravel content, VPD) and the covariate *A. macquariensis* cover were not significant in the dieback model (Fig. 4, Table B1.6., Appendix B). There was an apparent threshold between low humidity_{ext} and more freezing_{ext} events, below which no assessed sites recorded those conditions (Fig. 5). The interaction between freezing_{ext} and the presence of the < 5 % dieback class was significant (Table B1.6., Appendix B, $p = 0.002$), revealing a comparatively narrow band of conditions between humidity_{ext} and freezing_{ext} where healthy cushions (< 5 % dieback) occurred (Fig. 5).

Dieback progression classes: Active, Thinning, Advanced

Active dieback affected < 3.0 % (± 0.77 s.e.) of cushion cover island-wide, highest in the centre (5.3 % ± 1.5 s.e.) and lowest in the south (0.9 % ± 0.47 s.e.) (Table B1.4. Appendix B, Fig. 1). Island-wide, over four times the cushion cover was affected by Thinning (12.96 % ± 1.83 s.e.). Neither Active nor Thinning dieback varied significantly between regions ($X^2 = 4.40$, $df = 2$, p -value = 0.11; $X^2 = 1.71$, p -value = 0.43, $df = 2$ respectively; Fig. 1). Advanced dieback affected the most cushion cover of the three progression classes (13.72 % ± 2.50 s.e., Fig. 1, Table B1.4., Appendix B), differing between regions ($X^2 = 22.19$, $df = 2$, $p < 0.001$; north > centre $z = -3.12$, $p < 0.01$; north > south $z = 4.70$, $p < 0.001$; centre > south $z = 2.17$, $p = 0.03$; Fig. 1, Table B1.4., Appendix B). Advanced dieback was considerably higher in the north, increasing from 2.5 % (± 0.84 s.e.) cover in the south to 34.4 % (± 6.82 s.e.) in the north (Fig. 1., Table B1.4.).

(4) Recovery

Very low levels of Recovery were recorded island-wide (1.1 % ± 0.38 s.e.; Table 3). The proportion was nonetheless significantly different between regions ($X^2 = 15.76$, $p < 0.001$, $df = 2$, Fig. 1); highest in the north (4.1 %, ± 1.29 s.e.), followed by the centre ($z = -2.96$, $p < 0.01$) and then the south ($z = 3.89$, $p < 0.001$; Fig. 1.).

Cushion recovery was significantly higher at sites with high proportions of Black dieback ($p = 0.02$, deviance explained = 36.1 %) (Fig. 3b., Table B1.5.). While there was no significant effect of other predictors, response curves suggest that Recovery was also more likely to occur

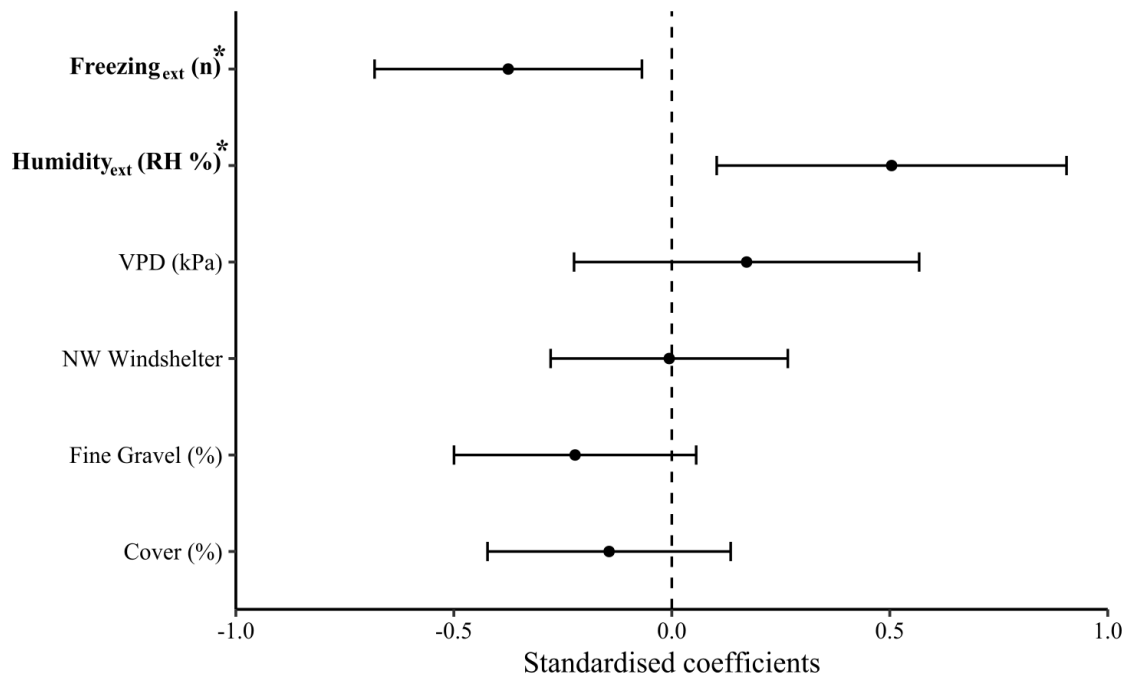


Fig. 4. Relative effect size of correlates of *Azorella macquariensis* dieback, positive (to the right of zero) and negative (to the left). Standardised regression coefficients (± 95 CI) from beta regression models, using growing season (Oct – Mar) microclimate and terrain variables. Significant variables indicated in bold (*, $p < 0.05$). Humidity_{ext} (average daily 95th percentile of relative humidity, %), VPD (average daily vapour pressure deficit, kPa) and Freezing_{ext} (number of days with temperatures < 0 °C).

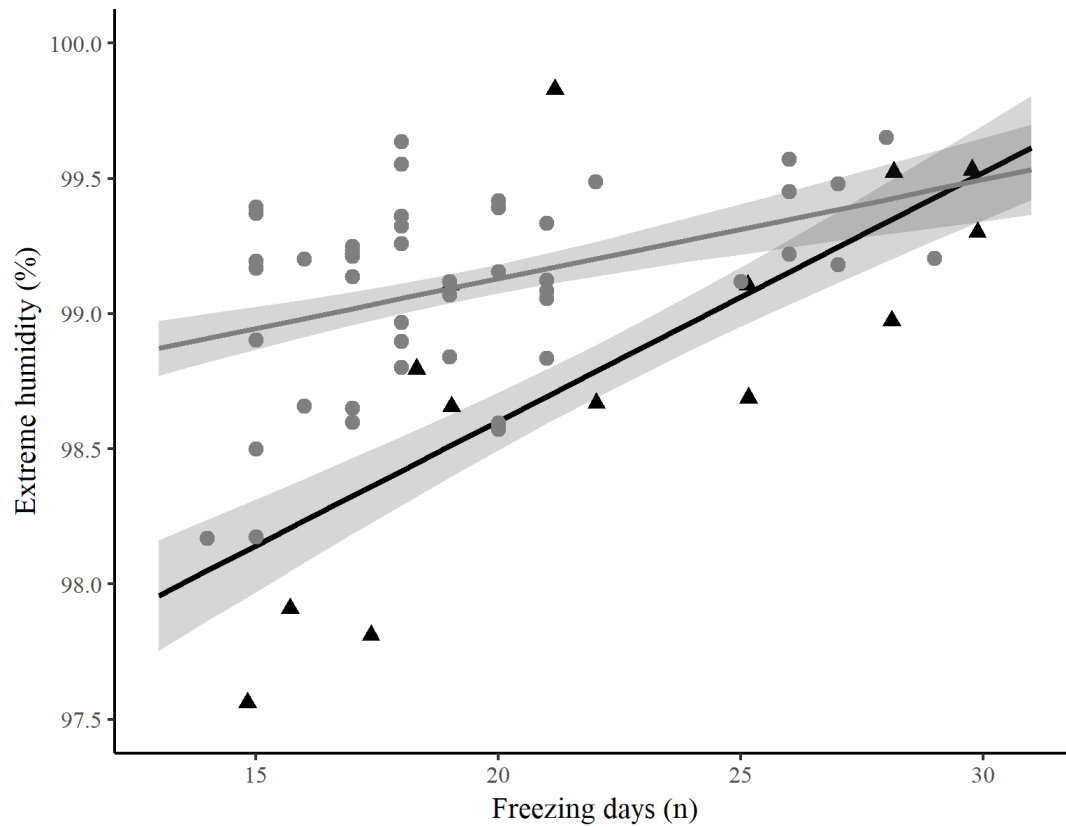


Fig. 5. Relationship between Extreme humidity (average daily 95th percentile of relative humidity, with 95 % confidence interval) and Freezing days (number of days < 0°C) during the growing season (Oct – Mar) for sites with < 5 % (black triangles) and ≥ 5 % (grey circles) *Azorella macquariensis* dieback. Generalised linear regression lines showing a significant interaction between Freezing days and sites with < 5 % or ≥ 5 % dieback ($p = 0.002$).

at sites with lower fine gravel content (conversely, fine earth fraction and higher vegetation cover) and higher shelter from strong northwest winds (Fig. 3b.).

Discussion

The microclimate model found that current *A. macquariensis* dieback extent was primarily explained by the pathogen hypothesis, where dieback was correlated with microclimate conditions conducive to disease outbreak (see Garret et al. 2016). Dieback extent was highest under a low number of freezing_{ext} days and high humidity_{ext}. This result, in combination with new island-wide microclimate data and the significant relationship between location and condition, provides a plausible explanation for the low levels of dieback in extensive southern populations, defining natural refugia. However, disease outbreaks require not only the environmental conditions to be conducive to the pathogen, but also a susceptible host and/or more virulent pathogen (see Garrett et al. 2016). Therefore, the synergistic effects of a warmer, wetter winter that favours pathogens combined with a warmer, more variable summer growing season that causes plant water-stress, are contributing to ongoing *A. macquariensis* dieback across Macquarie Island.

The value and insights from detailed cushion condition classes

The development of clearly discernible and repeatable fine-scale *A. macquariensis* condition classes has provided a more nuanced understanding of the drivers of dieback, and will also enable improved repeatability of population monitoring. This study separated naturally occurring wind-scour from ‘black’ dieback, which were both previously described under ‘grey’ damage by Whinam et al. (2014). The addition of active, thinning and advanced dieback progression classes provides a measure of temporal progression of condition describing the increase of dieback severity, and an estimate of time since infection (range 1 – 3+ years). This provides an important step forward, required to determine temporal trends and estimate the rate of cushion cover loss across the island.

Two-thirds of all cushion cover was healthy, predominantly with smooth unbroken surfaces. However, the canopies of individual cushions were naturally variable. Historically cushions have had varying levels of natural unevenness (unpub.1970s slides, G. Copson), although it is unclear whether unevenness was exacerbated under extreme water stress, as seen prior to 2008 (Bergstrom et al. 2015). Further work is needed to better understand this condition subclass.

The naturally occurring wind-scour affected very little of the cushion surface and was recorded at a similar level to that observed prior to disease outbreak (see Selkirk 2012). Despite not being related to cold temperatures, it was most prevalent toward the south of the island at sites exposed to the southwest winds.

The recent decline in cushion condition was represented by five subclasses, capturing the high variation in cushion decline from individual cushion to island-wide scales. Active dieback is ongoing across all regions and at a rate similar to the comparative ‘yellow’ damage documented in 2010 (Whinam et al. 2014). The separation of the common ‘grey’ damage (Whinam et al. 2014) into this study’s very rare wind-scour and most common black class, suggests that a large amount of pathogen dieback was already present in 2010. It is likely that cushion cover eroded to isolated roots and peat-patterning by wind and to a lesser extent during heavy rainfall/flooding events (subclass ‘ablated’), following a loss of canopy integrity from prior dieback, is under-represented in this study across Macquarie Island. This class is unlikely to persist over extended periods of time in exposed areas, which reduces the ability to estimate cushion cover pre-dieback. Cover-loss is typified by this process of ablation of advanced dieback across the island.

This study is the first island-wide assessment of *A. macquariensis* recovery, first locally observed by Whinam et al. (2014) in the north of the island. Recovery is occurring at low levels across the island and is highest in the north ($4.1 \pm 1.29\%$). Time since dieback (or presence of ‘black’ cushions) was the best predictor of recovery, which was regularly observed in dead cushion material as new seedlings or surviving rosettes. This pattern of recovery indicates that the pathogens responsible for dieback are only active at, or just in front, of the chlorosis line, providing capacity for recolonization of recently affected sites and cushions. However, multiple ‘waves’ of dieback have been recorded across previously and currently affected sites and cushions (Dickson et al. 2019; Bergstrom et al. in press). Therefore, to allow *A. macquariensis* to fully recover, the period between dieback ‘waves’ will need to be long enough to allow cushion regrowth and recruitment. The increasing frequency of dieback events for multiple species under climate change, suggests that for slow-growing species such as *A. macquariensis*, there may not be the required time to recover and thus maintain their former distribution (see Hughes et al. 2018).

The dieback progression classes confirm that there is a latitudinal gradient in cushion condition down the island, as hypothesised by Dickson et al. (2019). Old advanced dieback and

associated cover loss are concentrated in the north of Macquarie Island, while active dieback is highest in the centre and cushions are healthiest in the south. The latitudinal distribution of dieback progression classes appear indicative of a temporal dieback progression down the island. However, dieback was recorded across the extent of the island from the first season of observation in 2008/09 (Bergstrom 2013, updated 2014; Bergstrom et al. 2015) and the low proportion of southern cushions affected by dieback has remained relatively constant over time (Dickson et al. 2019). This suggests that rather than spreading from a northern infection point, dieback progression or pathogen virulence is higher in the north under more suitable conditions.

Correlates of dieback: determining support for the water-stress or pathogen hypothesis

The decadal reduction in summer plant available water has been considered the primary driver of *A. macquariensis* decline, with weakened cushions more susceptible to secondary pathogenic infection (Bergstrom et al. 2015). However, Dickson et al. (2019) found no relationship between terrain variables that are likely to affect relative plant water availability and cushion condition. This implied either (i) that terrain variables used were unsuitable surrogates for water stress, or (ii) that dieback might be better currently explained by conditions associated with pathogen ecology. Cushion dieback is related to microclimate extremes or lack thereof, with more dieback at sites experiencing higher humidity_{ext} and fewer freezing_{ext} days, supporting the hypothesis (ii) that dieback extent is better explained by pathogen ecology. Variables likely to affect plant water stress (VPD – highly correlated with hot_{ext}, wind exposure and soil gravel content) were not important to dieback in the model. Healthy cushions ($\leq 5\%$ dieback) occurred within a narrow band of freezing_{ext} and humidity_{ext} values. Healthy condition was maintained with high freezing_{ext} days despite very high humidity_{ext}, or conversely, cushions could tolerate a lower number of freezing_{ext} days when humidity_{ext} was comparatively low. Together these results support the pathogen hypothesis, where dieback is currently predicted by pathogen ecology, rather than water stress.

High humidity is known to promote plant pathogens, while freezing days suppress them, with responses varying amongst taxonomic groups (Harvell et al. 2002; Chakraborty 2013; Garrett et al. 2016; Burgess et al. 2019). Water moulds (Oomycetes) and fungal pathogens are both generally promoted under warmer, wetter climates (Woods et al. 2005; Welsh et al. 2014; Homet et al. 2019), making them likely candidates for the pathogens affecting cushion dieback. However, given the large number of potential taxa identified by Bergstrom et al. (2015) it is also possible that dieback is caused by a change in a consortium of microbes, similar to coral

black or white band disease where the microbial community change causes dieback to move in a band across the coral surface (see Gignoux-Wolfsohn and Vollmer 2015; Sato et al. 2016).

Leaf saturation is important in disease outbreaks (see Huber and Gillespie 1992). This is currently best represented at a site-level by relative humidity (RH), as a proxy for atmospheric water. Macquarie Island has a very high daily mean humidity (data loggers annual RH daily mean $95.75 \% \pm 1.05$; Table B1.1, Appendix B), however, there are fluctuations between and within sites (data logger RH full range 25.99 – 100 %). Therefore, while the range in average daily humidity_{ext} quantified across sites on Macquarie Island was 2.27 %, as with many other climate averages, this range should be interpreted in terms of its relative difference. In addition to representing an average around which there is variation, the range of humidity_{ext} also represents approximately one-fifth of observed variation in both the mean diurnal and mean daily minimum relative humidity (Table B1.1, Appendix B). Cumulatively over time, this variation in extreme humidity may well represent a biologically significant shift in humidity, as suggested by Fig. 4.

Microclimate and the potential for natural refugia

The landscape-scale distribution of dieback is, at least partially, driven by macro-scale weather conditions. The southern plateau is higher in elevation and regularly shrouded in cloud (Selkirk et al. 1990). Therefore, it was thought likely that cooler temperatures, potentially with more available atmospheric water, explained the extensive and healthier southern *A. macquariensis* populations (Dickson et al. 2019). The microclimate data presented here confirm that the southern region is significantly colder with more freezing days. There is a significant negative temperature gradient down the island (north-south -0.5°C), in addition to the expected -0.7°C per 100 m in elevation. However, the availability of atmospheric water (represented here by relative humidity) was comparatively stable down the island, with the south only slightly more humid (dry_{ext}). This suggests that the latitudinal gradients of cushion cover and dieback identified by Dickson et al. (2019), and the variation in cushion condition shown here, may be driven by the prevalence of freezing days rather than available atmospheric water. Therefore, it appears that the extreme cold temperatures in the south have provided some refuge from the rapidly progressing and extensive dieback (see Marçais et al. 1996; Harvell et al. 2002; Burgess et al. 2017). Encouragingly cold refugia have been identified across 15 % of the island's plateau, with lower temperatures and VPD than expected, due to the influence of topography (Baker et

al. unpublished)¹. The average number of freezing days recorded at the Bureau of Meteorology weather station in the north of the island have remained constant since 1948 (Table B1.3., Appendix B) and maintained the historical annual mean of 99 days (Löffler 1984). It is unclear whether this general trend of stable cold temperatures can be extrapolated across the island to provide further insight into disease emergence, as there is no southern weather station. Regardless, under the current climate trajectory it is unclear how long these cold refugia will persist.

Complexity of pathogen outbreaks and regional conditions

Disease is unlikely to be responding in isolation or as a straightforward linear relationship with one or several different drivers. Rather, disease and hosts are widely recognised to have highly complex interactions between climate, environment and pathogen variables (Chakraborty et al. 2000; Rohr et al. 2011). Disease outbreaks require the presence of at least two changes in the axes of the disease triangle (Fig. 6), whether that is a more facilitative environment for disease, a more susceptible host, and/or more virulent pathogen with appropriate vectors (Cahill et al. 2008; Garrett et al. 2016). The ability of plants to resist and recover from novel pathogens can be compromised when faced with a combination of novel extreme events such as drought, flooding, and frost (Stenlid and Oliva 2016). *Azorella macquariensis* dieback has occurred with the change of at least two axes of the disease triangle, where the cushion is more susceptible (stressed) and the environment is more conducive to novel pathogens, where it is wetter with higher maximum temperatures.

It is likely that both additive and multiplicative effects of novel climate change and related extreme events are driving cushion dieback, rather than simply water-stress. While it is likely that the extended period of summer plant water deficit conditions prior to the emergence of dieback reduced the cushion's defence to disease (Bergstrom et al. 2015), cushions appeared to regain turgidity with more available water post-2010 (Bergstrom et al. in press). However, the increase in plant available water has yet to be tested. Nevertheless, the regional climate is still increasingly variable with a drier atmosphere (Adams 2009) and significantly higher maximum and extreme maximum temperatures during the growing season (Table B1.3., Appendix B).

¹ Baker, D.J., Dickson, C.R., Bergstrom, D.M., Whinam, J., McGeoch, M.A., submitted. Assessing microrefugial potential for cold-adapted terrestrial biodiversity in the sub-Antarctic xx xx, xx. For this paper I collected the data, contributed to the study design and the manuscript.

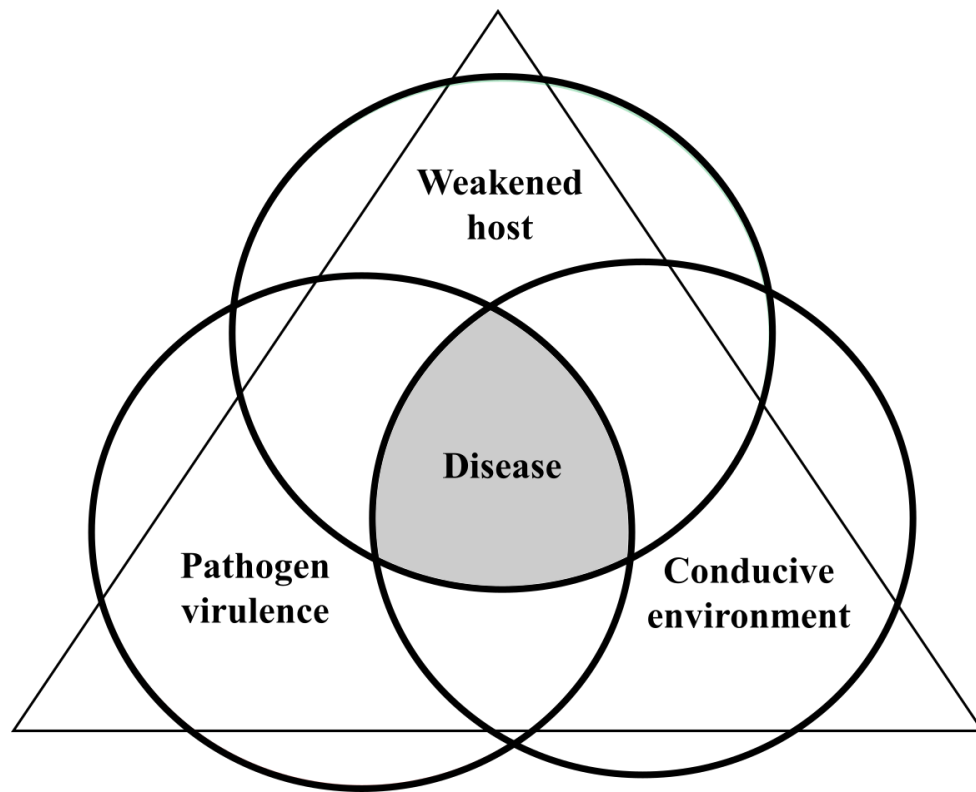


Fig. 6. Plant and animal diseases occur as a result of an interaction between the weakened host, a virulent pathogen and a more conducive environment for pathogenic organisms, these interactions are becoming increasingly common under climate change conditions (see Garrett et al. 2016).

Therefore, *A. macquariensis*, as a species susceptible to rapid water-loss (Rolland et al. 2015), is likely still more water-stressed under present conditions than it was under historical conditions. In contrast the system is increasingly saturated during winter when the cushion is dormant. There has been a 55 % increase in winter rainfall since the 1970s (Bergstrom et al. 2015), and maximum temperatures are significantly warmer (Table B1.3., Appendix B). Other species have likewise been shown to be more susceptible to disease under a similar combination of novel drought and waterlogging events (Corcobado et al. 2014). It seems increasingly likely that the prolonged drought-like conditions may have triggered the emergence of disease, and the wetter, warmer winters maintain the pathogen, which continues to affect cushions weakened by an increasingly warm, variable growing season.

Conclusion

Changes in regional climate towards a system that is warmer and more variable in the summer growing season, and wetter and warmer in winter appears to be facilitating the ongoing dieback of *Azorella macquariensis* across Macquarie Island. These changes are both directly and indirectly threatening *A. macquariensis*' survival, by weakening the plant and increasing the virulence of an associated pathogen, respectively. Similar to other ecosystems, it appears that the climate-driven change in the secondary biotic interaction between *A. macquariensis* and the pathogen is posing the greatest threat to the cushions (see Cahill et al. 2013; Ockendon et al. 2014). Cushion dieback is more prevalent under extreme humidity and reduced by freezing events, conditions that are known to promote or restrict fungal or water-mould pathogen virulence (see Chakraborty et al. 2000; Harvell et al. 2002; Garrett et al. 2016). These differences in microclimate across regions of the island play a key role in explaining recent and current patterns and trends in the decline of *A. macquariensis*. Under current climate conditions, where Macquarie Island is more variable, warmer and wetter than historically experienced, dieback is expected to remain persistent on the island, increasing at the slowest rate in the south, but potentially outpacing recovery in the long-term. The inclusion of both refined cushion condition classes and microclimate within an ongoing monitoring program are considered management priorities. The extent of *A. macquariensis* decline in response to a changed regional climate, emphasises the need to track and better manage shifting baselines and the potential regime shift on Macquarie Island's fellfield plateau, and more generally across sub-Antarctic fellfield ecosystems. Early detection of change within these remote high latitude systems provides the best ability to successfully address future climate-driven threats and maintain their unique character.

References

- Adams, N., 2009. Climate trends at Macquarie Island and expectations of future climate change in the sub-Antarctic. *Papers and proceedings of the Royal Society of Tasmania* 143, 1-8.
- Adamson, D., Whetton, P., Selkirk, P.M., 1988. An analysis of air temperature records for Macquarie Island: decadal warming, enso cooling and southern hemisphere circulation patterns. *Papers and proceedings of the Royal Society of Tasmania* 122, 107-112.
- Allen, R.G., Pereira, L.S., Raes, D., Smith, M., 1998. Crop evapotranspiration-Guidelines for computing crop water requirements-FAO Irrigation and drainage paper 56. Fao, Rome 300, D05109.
- Anderson, P.K., Cunningham, A.A., Patel, N.G., Morales, F.J., Epstein, P.R., Daszak, P., 2004. Emerging infectious diseases of plants: pathogen pollution, climate change and agrotechnology drivers. *Trends in Ecology & Evolution* 19, 535-544.
- Ashcroft, M.B., Gollan, J.R., 2012. Fine-resolution (25 m) topoclimatic grids of near-surface (5 cm) extreme temperatures and humidities across various habitats in a large (200 x 300 km) and diverse region. *International Journal of Climatology* 32, 2134-2148.
- Badano, E.I., Jones, C.G., Cavieres, L.A., Wright, J.P., 2006. Assessing impacts of ecosystem engineers on community organization: a general approach illustrated by effects of a high-Andean cushion plant. *Oikos* 115, 369-385.
- Baker, D.J., Dickson, C.R., Bergstrom, D.M., Whinam, J., McGeoch, M.A., unpublished. Are microrefugia likely to exist as conservation features for cold-adapted species across the sub-Antarctic islands? xx xx, xx.
- Barton, K., Barton, M.K., 2018. Package 'MuMIn': Multi-Model Inference. Version: 1.40.4. CRAN, <https://CRAN.R-project.org/package=MuMIn>.
- Bebber, D.P., Ramotowski, M.A.T., Gurr, S.J., 2013. Crop pests and pathogens move polewards in a warming world. *Nature Climate Change* 3, 985.
- Bergstrom, D.M., 2013, updated 2014. Macquarie Is. *Azorella* dieback 5 m x 5 m quadrats 2008-2012, ed. Australian Antarctic Data Centre - CAASM Metadata., <http://dx.doi.org/10.4225/15/50FF1931B92C1>.
- Bergstrom, D.M., Bricher, P.K., Raymond, B., Terauds, A., Doley, D., McGeoch, M.A., (. . .) Ball, M.C., 2015. Rapid collapse of a sub-Antarctic alpine ecosystem: the role of climate and pathogens. *Journal of Applied Ecology* 52, 774-783.

- Bergstrom, D.M., Dickson, C.R., Baker, D.J., Whinam, J., Selkirk, P.M., McGeoch, M.A., in press. Ecosystem collapse on a sub-Antarctic island, In *Ecosystem Collapse and Climate Change*. eds J.G. Canadell, R.B. Jackson, p. xxx. Ecological Studies, Springer-Nature, xxxx.
- Bivand, R., Altman, M., Anselin, L., Assunção, R., Berke, O., Bernat, A., (. . .) Yu, D., 2017. Package ‘spdep’: Spatial Dependence: Weighting Schemes, Statistics and Models. Version 0.7-4. . CRAN, <https://CRAN.R-project.org/package=spdep>.
- Bland, L.M., Rowland, J.A., Regan, T.J., Keith, D.A., Murray, N.J., Lester, R.E., (. . .) Nicholson, E., 2018. Developing a standardized definition of ecosystem collapse for risk assessment. *Frontiers in Ecology and the Environment* 16, 29-36.
- Bonan, G.B., 2008. *Ecological climatology : concepts and applications*, 2nd ed. edn. Cambridge : Cambridge University Press, Cambridge.
- Boyd, I.L., Freer-Smith, P.H., Gilligan, C.A., Godfray, H.C.J., 2013. The Consequence of Tree Pests and Diseases for Ecosystem Services. *Science* 342, 1235773.
- Brenning, A., Bangs, D., Becker, M., Schratz, P., Polakowski, F., 2018. Package ‘RSAGA’, Version 1.3.0, <https://github.com/r-spatial/RSAGA>.
- Bricher, P.K., Lucieer, A., Shaw, J., Terauds, A., Bergstrom, D.M., 2013. Mapping Sub-Antarctic Cushion Plants Using Random Forests to Combine Very High Resolution Satellite Imagery and Terrain Modelling. *Plos One* 8, 1-15.
- Brolsma, H., 2008. Macquarie Island AIRSAR DEM (Digital Elevation Model). <http://data.aad.gov.au/aadc/metadata/>.
- Bureau of Meteorology, 2019. Climate statistics for Australian locations, Monthly climate statistics Macquarie Island, http://www.bom.gov.au/climate/averages/tables/cw_300004.shtml , accessed 3April 2019.
- Burgess, T.I., McDougall, K.L., Scott, P.M., Hardy, G.E.S., Garnas, J., 2019. Predictors of *Phytophthora* diversity and community composition in natural areas across diverse Australian ecoregions. *Ecography* 42, 565-577.
- Burgess, T.I., Scott, J.K., Mcdougall, K.L., Stukely, M.J.C., Crane, C., Dunstan, W.A., (. . .) Hardy, G.E.S.J., 2017. Current and projected global distribution of *Phytophthora cinnamomi*, one of the world's worst plant pathogens. *Global Change Biology* 23, 1661-1674.
- Cahill, A.E., Aiello-Lammens, M.E., Fisher-Reid, M.C., Hua, X., Karanewsky, C.J., Yeong Ryu, H., (. . .) Wiens, J.J., 2013. How does climate change cause extinction? *Proceedings of the Royal Society B: Biological Sciences* 280, 20121890.

- Cahill, D.M., Rookes, J.E., Wilson, B.A., Gibson, L., McDougall, K.L., 2008. *Phytophthora cinnamomi* and Australia's biodiversity: impacts, predictions and progress towards control. Australian Journal of Botany 56, 279-310.
- Cerfonteyn, M.E., Le Roux, P.C., Van Vuuren, B.J., Born, C., 2011. Cryptic spatial aggregation of the cushion plant *Azorella selago* (Apiaceae) revealed by a multilocus molecular approach suggests frequent intraspecific facilitation under sub-Antarctic conditions. American Journal of Botany 98, 909-914.
- Chakraborty, S., 2013. Migrate or evolve: options for plant pathogens under climate change. Global Change Biology 19, 1985-2000.
- Chakraborty, S., Tiedemann, A.V., Teng, P.S., 2000. Climate change: potential impact on plant diseases. Environmental Pollution 108, 317-326.
- Chau, J.H., Born, C., McGeoch, M.A., Bergstrom, D., Shaw, J., Terauds, A., (. . .) Jansen van Vuuren, B., 2019. The influence of landscape, climate and history on spatial genetic patterns in keystone plants (*Azorella*) on sub-Antarctic islands. Molecular Ecology 28, 3291-3305.
- Cohen, J.M., Civitello, D.J., Venesky, M.D., McMahon, T.A., Rohr, J.R., 2019. An interaction between climate change and infectious disease drove widespread amphibian declines. Global Change Biology 25, 927-937.
- Conrad, O., Bechtel, B., Bock, M., Dietrich, H., Fischer, E., Gerlitz, L., (. . .) Böhner, J., 2015. System for automated geoscientific analyses (SAGA) v. 2.1. 4. Geoscientific Model Development 8, 1991-2007.
- Corcobado, T., Cubera, E., Juárez, E., Moreno, G., Solla, A., 2014. Drought events determine performance of *Quercus ilex* seedlings and increase their susceptibility to *Phytophthora cinnamomi*. Agricultural and Forest Meteorology 192-193, 1-8.
- Córdova, M., Céleri, R., Shellito, C.J., Orellana-Alvear, J., Abril, A., Carrillo-Rojas, G., 2016. Near-Surface Air Temperature Lapse Rate Over Complex Terrain in the Southern Ecuadorian Andes: Implications for Temperature Mapping. Arctic, Antarctic, and Alpine Research 48, 673-684.
- Dickson, C.R., Baker, D.J., Bergstrom, D.M., Bricher, P.K., Brookes, R.H., Raymond, B., (. . .) McGeoch, M.A., 2019. Spatial variation in the ongoing and widespread decline of keystone plant species. Austral Ecology 44, 891-905.
- Dinno, A., Dinno, M.A., 2017. Package 'dunn.test'. Version 1.3.5., <https://cran.r-project.org/web/packages/dunn.test/dunn.test.pdf>.
- Fisher, M.C., Henk, D.A., Briggs, C.J., Brownstein, J.S., Madoff, L.C., McCraw, S.L., Gurr, S.J., 2012. Emerging fungal threats to animal, plant and ecosystem health. Nature 484, 186.

- Fitzgerald, N.B., Kirkpatrick, J.B., 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.
- Garrett, K.A., Nita, M., De Wolf, E.D., Esker, P.D., Gomez-Montano, L., Sparks, A.H., 2016. Chapter 21 - Plant Pathogens as Indicators of Climate Change, In *Climate Change* (Second Edition). ed. T.M. Letcher, pp. 325-338. Elsevier, Boston.
- Gignoux-Wolfsohn, S.A., Vollmer, S.V., 2015. Identification of Candidate Coral Pathogens on White Band Disease-Infected Staghorn Coral. *Plos One* 10, e0134416.
- Graae, B.J., Frenne, P.D., Kolb, A., Brunet, J., Chabrierie, O., Verheyen, K., (. . .) Milbau, A., 2012. On the use of weather data in ecological studies along altitudinal and latitudinal gradients. *Oikos* 121, 3-19.
- Harvell, C.D., Mitchell, C.E., Ward, J.R., Altizer, S., Dobson, A.P., Ostfeld, R.S., Samuel, M.D., 2002. Climate Warming and Disease Risks for Terrestrial and Marine Biota. *Science* 296, 2158-2162.
- Hoberg, E.P., Brooks, D.R., 2015. Evolution in action: climate change, biodiversity dynamics and emerging infectious disease. *Philosophical Transactions of the Royal Society B: Biological Sciences* 370, 20130553.
- Homet, P., González, M., Matías, L., Godoy, O., Pérez-Ramos, I.M., García, L.V., Gómez-Aparicio, L., 2019. Exploring interactive effects of climate change and exotic pathogens on *Quercus suber* performance: Damage caused by *Phytophthora cinnamomi* varies across contrasting scenarios of soil moisture. *Agricultural and Forest Meteorology* 276-277, 107605.
- Huber, L., Gillespie, T.J., 1992. Modeling Leaf Wetness in Relation to Plant Disease Epidemiology. *Annual Review of Phytopathology* 30, 553-577.
- Hughes, T.P., Anderson, K.D., Connolly, S.R., Heron, S.F., Kerry, J.T., Lough, J.M., (. . .) Wilson, S.K., 2018. Spatial and temporal patterns of mass bleaching of corals in the Anthropocene. *Science* 359, 80-83.
- Inkscape Project, 2018. Inkscape, v0.92.3. URL:<https://inkscape.org/>
- Körner, C., Hiltbrunner, E., 2018. The 90 ways to describe plant temperature. *Perspectives in Plant Ecology, Evolution and Systematics* 30, 16-21.
- le Roux, P.C., McGeoch, M.A., 2010. Interaction intensity and importance along two stress gradients: adding shape to the stress-gradient hypothesis. *Oecologia* 162, 733-745.
- le Roux, P.C., McGeoch, M.A., Nyakatya, M.J., Chown, S.L., 2005. Effects of a short-term climate change experiment on a sub-Antarctic keystone plant species. *Global Change Biology* 11, 1628-1639.

- Lembrechts, J.J., Lenoir, J., Roth, N., Hattab, T., Milbau, A., Haider, S., (. . .) Nijs, I., 2019. Comparing temperature data sources for use in species distribution models: From in-situ logging to remote sensing. *Global Ecology and Biogeography* 28, 1578-1596.
- Löffler, E., 1984. Macquarie Island: A wind - molded natural landscape in the subantarctic. *Polar Geography and Geology* 8, 267-286.
- Marçais, B., Dupuis, F., Desprez-Loustau, M., 1996. Modelling the influence of winter frosts on the development of the stem canker of red oak, caused by *Phytophthora cinnamomi*. *Ann. For. Sci.* 53, 369-382.
- Ockendon, N., Baker, D.J., Carr, J.A., White, E.C., Almond, R.E.A., Amano, T., (. . .) Pearce-Higgins, J.W., 2014. Mechanisms underpinning climatic impacts on natural populations: altered species interactions are more important than direct effects. *Global Change Biology* 20, 2221-2229.
- Orchard, A.E., 1989. *Azorella* Lamarck (Apiaceae) on Heard and Macquarie Islands, with description of a new species, *A. macquariensis*. *Muelleria* 7, 15-20.
- Pauchard, A., Milbau, A., Albiñ, A., Alexander, J., Burgess, T., Daehler, C., (. . .) Kueffer, C., 2016. Non-native and native organisms moving into high elevation and high latitude ecosystems in an era of climate change: new challenges for ecology and conservation. *Biological Invasions* 18, 345-353.
- Pendlebury, S.F., Barnes-Keoghan, I.P., 2007. Climate and climate change in the sub-Antarctic. *Papers and proceedings of the Royal Society of Tasmania* 141, 67-82.
- R Core Team, 2019. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.
- Ripley, B., Venables, B., Bates, D.M., Hornik, K., Gebhardt, A., Firth, D., 2019. Package 'MASS': Support Functions and Datasets for Venables and Ripley's MASS, v7.3-51.4. CRAN, <https://cran.r-project.org/web/packages/MASS/MASS.pdf>.
- Rohr, J.R., Dobson, A.P., Johnson, P.T.J., Kilpatrick, A.M., Paull, S.H., Raffel, T.R., (. . .) Thomas, M.B., 2011. Frontiers in climate change–disease research. *Trends in Ecology & Evolution* 26, 270-277.
- Rolland, V., Bergstrom, D.M., Lenne, T., Bryant, G., Chen, H., Wolfe, J., (. . .) Ball, M.C., 2015. Easy Come, Easy Go: Capillary Forces Enable Rapid Refilling of Embolized Primary Xylem Vessels. *Plant Physiology* 168, 1636-1647.

- Rueden, C.T., Schindelin, J., Hiner, M.C., DeZonia, B.E., Walter, A.E., Arena, E.T., Eliceiri, K.W., 2017. ImageJ2: ImageJ for the next generation of scientific image data. *BMC Bioinformatics* 18, 529.
- Sato, C.F., Lindenmayer, D.B., 2018. Meeting the Global Ecosystem Collapse Challenge. *Conservation Letters* 11, e12348.
- Sato, Y., Civiello, M., Bell, S.C., Willis, B.L., Bourne, D.G., 2016. Integrated approach to understanding the onset and pathogenesis of black band disease in corals. *Environmental Microbiology* 18, 752-765.
- Selkirk, P.M., 2012. Plateau Vegetation On Sub-Antarctic Macquarie Island. *Papers and proceedings of the Royal Society of Tasmania* 146, 71-79.
- Selkirk, P.M., Seppelt, R.D., Selkirk, D.R., 1990. Subantarctic Macquarie Island: environment and biology. Cambridge Press University Press, Cambridge.
- Sicard, A., Zeilinger, A.R., Vanhove, M., Schartel, T.E., Beal, D.J., Daugherty, M.P., Almeida, R.P.P., 2018. *Xylella fastidiosa*: Insights into an Emerging Plant Pathogen. *Annual Review of Phytopathology* 56, 181-202.
- Sonter, R.O., Semple, W.S., Lawrie, J.W., 2000. Soils, vegetation and land use, In *Soils: their properties and management*. eds P.E. Charman, B.W. Murphy, pp. 271-286. Oxford University Press, Melbourne.
- Stenlid, J., Oliva, J., 2016. Phenotypic interactions between tree hosts and invasive forest pathogens in the light of globalization and climate change. *Philosophical Transactions of the Royal Society B: Biological Sciences* 371, 20150455.
- Taylor, B.W., 1955. The flora, vegetation and soils of Macquarie Island., In *ANARE Reports, Series B*, 11. pp. 1-192. Australian Antarctic Division, Melbourne.
- Tweedie, C.E., Bergstrom, D.M., 2000. A climate change scenario for surface air temperature at subantarctic Macquarie Island (ed.), In *Antarctic Ecosystems: Models for Wider Understanding*. eds W. Davison, C. Howard-Jones, P. Broady, pp. 272-281. Canterbury University Press, Canterbury.
- Welsh, C., Lewis, K.J., Woods, A.J., 2014. Regional outbreak dynamics of *Dothistroma* needle blight linked to weather patterns in British Columbia, Canada. *Canadian Journal of Forest Research* 44, 212-219.
- Whinam, J., Abdul-Rahman, J.A., Visoiu, M., di Folco, M.B.F., Kirkpatrick, J.B., 2014. Spatial and temporal variation in damage and dieback in a threatened subantarctic cushion species. *Australian Journal of Botany* 62, 10-21.

- Wood, S.N., 2017. Generalized additive models: an introduction with R. Chapman and Hall/CRC, New York.
- Woods, A., Coates, K.D., Hamann, A., 2005. Is an Unprecedented Dothistroma Needle Blight Epidemic Related to Climate Change? *Bioscience* 55, 761-769.
- Zeileis, A., Cribari-Neto, F., Gruen, B., Kosmidis, I., Simas, A.B., Rocha, A.V., Zeileis, M.A., 2016. betareg: Beta Regression. Version 3.1-0, <https://CRAN.R-project.org/package=betareg>

Appendix B: Supplementary abiotic and biotic data, and modelled response of *Azorella macquariensis* condition to microclimate and terrain variables.

Table B1.1. The mean daily temperature (°C), relative humidity (%) and calculated vapour pressure deficit (Pa) statistics from data-loggers located across the 62 plateau (above 142 m asl) sites on Macquarie Island, presented at a yearly, growing season (October to March) and winter senescence season (April to September) between December 2016 and 2017.

Microclimate variable	N	Min.	Max.	Mean (\pm s.d.)
Yearly relative humidity (%)				
Daily mean	62	93.27	97.88	95.75 (\pm 1.05)
Mean daily minimum	62	85.48	94.10	89.99 (\pm 2.10)
Mean daily maximum	62	98.44	99.85	99.25 (\pm 0.33)
Mean daily diurnal change	62	5.65	12.96	9.25 (\pm 1.87)
Growing season relative humidity (%)				
Daily mean	62	90.11	96.44	93.21 (\pm 1.52)
Mean daily minimum	62	78.16	90.40	85.14 (\pm 2.90)
Mean daily 5th percentile	62	81.23	92.49	87.63 (\pm 2.65)
Mean daily 95th percentile	62	97.56	99.83	99.04 (\pm 0.45)
Mean daily maximum	62	96.56	99.69	98.43 (\pm 0.70)
Mean daily diurnal change	62	8.90	20.03	13.29 (\pm 2.53)
Winter relative humidity (%)				
Daily mean	62	94.77	99.23	97.25 (\pm 0.91)
Mean daily minimum	62	88.22	97.37	92.83 (\pm 1.94)
Mean daily 5th percentile	62	89.84	98.12	94.09 (\pm 1.69)
Mean daily 95th percentile	62	98.75	99.99	99.65 (\pm 0.22)
Mean daily maximum	62	99.02	100.00	99.75 (\pm 0.17)
Mean daily diurnal change	62	2.63	11.15	6.92 (\pm 1.79)
Yearly temperature (°C)				
Daily mean	62	2.94	4.57	3.95 (\pm 0.39)
Mean daily minimum	62	1.10	2.73	1.96 (\pm 0.34)
Mean daily maximum	62	4.74	7.31	6.08 (\pm 0.56)
Mean daily diurnal change	62	3.48	5.40	4.13 (\pm 0.40)
Growing season temperature (°C)				
Daily mean	62	4.74	6.86	6.06 (\pm 0.48)
Number of days <0°C	62	14.00	30.00	20.03 (\pm 4.39)
Mean daily minimum	62	2.60	4.39	3.63 (\pm 0.38)
Mean daily 5th percentile	62	2.31	3.89	3.11 (\pm 0.35)
Mean daily 95th percentile	62	6.06	9.65	7.54 (\pm 0.82)
Mean daily maximum	62	6.95	10.96	8.82 (\pm 0.87)
Mean daily diurnal change	62	4.00	7.42	5.2 (\pm 0.76)
Winter temperature (°C)				
Daily mean	62	1.85	3.36	2.71 (\pm 0.36)
Number of days <0°C	62	43.00	80.00	60.74 (\pm 8.06)
Mean daily minimum	62	0.20	1.75	0.97 (\pm 0.33)
Mean daily 5th percentile	62	0.35	1.90	1.12 (\pm 0.33)

Microclimate variable	N	Min.	Max.	Mean (\pm s.d.)
Mean daily 95th percentile	62	3.16	4.76	4.11 (\pm 0.39)
Mean daily maximum	62	3.42	5.27	4.47 (\pm 0.44)
Mean daily diurnal change	62	3.07	4.20	3.5 (\pm 0.22)
Vapour pressure deficit (Pa)				
Growing season daily mean	62	0.04	0.17	0.08 (\pm 0.03)
Winter daily mean	62	0.01	0.05	0.03 (\pm 0.01)

Table B1.2. Modelled relationship between temperature (°C) and northing (m) with elevation (m) for the annual, growing season (October – March) and winter senescence season (April – September) periods on Macquarie Island (MI). Significant variables in bold ($p < 0.05$).

	Estimate	Std. Error	t value	p-value	Temp. (°C) lapse.km ⁻¹	Temp. (°C) Gradient. MI Extent
<i>Annual mean</i>						
Intercept	-25.79	9.01	-2.86	0.006		
Northing (m)	7.96E-06	2.28E-06	3.50	<0.001	0.008 (± 0.023)	0.26 (±0.08)
Elevation (m)	-7.36E-03	3.95E-04	-18.64	<0.001	-7.36 (±0.39)	
Adj. R ² = 0.8779, F _(2,59) = 220.4, $p < 2.2\text{e-}16$						
<i>Annual mean minimum</i>						
Intercept	-24.27	9.21	-2.64	0.011		
Northing (m)	7.01E-06	2.33E-06	3.01	0.004	0.007 (±0.023)	0.23 (±0.08)
Elevation (m)	-6.27E-03	4.03E-04	-15.54	<0.001	-6.27 (±0.40)	
Adj. R ² = 0.8337, F _(2,59) = 153.9, $p < 2.2\text{e-}16$						
<i>Annual mean maximum</i>						
Intercept	-31.48	21.64	-1.46	0.151		
Northing (m)	1.01E-05	5.47E-06	1.84	0.071	0.007 (±0.006)	0.33 (±0.18)
Elevation (m)	-9.47E-03	9.47E-04	-9.99	<0.001	-9.47 (±0.95)	
Adj. R ² = 0.6708, F _(2,59) = 63.14, $p < 2.186\text{e-}15$						
<i>Growing season mean</i>						
Intercept	-51.38	17.96	-2.86	0.006		
Northing (m)	1.50E-05	4.54E-06	3.30	0.002	0.015 (±0.005)	0.49 (±0.15)
Elevation (m)	-7.63E-03	7.87E-04	-9.69	<0.001	-7.63 (±0.95)	
Adj. R ² = 0.6892, F _(2,59) = 68.64, $p < 3.983\text{e-}16$						
<i>Growing season mean minimum</i>						
Intercept	-48.81	14.19	-3.44	0.001		
Northing (m)	1.36E-05	3.59E-06	3.80	<0.001	0.014 (±0.003)	0.45 (±0.12)
Elevation (m)	-5.83E-03	6.22E-04	-9.38	<0.001	-5.83 (±0.62)	
Adj. R ² = 0.6888, F _(2,59) = 68.5, $p < 4.149\text{e-}16$						
<i>Growing season mean maximum</i>						
Intercept	-52.45	44.22	-1.19	0.240		
Northing (m)	1.62E-05	1.12E-05	1.45	0.153	0.016 (±0.011)	0.53 (±0.37)
Elevation (m)	-1.14E-02	1.94E-03	-5.88	<0.001	-11.39 (±1.9)	
Adj. R ² = 0.4204, F _(2,59) = 23.12, $p < 3.854\text{e-}08$						

	Estimate	Std. Error	t value	p-value	Temp. (°C) lapse.km ⁻¹	Temp. (°C) Gradient. MI Extent
<i>Winter senescence season mean</i>						
Intercept	-14.10	5.52	-2.56	0.013		
Northing (m)	4.68E-06	1.39E-06	3.36	0.001	0.005 (±0.001)	0.15 (±0.05)
Elevation (m)	-7.29E-03	2.42E-04	-30.16	<0.001	-7.29 (±0.24)	
Adj. R ² = 0. 9466, F _(2,59) = 541.9, <i>p</i> < 2.2e-16						
<i>Winter senescence season mean minimum</i>						
Intercept	-12.13	7.10	-1.71	0.093		
Northing (m)	3.70E-06	1.79E-06	2.06	0.043	0.004 (±0.002)	0.12 (±0.06)
Elevation (m)	-6.59E-03	3.11E-04	-21.19	<0.001	-6.59 (±0.31)	
Adj. R ² = 0. 8963, F _(2,59) = 264.6, <i>p</i> < 2.2e-16						
<i>Winter senescence season mean maximum</i>						
Intercept	-23.88	10.80	-2.21	0.031		
Northing (m)	7.68E-06	2.73E-06	2.81	0.007	0.008 (±0.003)	0.25 (±0.09)
Elevation (m)	-8.47E-03	4.73E-04	-17.90	<0.001	-8.47 (±0.47)	
Adj. R ² = 0. 8703, F _(2,59) = 198.0, <i>p</i> < 2.2e-16						

Table. B1.3. Change in temperature variables at Macquarie Island Bureau of Meteorology weather station between 1948 and 2018, with the exception of extreme minimum 1948 to 2015. Extreme max. (highest monthly maximum), mean max. (mean monthly maximum), mean min. (mean monthly minimum), extreme min. (lowest monthly minimum), and Mean Days Ground $\leq -1^{\circ}\text{C}$ (mean monthly number of frost days, ground temperature $\leq -1^{\circ}\text{C}$). Monthly linear models showing the adjusted R^2 , F, degrees of freedom and p values for all temperature variables. With the exception of negative binomial models for the Mean days Ground $\leq -1^{\circ}\text{C}$ showing the z value, degrees of freedom and p -value. Significant variables in bold ($p < 0.05$). Significant increase in bold, * $p < 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$.

Temperature	Jan	Feb	Mar	Apr	May	Jun
	**	***	***	**	**	
Extreme max.	Adj. $R^2 = 0.09$, $F_{(1,69)} 7.91$, $p = 0.01$	Adj. $R^2 = 0.16$, $F_{(1,68)} 14.54$, $p < 0.001$	Adj. $R^2 = 0.13$, $F_{(1,69)} 11.62$, $p = 0.001$	Adj. $R^2 = 0.08$, $F_{(1,69)} 7.46$, $p = 0.01$	Adj. $R^2 = 0.12$, $F_{(1,69)} 10.22$, $p = 0.002$	Adj. $R^2 = 0.02$, $F_{(1,69)} 2.7$, $p = 0.10$
	*	***	**	***	*	*
Mean max.	Adj. $R^2 = 0.06$, $F_{(1,69)} 5.34$, $p = 0.02$	Adj. $R^2 = 0.15$, $F_{(1,68)} 13.22$, $p < 0.001$	Adj. $R^2 = 0.13$, $F_{(1,68)} 10.88$, $p = 0.002$	Adj. $R^2 = 0.16$, $F_{(1,69)} 14.74$, $p < 0.001$	Adj. $R^2 = 0.06$, $F_{(1,69)} 5.52$, $p = 0.02$	Adj. $R^2 = 0.06$, $F_{(1,69)} 5.39$, $p = 0.02$
		***	*	***		
Mean min.	Adj. $R^2 = 0.006$, $F_{(1,69)} 1.43$, $p = 0.24$	Adj. $R^2 = 0.12$, $F_{(1,69)} 10.82$, $p = 0.001$	Adj. $R^2 = 0.06$, $F_{(1,68)} 5.60$, $p = 0.02$	Adj. $R^2 = 0.13$, $F_{(1,69)} 11.26$, $p = 0.001$	Adj. $R^2 < 0.001$, $F_{(1,69)} 1.04$, $p = 0.31$	Adj. $R^2 = 0.01$, $F_{(1,69)} 1.65$, $p = 0.20$
Extreme min.	Adj. $R^2 = -0.01$, $F_{(1,69)} 0.05$, $p = 0.82$	Adj. $R^2 = -0.01$, $F_{(1,68)} 0.44$, $p = 0.51$	Adj. $R^2 = 0.03$, $F_{(1,69)} 3.12$, $p = 0.08$	Adj. $R^2 = -0.004$, $F_{(1,69)} 0.67$, $p = 0.42$	Adj. $R^2 = -0.02$, $F_{(1,69)} 2.53$, $p = 0.12$	Adj. $R^2 = -0.01$, $F_{(1,69)} 0.05$, $p = 0.83$
Mean Days Ground $\leq -1^{\circ}\text{C}$	na	na	na	$z = -1.58$, df = 60, $p = 0.11$	$z = -0.47$, df = 61, $p = 0.64$	$z = 0.51$, df = 59, $p = 0.61$

Table B1.3. continued.

Temperature	Jul	Aug	Sep	Oct	Nov	Dec
	***	**				
Extreme max.	Adj. R² = 0.14, F_(1,69) 12.3, p = 0.001	Adj. R² = 0.10, F_(1,69) 8.86, p = 0.004	Adj. R ² = 0.03, F _(1,69) 3.37, p = 0.07	Adj. R ² = 0.01, F _(1,69) 1.59, p = 0.21	Adj. R ² = 0.02, F _(1,69) 2.12, p = 0.15	Adj. R ² = 0.03, F _(1,69) 3.36, p = 0.07
		**	*	**	**	**
Mean max.	Adj. R ² = 0.01, F _(1,69) 1.67, p = 0.20	Adj. R² = 0.08, F_(1,69) 7.31, p = 0.01	Adj. R² = 0.04, F_(1,69) 3.91, p = 0.05	Adj. R² = 0.12, F_(1,69) 10.31, p = 0.002	Adj. R² = 0.08, F_(1,69) 7.06, p = 0.01	Adj. R² = 0.09, F_(1,69) 7.59, p = 0.01
		*	**			
Mean min.	Adj. R ² = -0.01, F _(1,69) 0.50, p = 0.48	Adj. R² = 0.06, F_(1,69) 5.69, p = 0.02	Adj. R² = 0.08, F_(1,69) 7.02, p < 0.01	Adj. R ² = 0.003, F _(1,69) 1.24, p = 0.27	Adj. R ² = 0.006, F _(1,69) 1.43, p = 0.24	Adj. R ² = 0.04, F _(1,69) 3.65, p = 0.06
Extreme min.	Adj. R ² = -0.01, F _(1,69) 0.05, p = 0.82	Adj. R ² = 0.006, F _(1,69) 1.45, p = 0.23	Adj. R ² = 0.02, F _(1,69) 2.18, p = 0.15	Adj. R ² = -0.01, F _(1,69) 0.14, p = 0.71	Adj. R ² = -0.01, F _(1,69) 0.05, p = 0.82	Adj. R ² = -0.01, F _(1,69) 0.20, p = 0.66
Mean Days Ground ≤ -1°C	z = -0.38, df = 61, p = 0.70	z = -0.10, df = 61, p = 0.92	z = -1.51, df = 61, p = 0.25	z = -0.58, df = 57, p = 0.56	z = 1.04, df = 60, p = 0.30	na

Table B1.4. *Azorella macquariensis* summary statistics for total cover and proportion of each condition class, within six replicate plots at 62 sites across Macquarie Island. Condition classes presented at an island-wide level and within three equal latitudinal regions.

	N	Min.	Max.	Mean (\pm s.e.)	1st Q	Median	3rd Q
<i>Total Cover</i>							
Island-wide (m ²)							
Island-wide (%)	62	0.5	88.3	41.7 (\pm 2.73)	24.8	40.8	59.0
North (%)	15	6.0	43.4	20.4 (\pm 2.78)	13.9	18.4	24.6
Central (%)	29	0.5	71.7	39.5 (\pm 3.12)	29.1	39.3	48.5
South (%)	18	37.2	83.3	62.8 (\pm 3.46)	52.7	65.7	72.6
<i>Healthy (Smooth + Uneven + Healthy with Agrostis cover)</i>							
Island-wide (%)	62	6.0	100.0	67.76 (\pm 3.19)	51.6	67.8	89.4
North (%)	15	6.0	97.5	47.8 (\pm 6.57)	28.7	41.5	65.0
Central (%)	29	11.9	100.0	69.4 (\pm 4.14)	58.0	70.0	85.3
South (%)	18	37.5	99.9	81.8 (\pm 4.42)	75.5	87.7	96.1
<i>Healthy: Smooth</i>							
Island-wide (%)	62	1.7	95.7	58.6 (\pm 3.13)	41.2	60.7	79.2
North (%)	15	1.7	85.1	41.2 (\pm 6.55)	21.9	40.7	57.2
Central (%)	29	11.2	95.7	57.5 (\pm 4.00)	44.5	59.4	73.8
South (%)	18	32.3	94.5	75.0 (\pm 4.33)	69.2	79.3	88.3
<i>Healthy: Uneven</i>							
Island-wide (%)	62	0.00	40.2	2.9 (\pm 1.11)	0.00	0.00	0.00
North (%)	15	0.00	30.8	2.2 (\pm 2.05)	0.00	0.00	0.00
Central (%)	29	0.00	40.2	4.6 (\pm 2.06)	0.00	0.00	0.00
South (%)	18	0.00	10.1	0.6 (\pm 0.56)	0.00	0.00	0.00
<i>Healthy: with Agrostis cover</i>							
Island-wide (%)	62	0.0	20.6	6.3 (\pm 0.64)	1.9	5.5	9.3
North (%)	15	0.0	14.1	4.5 (\pm 1.18)	1.0	2.6	6.9
Central (%)	29	0.8	17.6	7.3 (\pm 0.89)	4.0	6.8	9.7
South (%)	18	0.5	20.6	6.3 (\pm 1.31)	2.0	5.1	9.2
<i>Wind-scour</i>							
Island-wide	62	0.00	13.4	1.5 (\pm 0.30)	0.1	0.5	1.5
North	15	0.00	5.1	0.8 (\pm 0.34)	0.0	0.3	1.2
Central	29	0.00	4.7	0.9 (\pm 0.20)	0.1	0.5	1.4
South	18	0.08	13.4	2.9 (\pm 0.89)	0.5	1.0	3.5

	N	Min.	Max.	Mean (\pm s.e.)	1st Q	Median	3rd Q
<i>Dieback (Active + Thinning + Advanced)</i>							
Island-wide	62	0.00	86.9	29.7 (\pm 3.08)	7.5	26.5	46.5
North	15	1.36	86.8	47.3 (\pm 5.84)	33.4	51.0	63.0
Central	29	0.00	86.9	29.5 (\pm 4.10)	12.0	29.4	39.9
South	18	0.00	62.1	15.2 (\pm 4.62)	0.1	7.4	21.9
<i>Active Dieback (Brown)</i>							
Island-wide (%)	62	0.00	26.9	3.0 (\pm 0.77)	0.00	0.1	2.5
North	15	0.00	6.7	1.1 (\pm 0.49)	0.00	0.0	1.4
Central	29	0.00	26.9	5.3 (\pm 1.5)	0.00	0.8	8.1
South	18	0.00	7.7	0.9 (\pm 0.47)	0.00	0.00	0.4
<i>Thinning Dieback (Olive + Agrostis cover on dieback)</i>							
Island-wide (%)	62	0.00	54.3	13.0 (\pm 1.83)	1.1	7.7	21.8
North	15	0.00	52.1	11.8 (\pm 3.7)	2.2	4.9	17.7
Central	29	0.00	47.4	14.2 (\pm 2.5)	1.6	12.7	23.0
South	18	0.00	54.3	11.8 (\pm 3.87)	0.1	6.4	16.9
<i>Olive</i>							
Island-wide (%)	62	0.00	51.6	10.8 (\pm 1.62)	0.2	4.8	18.1
North	15	0.00	51.6	10.2 (\pm 3.81)	0.0	2.2	16.6
Central	29	0.00	37.6	11.6 (\pm 2.18)	0.8	11.2	19.5
South	18	0.00	44.9	10.0 (\pm 3.11)	0.1	5.5	15.2
<i>Agrostis cover on dieback</i>							
Island-wide (%)	62	0.00	11.6	2.2 (\pm 0.38)	.00	1.2	2.7
North	15	0.00	10.7	1.7 (\pm 0.70)	0.00	1.1	2.2
Central	29	0.00	10.7	2.7 (\pm 0.53)	0.32	2.0	3.4
South	18	0.00	11.6	1.9 (\pm 0.83)	0.00	0.3	1.4
<i>Advanced Dieback (Black + Ablated)</i>							
Island-wide (%)	62	0.00	85.6	13.7 (\pm 2.50)	0.7	4.7	16.4
North	15	1.3	85.6	34.4 (\pm 6.82)	12.8	34.6	55.1
Central	29	0.00	43.8	10.0 (\pm 2.39)	1.2	3.7	11.9
South	18	0.00	12.4	2.5 (\pm 0.84)	0.00	0.7	3.1
<i>Black</i>							
Island-wide (%)	62	0.00	53.6	9.7 (\pm 1.91)	0.00	2.1	12.3
North	15	0.27	55.6	23.9 (\pm 5.55)	3.88	16.5	43.8
Central	29	0.00	33.6	6.9 (\pm 1.87)	0.00	1.8	8.6
South	18	0.00	12.4	2.4 (\pm 0.84)	0.00	0.2	3.0

	N	Min.	Max.	Mean (\pm s.e.)	1st Q	Median	3rd Q
<i>Advanced Dieback continued.</i>							
<i>Ablated</i>							
Island-wide (%)	62	0.00	50.5	4.0 (\pm 1.18)	0.00	0.0	2.3
North	15	0.00	50.5	10.5 (\pm 4.11)	0.00	1.7	10.4
Central	29	0.00	17.3	3.1 (\pm 0.97)	0.00	0.5	4.2
South	18	0.00	1.4	0.2 (\pm 0.09)	0.00	0.0	0.00
<i>Recovery</i>							
Island-wide	62	0.00	15.3	1.1 (\pm 0.38)	0.00	0.00	0.3
North	15	0.00	15.3	4.1 (\pm 1.29)	0.00	1.8	7.1
Central	29	0.00	3.0	0.3 (\pm 0.11)	0.00	0.00	0.3
South	18	0.00	0.2	0.02 (\pm 0.01)	0.00	0.00	0.00

Table B1.5. Relationship between summer growing season (Oct – Mar) microclimate and terrain variables and (a) the presence of wind-scour on *Azorella macquariensis* and, (b.) the presence of *A. macquariensis* recovery. Generalised additive models showing the estimated degrees of freedom (edf), Red df, and X^2 for predictor variables. Significant variables in bold ($p < 0.05$).

	edf	Ref df	X^2	p
a) Wind-scour				
<i>Azorella</i> cover (m²)	1	1	9.415	0.002
SW wind-shelter (0-1)	1	1	5.365	0.021
Freezing _{ext} days (n)	2.03	2.50	0.411	0.840
Fine gravel (%)	2.19	2.77	1.618	0.612
R-sq.(adj) = 0.557 Deviance explained = 61.2%				
-REML = 13.968, Scale est. = 1, n = 62				
b) Recovery				
Black dieback subclass (%)	1	1	5.104	0.024
Vapour pressure deficit (VPD, kPa)	2.32	2.88	1.411	0.597
Fine gravel content (%)	1	1	1.904	0.168
NW wind-shelter (0 - 1)	1	1	0.561	0.454
<i>Dieback</i> class (%)	1	1	0.569	0.451
R-sq.(adj) = 0.343 Deviance explained = 36.1%				
-REML = 28.106, Scale est. = 1, n = 62				

Table B1.6. Relationship between growing season (Oct – Mar) microclimate and terrain variables and the proportion of *Azorella macquariensis* with dieback (%). Beta regression models showing the estimated coefficients with standard error and Wald’s z-value for predictor variables. Relationship between mean growing season humidity_{ext} (mean daily 95th percentile of relative humidity, %) and freezing_{ext} (days < 0°C) at low (< 5 %) and high (≥ 5 %) dieback, general linear model showing estimated coefficients with standard error and t-value for predictor variables. Significant variables in bold ($p < 0.05$).

Variable	Estimated coefficient	Std. Error	z	p
a) <i>Azorella</i> dieback				
Intercept	-0.92	0.13	-6.93	<0.000
Humidity_{ext} (%)	0.50	0.20	2.46	0.014
Freezing_{ext} (n)	-0.38	0.16	-2.40	0.017
Fine Gravel (%)	-0.22	0.14	-1.57	0.118
Vapour pressure deficit (VPD, kPa)	0.17	0.20	0.85	0.396
<i>Azorella</i> cover (%)	-0.14	0.14	-1.01	0.312
NW Wind shelter	-0.01	0.14	-0.04	0.966
b) <i>Humidity</i>				
	Est. coef.	s.e.	t	p
Intercept	96.76	0.44	220.84	<0.001
Freezing_{ext} (n)	0.09	0.02	4.81	<0.001
Dieback < 5 %	1.63	0.51	3.18	0.002
Freezing_{ext} (n) : Dieback < 5 %	-0.06	0.02	-2.36	0.022
Adj. R ² = 0. 3591, F _(3,58) = 12.39, $p < 2.275\text{e-}06$				

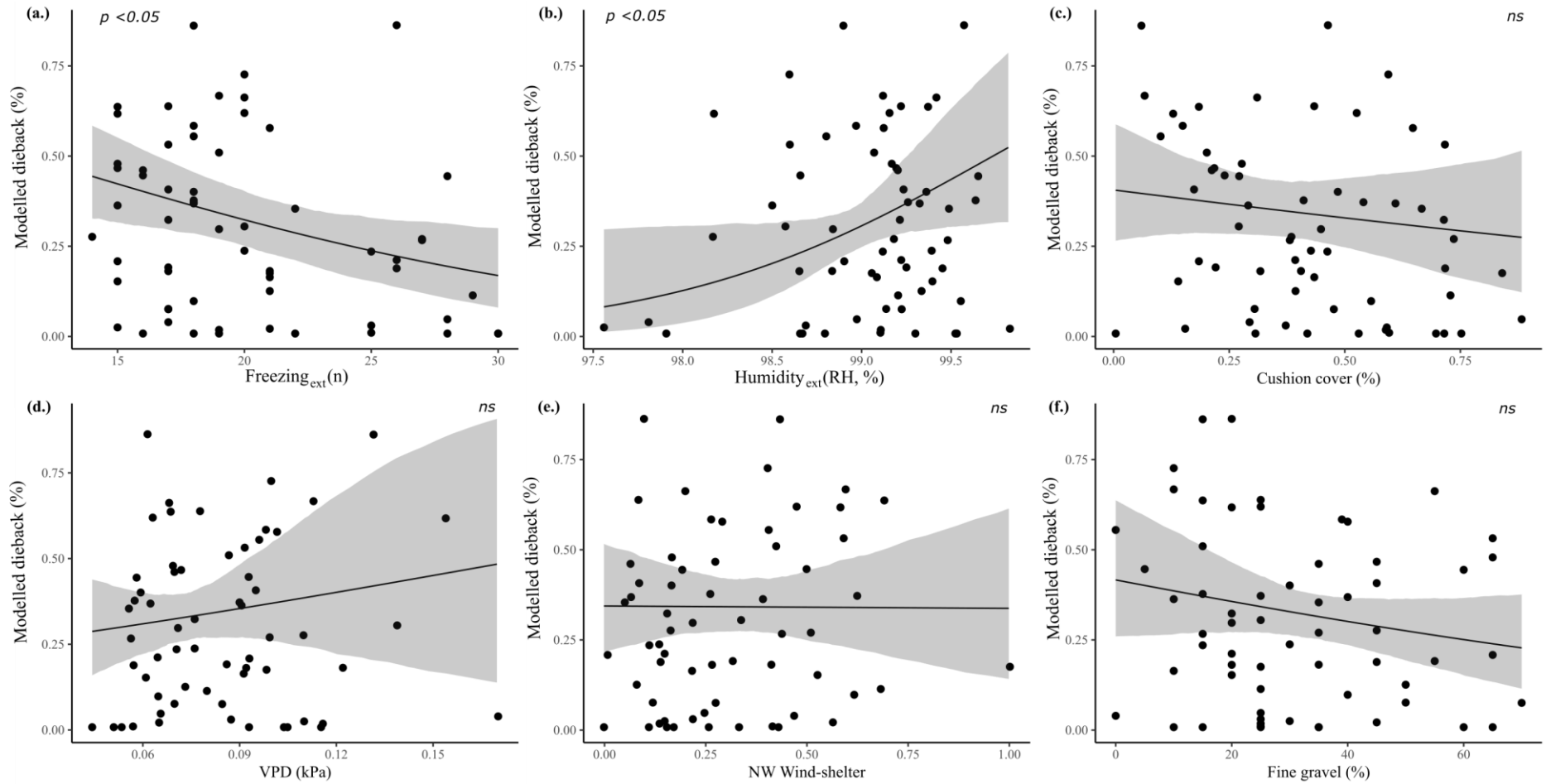


Fig. B1.1. Mean modelled *Azorella macquariensis* dieback as a proportion of total cushion cover (%) (bootstrapped 95 % confidence interval) over: (a) Freezing_{ext} (days <0°C), (b) Humidity_{ext} (daily mean 95th percentile of relative humidity, %), (c) Cushion cover (%), (d) VPD (mean daily vapour pressure deficit, kPa), (e) NW Wind-shelter (no units), and (f) Fine gravel content (%). All Figs over-laid with the recorded *A. macquariensis* dieback.

Chapter 3

Understanding ecosystem change using qualitative modelling: sub-Antarctic fellfield on Macquarie Island

Introduction

Global environmental change is affecting the distribution of biodiversity across the planet (Pecl et al. 2017). Climate change has now been observed to alter biotic interactions (Tylianakis et al. 2008; Ockendon et al. 2014) and drive species range shifts (Chen et al. 2011; Pecl et al. 2017), leading to the formation of novel communities (le Roux and McGeoch 2008a). Large-scale ecological changes in response to environmental change, have been linked to the effects of climate change through either the loss of a dominant species or the effects across multiple species (Harris et al. 2018). Ecological regime shifts occur when a system moves from one system state to another (Scheffer and Carpenter 2003). The climate drivers of declines in species and communities are variable and often specific to the system. They can range from long-term climate presses (e.g. steady increase in temperature or rainfall) to short-term extreme event climate pulses (e.g. storms, wildfire), or a most often a combination of both (Harris et al. 2018). Biotic interactions may help to buffer both the direct and indirect effects of climate change by creating a differential response across the community, thus providing a compensatory mechanism and thereby improving the ecosystem's resilience to change (Suttle et al. 2007; Valiente-Banuet et al. 2015; Losapio and Schöb 2017). Islands may be particularly affected by the loss of individual plant species from the effects of climate change, as they often have less functional redundancy (Harter et al. 2015). Therefore, on islands, the loss of a single species can disproportionately affect ecological structure, function and biotic interactions (Harter et al. 2015). In particular, the loss of species that have a disproportionate effects on the ecosystem function (keystone species), may trigger substantial change to a system resulting in an ecological regime shift.

Regime shifts, defined as a shift from one stable state to another (Scheffer and Carpenter 2003), are hard to predict and may occur as a slow transition with the potential for recovery (Hughes et al. 2013), or as a rapid irreversible transition (Scheffer and Carpenter 2003; Ratajczak et al. 2017). Ecosystem collapse describes the endpoint of a slow or rapid irreversible ecosystem transition, and is defined as a system exceeding one or more bounded thresholds for which it is characterised (Keith et al. 2013; Bland et al. 2018; Sato and Lindenmayer 2018). Predominantly used in the context of the IUCN's Red List for Ecosystems (RLE), the term ecosystem collapse is used to express the irreversible loss of an ecosystem's character and associated ecosystem function in response to individual or series of threats (Keith et al. 2013; Bland et al. 2018; Sato and Lindenmayer 2018). However, identifying ecological thresholds

and determining the rate of regime shifts, and the ultimate ecosystem collapse, is challenging, as they are determined by complex biotic interactions with multiple drivers (Petraitis 2013).

The start of the first climate-driven, landscape-scale regime shift in the sub-Antarctic region, occurred with the contemporary island-wide dieback of the keystone endemic, *Azorella macquariensis* Orchard (Macquarie cushions, Apiaceae), and associated bryophytes on Macquarie Island (Whinam et al. 2014; Bergstrom et al. 2015). The island-wide dieback is ongoing, continuing to affect approximately a third of cushion cover on the island since it was first observed in 2008/09 (Dickson et al. 2019). In areas of extensive dieback, the loss of the keystone cushion is thought to be causing localised ecosystem collapse, with substantial denuding in some areas on the fellfield (Hoffmann et al. 2019; Bergstrom et al. in press). Dieback is hypothesised to be triggered and driven by the pathogenic infection of cushions weakened by a changed, more variable regional climate, i.e. characterised by higher evapotranspiration rates and less summer plant available water up to 2008 (Bergstrom et al. 2015). Though the system is no longer as visibly water-stressed, with cushions regaining turgidity and some recovery occurring, dieback continues under increasingly large pulses of rainfall and warming regional climate (Chapter 2). While the pathogen/s remains unidentified, 10 major groups of fungal, bacterial and oomycete taxa have been found in association with *A. macquariensis* dieback (Bergstrom et al. 2015).

As a keystone species, which facilitates biotic diversity and effects landform process (Bergstrom et al. 2015), the substantial reduction of cover is likely to have a large negative effect on biotic interactions important for ecosystem function. The loss of interactions and associated feedbacks on the *A. macquariensis*-dominated fellfield would reduce biotic complexity, and in turn negatively affect its resilience to climate change. Despite *A. macquariensis* demography and the surrounding fellfield ecosystem ecology being reasonably well understood (Taylor 1955a; Taylor 1955b; Ashton and Gill 1965; Selkirk et al. 1988; Selkirk et al. 1990; Bergstrom et al. 1997; Selkirk 2012; Bricher et al. 2013; Selkirk-Bell and Selkirk 2013; Whinam et al. 2014; Bergstrom et al. 2015; Dickson et al. 2019), the interactions in the system have not been well quantified. Therefore, currently ecosystem interactions and the mechanisms hypothesised to be driving ecosystem collapse on the island are untested, and subsequently the response of the system as a whole to climate change is poorly understood.

In systems where the direction of the interactions between different components are known, it is possible to use qualitative data to (i) make predictions about the types of responses and (ii)

subsequently test ecosystem response to different press perturbations (defined here as ongoing disturbances) (Ramsey and Veltman 2005; Raymond et al. 2011; Melbourne-Thomas et al. 2012; Marzloff et al. 2016; Sobocinski et al. 2018). This simulation-approach enables exploration of competing hypotheses about multiple threats in the ecosystem, by defining the probability of negative consequences across multiple model realisations. The Macquarie Island fellfield provides a good system to examine complex interactions in response to climate change (see Harter et al. 2015), because similar to other sub-Antarctic Islands its changing climate is well documented, and it has low biological diversity and comparatively low human disturbance (Selkirk et al. 1990; Bergstrom and Chown 1999).

Here the major abiotic and biotic interactions in the fellfield ecosystem of Macquarie Island are characterised and tested using qualitative and iterative system modelling methods. First, a qualitative network model (QNM) is used to (i) identify the interactions that have the largest impact on the keystone species *A. macquariensis*, and to (ii) predict alternative outcomes should current climate conditions be maintained and the island-wide *A. macquariensis* dieback continue unchecked. Second, a mechanistic state-transition diagram for *A. macquariensis* condition is then constructed using the outcome of the previous step, and in combination with empirical evidence on the system and the interactions within it. Together these models enable a structured and more precise understanding of the complex sets of interactions and responses of the ecosystem's keystone species to current and predicted environmental change. Here, use of these models enables a suite of system-wide hypotheses to be constructed for future testing. The results are used to identify research and monitoring priorities for understanding and early detection of further changes in the nature and functioning of the fellfield ecosystem on Macquarie Island.

Study system

Macquarie Island is a small (123.9 km²), remote sub-Antarctic island (158°55'E; 54°30'S). The flora and fauna of the oceanic island are adapted to historically stable, cool, wet and misty conditions, regulated by its location and rectangular shape (c.34 km by c. 5km long) (Selkirk et al. 1990). Over the past 40 years the regional climate has changed, resulting in a higher evapotranspiration rate from an increase in summer wind speed, sunshine hours (Bergstrom et al. 2015), against a drier, stormier atmosphere (Adams 2009). During this period, rainfall on the island has increased by 30%. However, rainfall is more variable, falling in larger events,

predominantly in the winter and saturating the peat soils (Scott and Kirkpatrick 2013; Bergstrom et al. 2015).

The island is characterised by low, highly undulating alpine plateau, ranging from 200 – 416 m above sea level (asl). The exposed mid to high plateau is dominated by a sparse fellfield ecosystem comprised of bryophytes and a low diversity of vascular plants. The ecosystem graduates from sparse fellfield to short-grasslands at lower elevation. The dominant fellfield cushion plant, *A. macquariensis*, with a mean cover of 47% (range 0 – 98%), is one of only 18 vascular plant species on the fellfield (Selkirk 2012). The cushion form and extent is highly variable, dependent on-site conditions, forming extensive mats in the south of the island and is a major component of Macquarie Island's iconic terraces (Orchard 1989; Selkirk 2012; Bricher et al. 2013). The cushion is particularly susceptible to water loss during its active summer growing season (Rolland et al. 2015) and has a winter dormancy period from ~April when leaves senesce before new leaves are produced in spring (Aug-Oct) (Taylor 1955a). The senesced leaves are held within the canopy of the cushion, forming a moist humic compost with the interstitial bryophytes, which provides an important source of available water and nutrients (Bergstrom et al. 2015).

Azorella macquariensis is considered a keystone species because, similar to other *Azorella* species, it facilitates a higher diversity and abundance of micro-arthropods and concentrates carbon through the deposition of humic material within its canopy (Bergstrom et al. 2015). The contribution of soil organic carbon and subsequent soil development is particularly important in the fellfield ecosystem, which has the lowest carbon accumulation rate on the island (Wilson et al. 2019). More generally, *Azorella* species have been shown to facilitate the diversity and abundance of vascular plants at moderate to high elevations (le Roux and McGeoch 2008b; Raath-Krüger et al. 2019) and micro-arthropods (Barendse and Chown 2001; Hugo et al. 2004). Facilitation of other species occurs through the amelioration of microclimate conditions, by buffering temperature extremes (Nyakatya and McGeoch 2008) and soil moisture content, while also improving nutrient availability (Anthelme et al. 2012).

Modelling Methods

Qualitative network modelling (QNM) is a method that can be used to assess the relative effect of different ecosystem components on each other (Levins 1974; Dambacher et al. 2003; Ramsey and Veltman 2005; Raymond et al. 2011). It provides a useful tool for analysing complex systems where the interaction (edge) direction or mechanism between components (nodes) is known, but the interaction strengths have not been quantified (Dambacher et al. 2003; Raymond et al. 2011; Melbourne-Thomas et al. 2012). The ability to focus on the model structure allows the exploration of direct and indirect effects from an extended perturbation (or ‘press’) in the system, including unexpected results from indirect effects (Raymond et al. 2011). The predator-prey (Lotka-Volterra) system of differential equations is used to describe the dynamics of n interacting nodes (normally species) and to create a community interaction matrix (Raymond et al. 2011). The effect of different perturbations can then be estimated by applying an extended press to the resultant negative inverse community matrix, when at equilibrium (Raymond et al. 2011). However, because natural systems are complex, there is regularly some ambiguity in the true model configuration. Qualitative network analysis (QNA), applied to the QNM using the R software package *QPress* (Melbourne-Thomas et al. 2012), was therefore used to advance understanding of the system by (1) describing the inverse community matrix from the user-defined model, (2) simulating the matrix using randomly generated edge (interaction) weights, then checking the resultant models for (3) numeric stability and (4) ecological validity against pre-described validation criteria, before (5) applying a press perturbation to the models, and aggregating the results to provide a proportional estimate of the response (Raymond et al. 2011; Melbourne-Thomas et al. 2012).

Qualitative network analysis (QNA) has been previously used to evaluate the complex response of a variety of ecosystems to management and threat perturbation, such as, drivers of survival decline in Salish Sea salmon populations (Sobocinski et al. 2018), management interventions for the Tasmanian reef ecosystems (Marzloff et al. 2016), and pest eradication strategies for the Macquarie Island terrestrial ecosystem (Raymond et al. 2011). QNA is used here to explore the complex interactions and response of the Macquarie Island fellfield ecosystem and its keystone species to current and projected climate change and associated indirect threats. This modelling technique provides the most suitable option because despite *A. macquariensis* and the fellfield ecosystem being comparatively well understood (see above), interaction strengths are unquantified and its response to environmental change is untested.

The following workflow was used to characterise and refine the qualitative network model (Melbourne-Thomas et al. 2012) for the *Azorella*-centred fellfield ecosystem (ACFE) so that it could be used to explore a number of hypotheses: (a) develop a conceptual model of healthy ACFE, which occurs under historical cool, misty and windy conditions (see Selkirk et al. 1990) and subsequent sub-models (healthy, active and advanced dieback), (b) analyse these three sub-models using qualitative network analysis to describe alternate states in the condition of the species, (c) gain insight on the ACFE response to defined scenarios (changes in the climate, pathogens, epiphyte density and a decline cushion condition) via further analysis, (d) use the results from analysis to revise the sub-models, and (e) use the revised models to interpret the response of the ACFE to the defined scenarios (Fig. 1).

i. *Azorella*-centred fellfield ecosystem conceptual model and sub-models

A conceptual model of the *Azorella*-centred fellfield ecosystem (ACFE) was assembled as a signed-graph (following Melbourne-Thomas et al. 2012) (Fig. 1a), with the assumption of *A. macquariensis* populations in a historical healthy condition. The model was limited to encompass only the fellfield ecosystem where *A. macquariensis* is the dominant vascular species. Therefore, the model excludes areas of short-grassland at lower elevations. The ‘nodes’ of the model represent biotic and abiotic ecosystem components, and ‘edges’ represent the interactions between those nodes or ecosystem components (following Melbourne-Thomas et al. 2012). Evidence from published literature and expert knowledge was used to determine the main components of the ACFE.

The draft ACFE model was reviewed at a workshop of relevant experts including active researchers from four Australian universities and four government agencies, encompassing expertise in *Azorella* biology and ecology, Macquarie Island ecology and geomorphology, plant physiology, and ecological modelling (see thesis acknowledgements for a full list of workshop participants). Experts discussed the potential interactions that occurred in the fellfield ecosystem, which had a degree of support in the literature (see Appendix C1 for a full list of considered interactions and associated literature). These interactions were subsequently classified as ‘major’ (i.e. the interaction had a significant impact on another node, that if excluded would change the system in its absence) or ‘minor’ (i.e. had no effect on the system if removed). Minor interactions were not included in the model.

The final Macquarie Island ACFE consisted of ten nodes, four abiotic and six biotic, associated with what were considered major interactions on the fellfield (Table 1, Fig. 2a, Table C1.1).

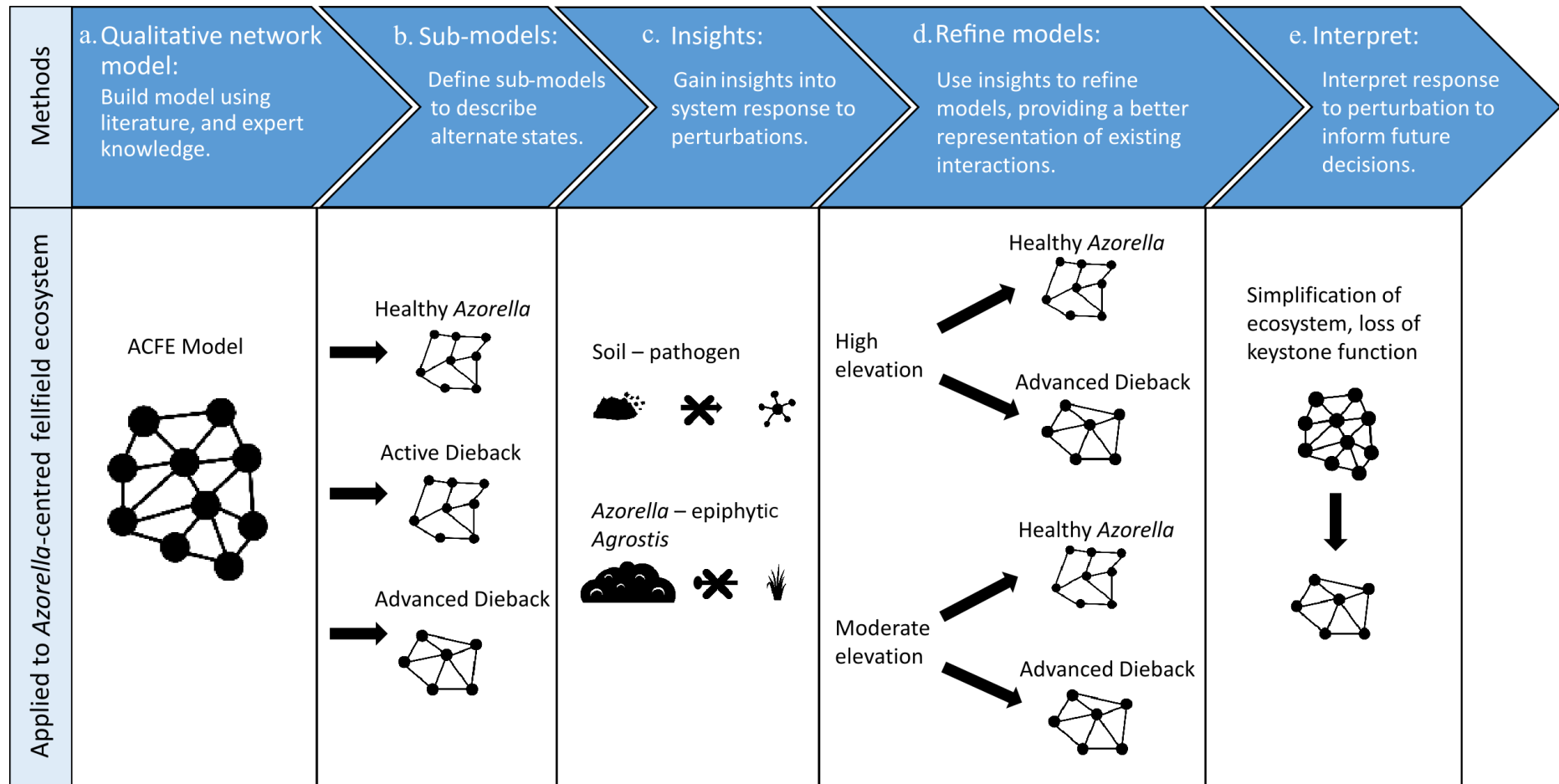


Fig. 1. Workflow for the development of the Macquarie Island *Azorella*-centred fellfield ecosystem (ACFE) qualitative network model and its subsequent analysis, insights gained, refinement and application.

Table 1. Major abiotic and biotic interactions within the *Azorella*-centred fellfield ecosystem (ACFE) on Macquarie Island under current climate conditions, determined from published literature and expert input. Major interactions are described as necessary to maintain current function. Abbreviated model nodes: Az: *Azorella macquariensis*; Bryo: bryophytes; EpiAgr: epiphytic monocots on *A. macquariensis*, predominantly *Agrostis magellanica* and *Luzula crinita*; EpiBry: interstitial bryophyte species within *A. macquariensis* canopy; MicAr: microarthropod species; MClim: current variable microclimate; Path: pathogens causing disease in *A. macquariensis*; Soil: water-holding capacity of soil; SOM: soil-organic matter; and, Texture: soil gravel content. Model abbreviations: 1: initial ACFE, (a) healthy, (b) active dieback, (c) advanced dieback. 2H: High elevation ACFE, (a) healthy, (b) advanced dieback. 2M: Moderate elevation ACFE, (a) healthy, (b) advanced dieback. Directional relationship indicated by symbols, positive (\rightarrow) and negative ($-\bullet$).

Interaction	Description	Models	Reference
Az \rightarrow EpiAgr	<i>Azorella</i> species facilitate epiphytes under abiotic stress; and under dieback.	1 a, b, c 2H a	Bonanomi et al. (2016), le Roux and McGeoch (2010), le Roux et al. (2013); Whinam et al. (2014)
Az \rightarrow EpiBry	Provision of habitat, amelioration of abiotic conditions.	1 a, b 2H a, 2M a	Bergstrom et al. (2015)
Az \rightarrow MicAr	<i>Azorella</i> ameliorates abiotic conditions for some species.	1 a, b 2H a, 2M a	Barendse and Chown (2001), Hugo et al. (2004), Bergstrom et al. (2015)
Az \rightarrow SOM	<i>A. macquariensis</i> increases soil organic matter (carbon).	1 a, b 2H a, 2M a	Bergstrom et al. (2015), Anthelme et al. (2012)
Bryo \rightarrow Az	Neighbouring bryophytes ameliorate abiotic conditions, reducing water loss.	1 a, b, c 2H a, b 2M a, b	Jagerbrand et al. (2011)
EpiAgr $-\bullet$ Az	When climate is warm or dieback is present epiphytes increase and cushion health decreases.	1 b, c, 2M a, b	le Roux et al. (2005), Whinam et al. (2014)
EpiBry \rightarrow Az	Maintains canopy integrity and cushion health.	1 a, b 2H a, 2M a	Bergstrom et al. (2015)
MicAr \rightarrow Soil	At healthy levels, increases soil development and beneficial soil properties.	1 a, b, c 2H a, b 2M a, b	Parisi et al. (2005), Stork and Eggleton (1992), Smith and Steenkamp (1990)
MClim $-\bullet$ Az	<i>Azorella</i> condition declines under warming and rainfall variability.	1 a, b, c 2H a, b 2M a, b	le Roux et al. (2005), Rolland et al. (2015), Bergstrom et al. (2015)

Interaction	Description	Models	Reference
MClim –● Bryo	Bryophyte health decreases under current variable climate.	1 a, b, c 2H a, b 2M a, b	Bergstrom et al. (2015)
MClim → EpiAgr	As climate warms, epiphytic <i>Agrostis magellanica</i> is advantaged.	1 a, b, c 2H a, b 2M a, b	le Roux and McGeoch (2008a), le Roux et al. (2005)
MClim –● EpiBry	Bryophyte health decreases under current variable climate.	1 a, b, c 2H a, b 2M a, b	Bergstrom et al. (2015), Gignac (2011)
MClim –● MicAr	Climate variability and periodic drying negatively affects some species.	1 a, b, c 2H a, b 2M a, b	McGeoch et al. (2006), Smith and Steenkamp (1990)
MClim → Path	Disease has increased under the current climate.	1 a, b, c 2H a, b 2M a, b	Bergstrom et al. (2015), Whinam et al. (2014), Dickson et al. (2019)
Path –● Az	Disease reduces <i>Azorella</i> cover.	1 a, b, c 2H a, b 2M a, b	Bergstrom et al. (2015), Whinam et al. (2014), Dickson et al. (2019)
Soil → Path	Higher pathogen presence in soils with higher water holding capacity.	1 a, b, c	Expert input
SOM → Soil	SOM increases water holding capacity of soil.	1 a, b, c 2H a, b 2M a, b	Sonter et al. (2000)
Texture –● Soil	Increasing gravel content reduces water holding capacity of soil.	1 a, b, c 2H a, b 2M a, b	Sonter et al. (2000)

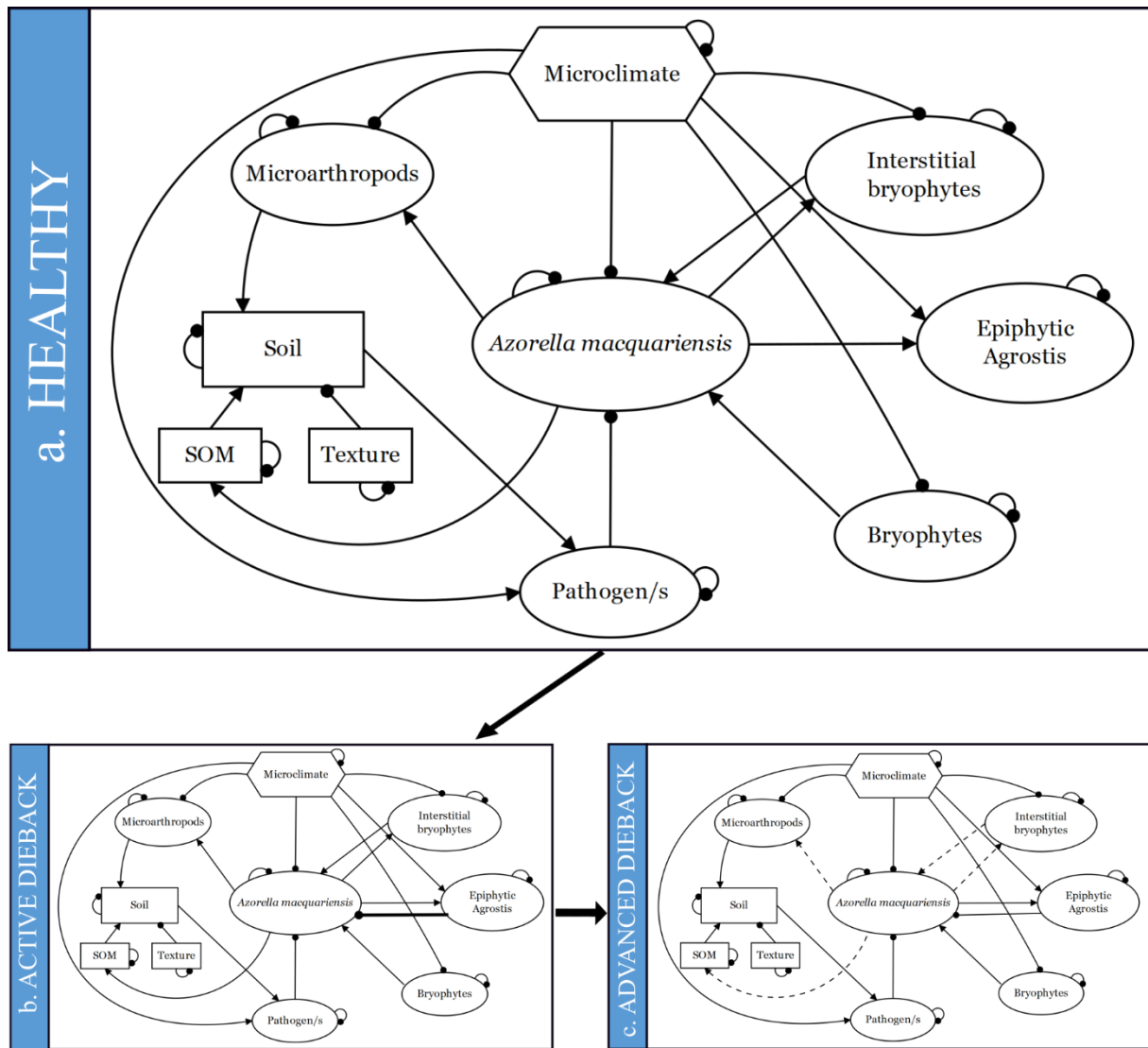


Fig. 2. Macquarie Island *Azorella*-centred fellfield ecosystem (ACFE) qualitative network model. ACFE sub-models shown for the three major *Azorella macquariensis* condition classes, healthy (a., primary model reviewed at workshop), active dieback (b.) and advanced dieback (c.). Interaction changes between condition models a. to b., and b. to c. are shown with the use of bold lines (insertion of interactions) and dotted lines (removal of interactions). Node abbreviations: Microclimate represents current climate conditions; Soil: water-holding capacity; Texture: gravel content; SOM; soil organic matter; Epiphyte *Agrostis*: includes *Agrostis magellanica* and *Luzula crinita*; all other nodes as presented. Only major interactions are included, directional positive (→), directional negative (→●), and self-limiting feedback loops (⬤).

Nodes represent biotic (taxonomic groups) or abiotic conditions unless otherwise specified. The ACFE is presented as a digraph (i.e. directed graph) using Dia (0.97.2) software, depicting positive (\rightarrow), negative ($-\bullet$) and self-limiting interactions (\bullet) (Fig. 2a). The ‘healthy’ ACFE was constructed as relevant to the historical weather conditions (MClim) that were consistently cool, misty, and windy (Selkirk et al. 1990). The Epiphytic *Agrostis* (EpiAgr) node represents the dominant vascular epiphytes of *A. macquariensis*, specifically the native graminoids *Ag. magellanica* (grass) and *Luzula crinita* (sedge).

The type of interaction (i.e. major/minor or positive/negative) can vary depending on assumed ecosystem state, for example between healthy cushions or cushions with advanced dieback. Therefore in addition to the ‘healthy’ ACFE model (Fig. 2a), two other sub-models (Fig. 1b) were specified to represent the two other main *A. macquariensis* condition classes, ‘active dieback’ (Fig. 2b) and ‘advanced dieback’ (Fig. 2c), as defined in Chapter 2. The number of interactions between different nodes of the ACFE were hypothesised and therefore set to decrease as cushion condition declined, supported by published literature and expert judgement. The active and advanced dieback ACFE sub-models are also presented as digraphs (Fig. 2).

It was hypothesised that the largest impact on *A. macquariensis* condition would occur under (i) increased pathogen activity (Chapter 2), followed by (ii) continued change of microclimate conditions under the current climate trajectory, which are thought to both stress *A. macquariensis* (Whinam et al. 2014; Bergstrom et al. 2015) and promote the pathogen (Chapter 2). It was expected that areas of advanced dieback would be least able to maintain the facilitative interactions from *A. macquariensis* and hence support pre-perturbation biotic processes and ecosystem function. In contrast, the native grass *Ag. magellanica* was expected to increase under the current climate change trajectory (le Roux and McGeoch 2008a), represented as higher temperatures and more episodic rainfall. This increase in *Ag. magellanica* cover was expected to negatively affect *A. macquariensis*, by causing higher cushion stem death from increased shading (see le Roux et al. 2005).

ii. Qualitative network analysis

Qualitative network analysis (QNA) was used to investigate the response of the three ACFE sub-models (digraphs, Fig. 2) representing healthy cushions, cushion with active and advanced dieback to changes in the climate, the unknown pathogens, epiphyte density and a decline in *A. macquariensis* condition (see Raymond et al. 2011; Melbourne-Thomas et al. 2012; Marzloff et al. 2016). Analysis was conducted in the R software package *QPress* (Melbourne-

Thomas et al. 2012) to explore the ACFE's resilience to foreseeable change and gain an understanding of key drivers of future change.

Each ACFE sub-model (healthy, active dieback, and advanced dieback; Fig. 2) digraph were described as a signed community matrix. *QPress* interprets digraphs as community matrices, which are simulated multiple times based on randomly generated edge weights of the same sign for non-zero nodes (between 0.01 and 1), including self-limitation effects for all nodes between -1 and -0.25 (Raymond et al. 2011). The resultant matrices are retained if they are numerically stable (i.e. have a stable equilibrium) based on the matrix's eigenvalues and are ecologically valid, i.e. respond in a predetermined way to a well understood perturbation (Melbourne-Thomas et al. 2012). The stable models are then used to determine the proportion of positive and negative responses of the model nodes to described press perturbations within the system, providing a measure of uncertainty. *QPress* allows the exploration of uncertainty within the network under different change scenarios (press perturbations) and under different assumptions about interactions in the ecosystem.

Each matrix was then simulated 5000 times, using randomised edge weights to generate a suite of alternate models (inverse community matrices) (Melbourne-Thomas et al. 2012; Marzloff et al. 2016; Sobocinski et al. 2018). Only numerically stable models that were consistent with ecological validation criteria were retained. The retained models were then used to assess the response of the ACFE to perturbations with unknown responses (Raymond et al. 2011; Melbourne-Thomas et al. 2012). The proportional response of each node in the model to different press perturbations was defined by the cumulative response of the alternate models (Raymond et al. 2011; Melbourne-Thomas et al. 2012). Positive press perturbations are defined as a sustained (continuous) increase in the specified node.

The hypothesised ACFE sub-model response (above) were tested using QNA for five positive press perturbations, herein referred to as scenarios. Scenarios included, (i) a climate trajectory of higher wind speed, increased sunshine hours, higher but more variable precipitation (Bergstrom et al. 2015) and higher maximum temperatures (Chapter 2) (MClim), (ii) higher pathogen activity (Path), (iii) higher cover of Epiphytic *Agrostis* (EpiAgr), (iv) MClim+Path, and (v) *Azorella* recovery (*Azorella*). The response of each node to each scenario within the three sub-models is displayed using a colour scale, from positive (red) to negative (blue) (following Marzloff et al. 2016). Those responses that were less than 80% positive or negative

were considered uncertain (grey). All analyses were performed using RStudio Desktop 1.2.1335 using R for Windows 3.5.0 (R Core Team 2019).

To refine the ACFE conceptual model for the purpose of further understanding the ecosystem response to different threats (scenarios) when *A. macquariensis* populations were in either healthy or advanced dieback condition, an iterative model development process was used based on the insights gained from the first QNA scenarios (Fig. 1).

State-transition condition diagram

The understanding of interactions on the Macquarie Island fellfield (Table 1) gained from the QNA were then combined with cushion condition classes (Chapter 2) to provide a mechanistic description of *A. macquariensis* dieback progression. This state-transition diagram, used prior to the development of a quantitative state-transition model, describes the change in transitional cushion condition (state) expanding on the hypothetical model of dieback drivers described in Hoffmann et al. (2019). Dieback progression is defined as the reduction in cushion condition, and provides the ability to estimate the potential for, and time to, cushion recovery or ablation from the system depending on site and climate conditions. This hypothetical system-wide model was constructed for the purpose of predicting feedback loops in the ACFE as well as a temporal dimension to change in the system.

Results

Qualitative Network Analysis and model refinement

The construction of the ACFE sub-models demonstrated that a decline in *A. macquariensis* condition to advanced dieback resulted in a large reduction of interactions between biotic components on the ACFE (Fig. 2a-c). Consequently, qualitative network analysis found that the microclimate scenario of increasing current climate trajectories had the most consistently strong negative impact on all components across all condition class sub-models, with the exception of soil texture and soil organic matter (Fig. 3c). Biotic components (i.e. epiphytes, bryophytes, micro-arthropods) and abiotic conditions (soil water holding capacity and organic matter) all decreased from the direct negative impact of climate, or indirectly through the decline in *A. macquariensis* condition under this scenario. Unexpectedly, the microclimate scenario resulted in a weakly negative or uncertain response by both the pathogens and *Epiphytic Agrostis* (Fig. 3a-c). Because this outcome was unexpected it was explored further

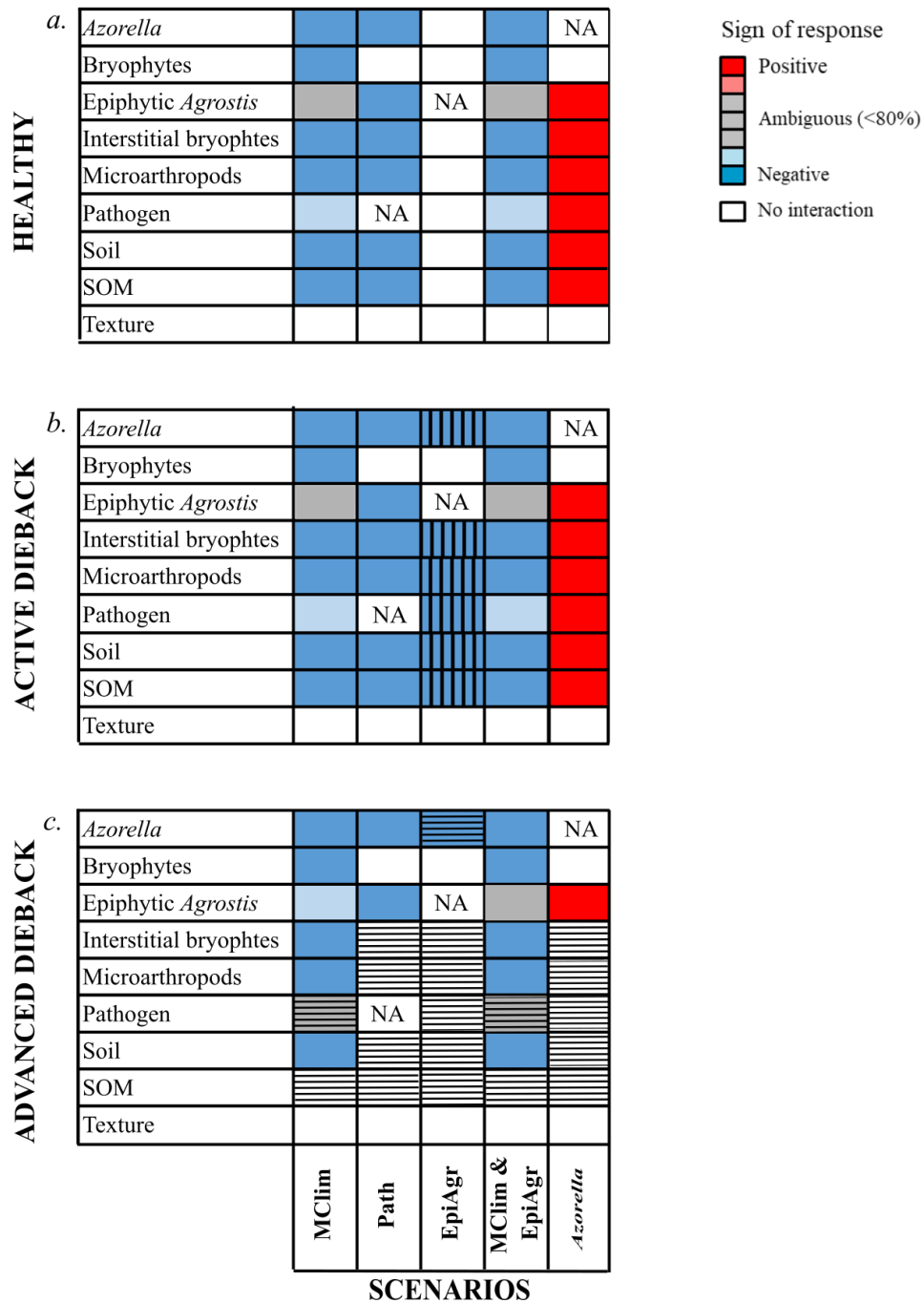


Fig. 3. Modelled ecological response of the Macquarie Island *Azorella*-centred fellfield ecosystem (ACFE) (y-axis) to scenarios (x-axis). ACFE sub-models shown for the three major *Azorella macquariensis* condition classes, healthy (a.), active dieback (b.) and advanced dieback (c.). Response scaled from positive (blue) to negative (red), with uncertain response (<80% of either direction) shaded in grey and no interaction white. Node response difference between condition sub-models indicated by vertical lines (model a. to b.) and horizontal lines (model b. to c.). Microclimate represents current climate conditions; Soil: water-holding capacity; Texture: gravel content; SOM; soil organic matter; Epiphytic *Agrostis*: includes *Ag. magellanica* and *Luzula crinita*; all other nodes as presented. Scenarios include, MClm (increased trajectory of current climate conditions), Path (increased pathogen activity), EpiAgr (increased epiphytic *Ag. magellanica* or *L. crinita* cover), and *Azorella* (*A. macquariensis* recovery or increase in cover).

independently using empirical tests of the interactions (Fig. 1c), followed by modification of sub-models interactions that emerged as being inconsistent with the results (Fig. 1d).

i. Insights gained from ACFE sub-models and used to define the revised models

Pathogen response to microclimate (MClim)

Running the microclimate scenario for all three ACFE sub-models resulted in a negative response by the pathogens (Fig. 3a-c). However, the pathogen has emerged on Macquarie Island over the past ten years along-side an increasingly wet, warm and variable climate (Bergstrom et al. 2015). Therefore, one or more assumptions in the ACFE model was shown to be incorrect. The positive interaction from soil (water holding capacity) to pathogens (Fig. 2a-c) was identified as the indirect cause of the negative pathogen response to a microclimate scenario. This link was therefore removed from all subsequent models (Fig. 1c), a decision consistent with the lack of support for a significant relationship between soil characteristics and cushion dieback extent in topographic (Dickson et al. 2019) and microclimate (Chapter 2) modelling.

Epiphytic Agrostis response to microclimate (MClim) and dieback

Similarly, Epiphytic *Agrostis* unexpectedly responded negatively to the microclimate scenario across all ACFE sub-models (Fig. 3a-c). Elsewhere in the sub-Antarctic the distribution of the native grass *Agrostis magellanica* Lam. (Poaceae) has moved upslope (le Roux and McGeoch 2008a) and increased in abundance (le Roux et al. 2005) in response to a warming climate. There has also been a significant increase in maximum temperature on Macquarie Island (Chapter 2; 0.7 ± 0.26 °C (SD), 1950 – 2010s). This rise in temperature has occurred concurrently with a significant increase in cover of *Ag. magellanica* and *L. crinita* on the coastal escarpments, irrespective of European rabbit (*Oryctolagus cuniculus*) grazing (Scott and Kirkpatrick 2013), implying that on Macquarie Island graminoids are also responding to a warmer environment. This suggests that one or more model assumptions (Fig. 4ab) were incorrect, triggering further analysis that focused on the relationships between *A. macquariensis*, dieback and Epiphytic *Agrostis* (Appendix C2).

This analysis provided valuable insights (Appendix C2), suggesting that the relationship between *A. macquariensis* and Epiphytic *Agrostis* changes with elevation and temperature (Fig. C2.1), where they had a higher cover and therefore were more competitive at the warmer lower elevation, which may also be true for graminoids off-cushion. To capture these empirical results about the change in relationships over elevation, the ‘original’ ACFE model was

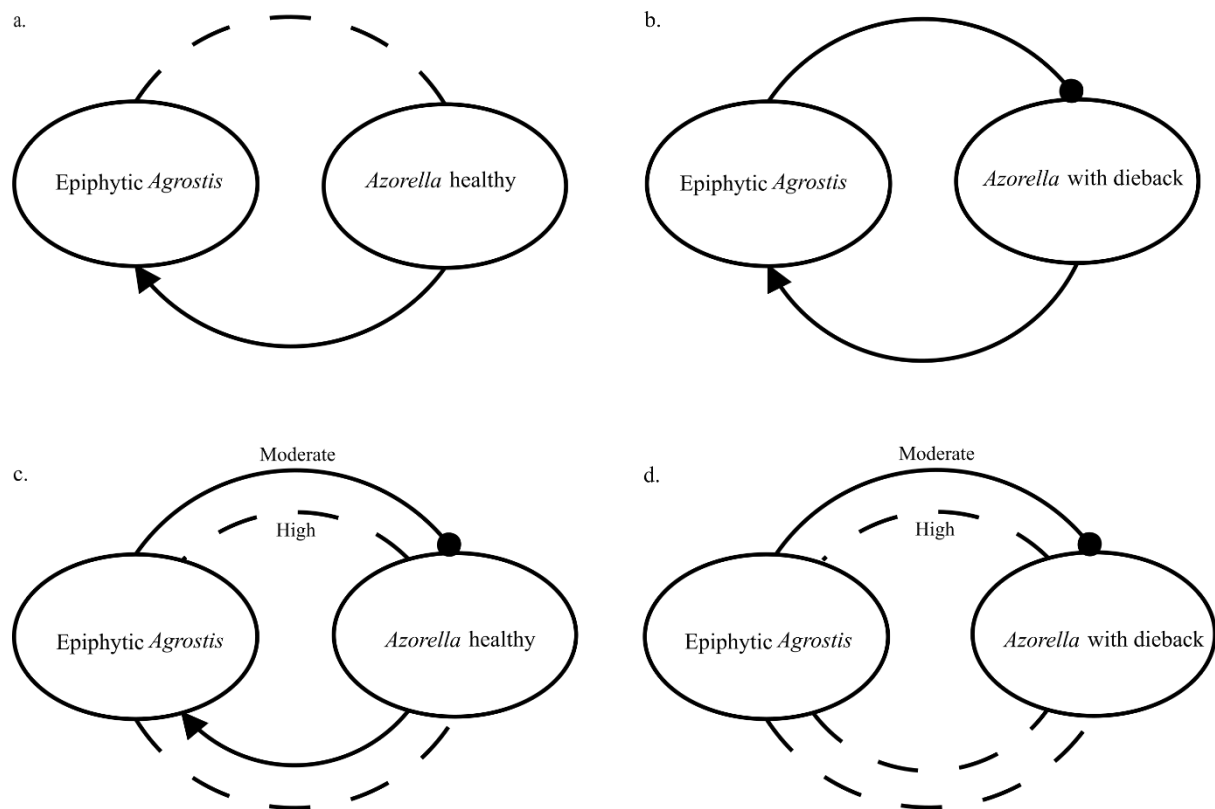


Fig. 4. Hypothesised relationships between the epiphytes *Agrostis magellanica* or *Luzula crinita* (Epiphytic *Agrostis*) and healthy *Azorella macquariensis* (*Azorella*) or *A. macquariensis* with dieback prior to analysis (a. and b., respectively). The revised relationships between the same components post-analysis of biotic and abiotic data for the island (Appendix C, Fig C2.1 c. and d.), where the outer links represent the interaction at a moderate elevation (240 – 270m asl) and inner links the interactions at high elevation (>270m asl) on Macquarie Island. Directional interactions presented major positive (\rightarrow), major negative ($--\bullet$), and minor ($- - -$). Minor interactions were not included in analysis.

modified for two different elevation classes; (1) moderate elevation, which is slightly less exposed and warmer with more grassland patches, and (2) high elevation, which is highly exposed, cold and windy (Fig. 4cd).

The presence of cushion dieback was not found to facilitate the establishment of Epiphytic *Agrostis*. There was a significant negative relationship between Epiphytic *Agrostis* and dieback ($p < 0.05$, Fig. C2.1, Appendix C2), consequently, the negative interactions between Epiphytic *Agrostis* and *A. macquariensis* were removed from all subsequent revised models (Fig. 1c). The hypothesised relationships between *A. macquariensis* (healthy and with dieback) and Epiphytic *Agrostis* at moderate and high elevation are described in Fig. 4cd.

ii. Refine: Development of moderate and high elevation ACFE

The ACFE revised models were defined for two elevations, moderate (~240-270m) and high (>270m asl) elevation fellfield, with two cushion condition classes, healthy and advanced dieback to account for the hypothesised change in interaction between Epiphytic *Agrostis* and *A. macquariensis* (Fig. 1d, Fig. 5). In the new models *Ag. magellanica* is defined as having a negative impact on cushions under warming conditions (see also (le Roux et al. 2005), which is hypothesised to occur at moderate elevation on Macquarie Island (Fig. 5ab). At the increasingly mild conditions at moderate elevation, the model suggests that Epiphytic *Agrostis* is no longer dependent on the facilitative effect from *A. macquariensis*, changing the relationship to minor (minor relationships were not included in analysis). However, at high elevation *Azorella* maintains its positive facilitative effect for Epiphytic *Agrostis* (Fig. 5c), which is not provided under advanced dieback (Fig. 5d). The Active dieback model was not pursued further, as the interactions were the same as the healthy condition model following the clarification of the relationship between dieback and Epiphytic *Agrostis*.

The four new revised models were subsequently simulated and four QNA scenarios run. The scenario MCLim + EpiAgr was not simulated for the new models (Fig. 5), as the original ACFE sub-models revealed that all nodes responded in the same direction, with the same strength, as for the singular MCLim scenario (Fig. 3).

iii. Interpret: Moderate & high elevation models

Structurally there was a sharp decline in the number of interactions from the healthy to advanced dieback ACFEs in both elevation classes, as *A. macquariensis* lost the ability to facilitate other biotic groups or abiotic conditions (Fig. 5). Consequently, in areas of advanced cushion dieback where *A. macquariensis* no longer had the capacity to facilitate other biotic

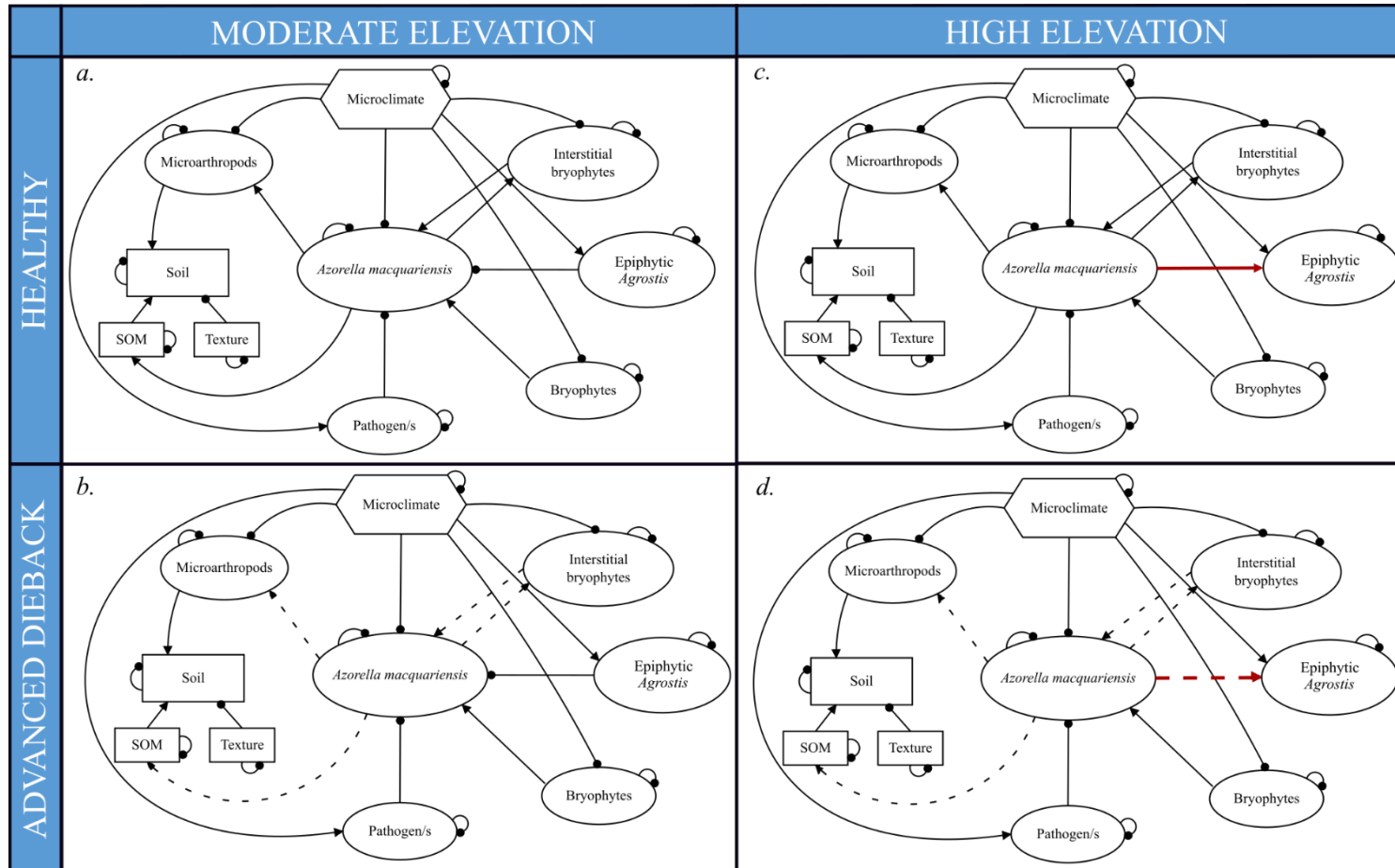


Fig. 5. Refined qualitative network model of the Macquarie Island *Azorella*-centred fellfield ecosystem (ACFE), shown for moderate (a., .b.) and high (c., d.) elevation with two major *A. macquariensis* condition classes, healthy (a., c.) and advanced (b., d.) dieback. Interaction changes between condition models shown using: a. to b. and c. to d. removal of interactions (---); a. to c. and b. to d., change in direction of relationship (---). Microclimate represents current climate conditions; Soil: water-holding capacity; Texture: gravel content; SOM; soil organic matter; Epiphyte *Agrostis*: includes *Agrostis magellanica* and *Luzula crinita*; all other nodes as presented. Only major interactions are included, directional positive (\rightarrow), directional negative ($-\bullet$), and self-limiting feedback loops (\bullet).

components of the ACFE, an increase in pathogen activity (Path) or an increase in Epiphytic *Agrostis* (EpiAgr) cover only negatively affected the condition of *A. macquariensis* (Fig. 6).

Analysis then demonstrated an increasingly warm, wet and variable microclimate (MClim) increased pathogen prevalence in all models and negatively affected the largest number of biotic and abiotic components (six) in both the healthy and advanced dieback models (Fig. 6a-d). *Azorella* and bryophytes were both directly negatively affected by a more variable microclimate, while interstitial bryophytes, micro-arthropods, SOM and soil (water holding capacity) were indirectly negatively affected by the reduced *Azorella* condition under a changed climate (see interactions Fig. 5), and hence it is inferred reduced facilitation. MClm resulted in an increase in Epiphytic *Agrostis* cover at moderate elevation (Fig. 6a,b) and a decline in Epiphytic *Agrostis* cover in healthy cushion populations at higher elevation, where it is weakly negatively affected by reduction in *Azorella* cover and hence less facilitation (Fig. 6c).

Scenario 2, an increase in pathogen activity (Path) negatively affected five and six components in the ACFE at moderate and high elevation, respectively (Fig. 6a,c), through the indirect negative effect of reduced facilitation by a reduction in *Azorella* condition (see Fig. 5). In Scenario 3 at high elevation an increase in the Epiphytic *Agrostis* (EpiAgr) cover had no negative effect on healthy *Azorella* condition or other elements of the system (Fig. 6c-d), as the species is facilitated by *Azorella* under high abiotic stress (consistent with le Roux and McGeoch 2010). However, at the moderate and slightly warmer elevation, an increase in Epiphytic *Agrostis* resulted in the decline of more than half the biotic and abiotic components of the ACFE (Fig. 6a-b): At the moderate elevation Epiphytic *Agrostis* had the same negative effect on the ACFE as an increase in pathogen activity (Fig. 6a-b).

In Scenario 4, *Azorella* recovery (*Azorella*) positively affected interstitial bryophytes, micro-arthropods and the quality of the soil (SOM and water holding capacity) in healthy *Azorella* populations at both moderate and high elevation (Fig. 6a,c). Conversely, in *Azorella* populations with advanced dieback, recovery (*Azorella*) no longer improved the previously facilitated ACFE components, as there are no remaining interactions in Fig. 6b – d. This is consistent with the expected response on the fellfield, where it takes an extended period of time (many years or decades) for the slow-growing *A. macquariensis* (see Taylor 1955a; Bergstrom et al. 1997) to regain cover and re-establish keystone interactions.

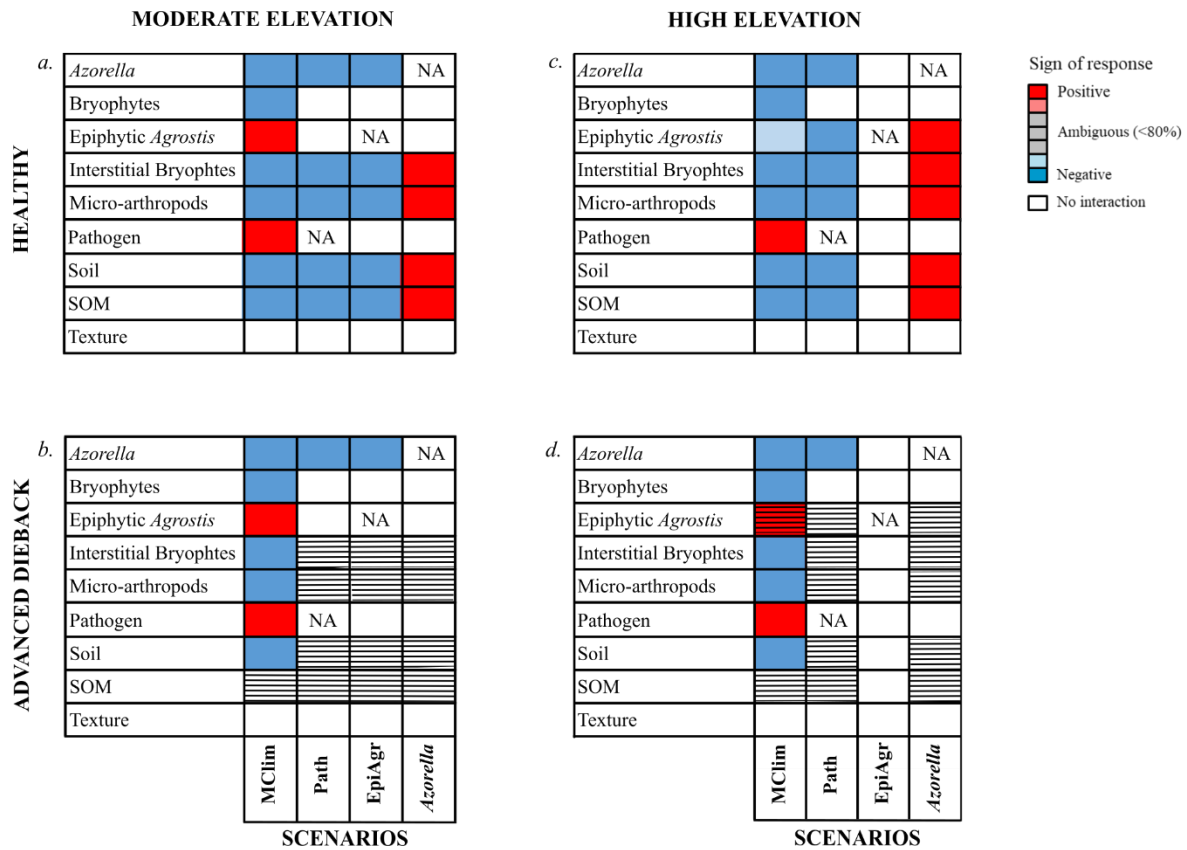


Fig. 6. Refined ecological response of the Macquarie Island *Azorella*-centred fellfield ecosystem (ACFE) (y-axis) to the four scenarios (x-axis). ACFE revised models shown for moderate (a., b.) and high (c., d.) elevation, in both healthy (a., c.) and advanced dieback (b., d.) condition classes. Response scaled from positive (blue) to negative (red), with uncertain response (<80% of either direction) shaded in grey and no interaction white. Node response difference between condition revised models within the same elevation class indicated by horizontal lines (model a. to b. and c. to d.). Microclimate represents current climate conditions; Soil: water-holding capacity; Texture: gravel content; SOM; soil organic matter; Epiphytic *Agrostis*: includes *Ag. magellanica* and *Luzula crinita*; all other nodes as presented. Scenarios include, MClm (increased trajectory of current climate conditions), Path (increased pathogen activity), EpiAgr (increased epiphytic *Ag. magellanica* or *L. crinita* cover), and *Azorella* (*A. macquariensis* recovery or increase in cover).

The state-transition condition diagram and its biological explanation

Incorporating the interactions supported by the ACFE qualitative network model, a state-transition diagram was compiled to show the progression of *A. macquariensis* dieback, from healthy to advanced dieback or recovery over a period of three or more years (Fig. 7a, x-axis). The progression of dieback was shown using condition classes (Fig. 7b, y-axis) described in Chapter 2. The four hypothesised mechanisms were described for each state (condition class) transition (Fig. 7c), including summer (growing season) plant available water (PAW), pathogens, wind and temperature. Summer PAW refers specifically to atmospheric water and the associated evapotranspiration rate (Bergstrom et al. 2015), while the pathogen presence is indicative of a warmer more saturated winter system (see Chapter 2).

Prior to island-wide *A. macquariensis* dieback, cushions were largely healthy (with or without epiphytes) (Fig. 7 i & iii), where they were primarily only affected by naturally occurring dieback, referred to here as wind-scour (Fig. 7 ii). Historically, < 10% of the cushion canopies near or in short-grasslands were physically damage by the now eradicated rabbits (Whinam et al. 2014). However, there was no relationship between rabbits and pathogen dieback (Bergstrom et al. 2015). Given their successful eradication, rabbits were not considered in this model.

Under reduced summer plant available water (PAW), pathogen infection and consequent Active dieback (Fig. 7 iv), occurs on healthy, uneven and wind-scoured cushions (Whinam et al. 2014; Bergstrom et al. 2015) (Fig. 7 iv). Active dieback was observed at a range of severities. Affecting all or some of the cushion branchlets, which then transitioned to permanent senescence following the visible progression of the yellow chlorosis line. Intraspecific resistance of plant populations to pathogens, such as *Phytophthora cinnamomi*, is known to occur in response to multiple environmental site conditions or the host species' genetic makeup (Cahill et al. 2008). Similarly, *A. macquariensis* may also express differing levels of resistance depending on genetic make-up and site conditions, though this has not been tested. Depending on the proportion of branchlet senescence there were two hypothesised outcomes, (i) if all of the branchlets were killed, the cushion progressed to advanced dieback (Fig. 7 vi), where extensive necrosis was observed two years post chlorosis line (Whinam et al. 2014), or (ii) if some branchlets survive and there is no additional pathogenic infection, the cushion may persist in the thinning condition (Fig. 7 v). Green leaves/branchlets were similarly observed on some cushions post chlorosis lines in 2013 (Whinam et al. 2014). It is also possible that the cushion

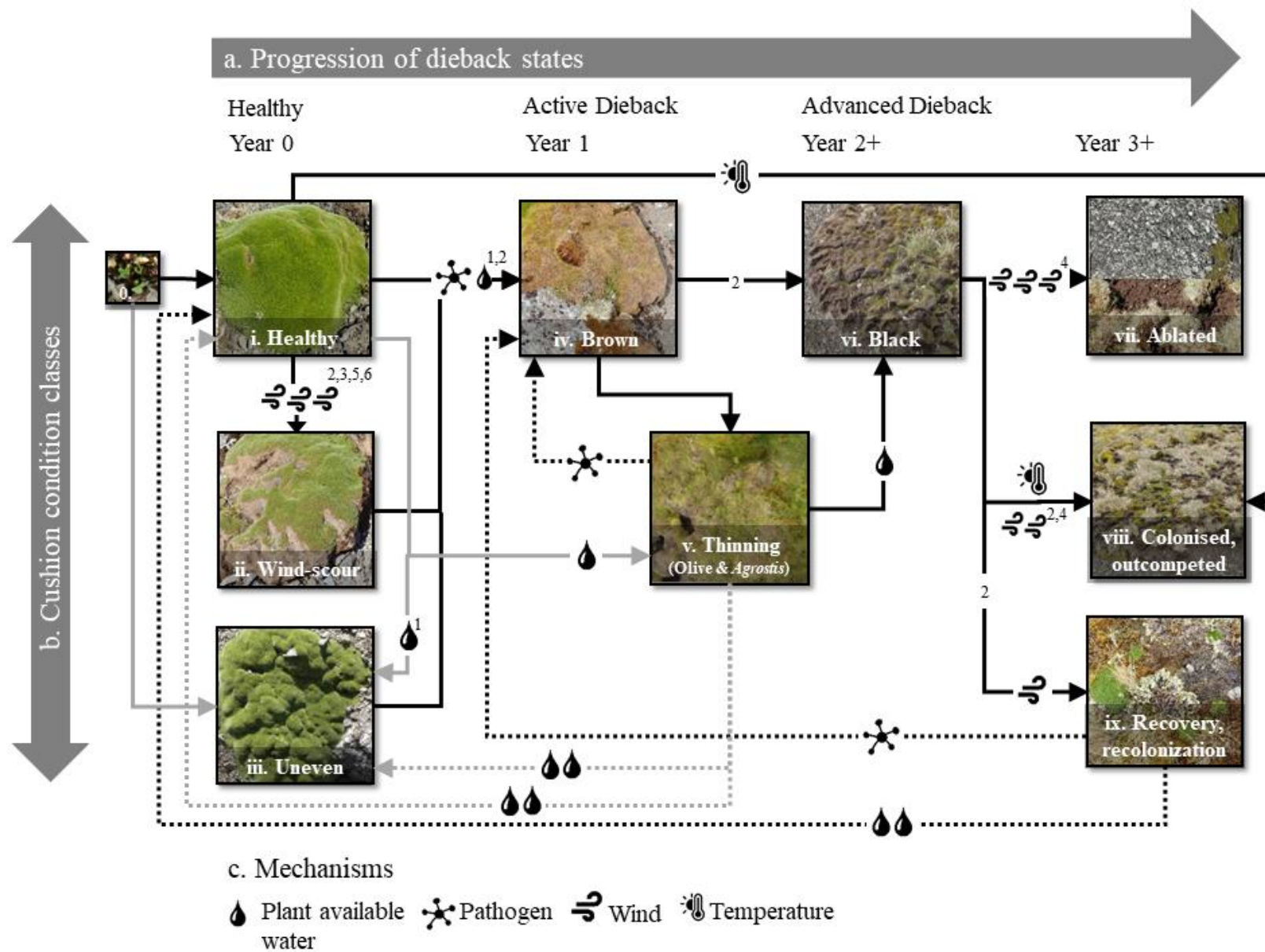


Fig. 7. Mechanistic state-transition diagram of *Azorella macquariensis* describing (a) dieback progression states and (b) condition classes, as determined by (c) mechanisms on Macquarie Island. Long-term average summer plant available water (PAW) indicated by two ‘waterdrop’ symbols, with a deficit in summer PAW relative to the long-term average shown with a single water drop. PAW predominately indicates atmospheric water, while the presence of the pathogen indicates warmer, more saturated conditions. Low, medium and high wind exposure indicated by one, two and three wind symbols, respectively. Arrows in the body of the graphic with broken lines represent feedbacks supported by the ACFE qualitative network model, black lines represent those state-transitions with evidence and grey lines are hypothesised. Condition classes (i-ix) from Chapter 2 and seedling (0). Numbers associated with progression and mechanisms refer to literature that discusses or provides evidence for the event. 1. Bergstrom et al. (2015); 2. Whinam et al. (2014); 3. Fitzgerald and Kirkpatrick (2017); 4. Hoffmann et al. (2019); 5. Selkirk-Bell and Selkirk (2013); 6. Ashton and Gill (1965).

could transition from healthy or wind-scour (Fig. 7 i-iii) to Thinning (Fig. 7 v) under extreme water stress, such as reduced summer PAW, however, this requires further research.

In 2010 uneven cushions were regularly soft, depressing on touch, and associated with brown discolouration (see Fig. 1b. in (Bergstrom et al. 2015)). The colouration is more consistent with individuals within the dieback condition classes of this thesis (Chapter 2). While there is a high natural variation of surface evenness (Chapter 2), unevenness may also occur when the cushion is stressed through a reduction in PAW (Fig. 7 iii) and a relaxation of the canopy (see Box 1), which appears to be permanent even once turgidity is recovered with more available PAW (Bergstrom et al. 2015; Bergstrom et al. in press). The bumps were more often conspicuous on cushions with dieback, as raised sections of canopy often displayed further advanced stages of dieback. It is hypothesised that this may be because when the area is already compromised by the pathogen, the raised areas have increased exposure and consequently a higher rate of water loss, which (i) potentially advances dieback or thinning of branchlets and leaves, and (ii) reduces the health of interstitial bryophytes/liverworts which were contributing the green colouration (see Chapter 2, Table 2: brown, olive and black sub-classes).

Once the cushion progresses to black (Fig. 7 vi, advanced dieback) there were three hypothesised outcomes. First, in areas of high wind on the exposed fellfield the cushion is ablated from the system (Hoffmann et al. 2019) (Fig. 7 vii). Second, under moderate wind and warmer conditions the cushion is likely to be colonised and outcompeted by graminoid (*Ag. magellanica* or *L. crinita*) epiphytes (Fig. 7 viii). Finally, recovery (Fig. 7 ix) of isolated living branchlets or new seedlings may occur in the dead cushion or bryophytes that retain their structural integrity. The presence of black (Fig. 7 vi) cushions is positively related to the presence of recovery (see Chapter 2) and implicitly suggests the site is comparatively sheltered, thus preventing their ablation. At the warmer low to moderate elevation sites healthy cushions (Fig. 7 i) were similarly hypothesised to be colonised and out-competed (Fig. 7 viii) by graminoids over time, irrespective of dieback.

Two recovery transitions (dashed line, Fig. 7) are described during average periods of PAW from dieback states, recovery (Fig. 7 ix, via iv) and thinning (Fig. 7 v) to healthy condition (Fig. 7 i or iii). However, the transition from thinning to healthy needs to be confirmed (Box 1). Seedlings and recovering branchlets that form the recovery condition class are observed to grow unaffected within advanced dieback, suggesting that the dieback is only active at the chlorosis line. The presence of two potential pathways of recovery is encouraging for the

species' survival, albeit likely to be both slow and patchy because of the species' ecology (Dickson et al. 2019). However, in the 10 years since cushion dieback was first observed, multiple waves of disease (chlorosis lines) have been documented at sites and on individual cushions (see Fig 2E in (Bergstrom et al. in press). Therefore it is possible for future disease fronts to move through the same area, transitioning (Fig. 7, dashed lines) the remaining thinning (Fig. 7 v) or recovering (Fig. 7 ix) cushions back to active/brown (Fig. 7 iv) dieback.

Box 1: Research and monitoring priorities to identify the rate of future change to *Azorella macquariensis* and the associated fellfield ecosystem.

The Macquarie Island fellfield ecosystem is clearly changing under current climate conditions. The extensive and rapid dieback of the dominant cushion plant has resulted in some high elevation fellfield areas being reduced back to gravel and bryophytes, and the simultaneous (but independent) encroachment of short-grasslands upslope from low to moderate elevation. While state-transitions and feedback loops of both recovery and additional dieback have been identified, the rate of change is still unclear. The following research and monitoring priorities emerged from the qualitative models and will be essential to understanding the rate and direction of change in the Macquarie Island fellfield ecosystem:

- (i) **Repeat biennial monitoring using the defined cushion classes to determine the rate and direction of change of *A. macquariensis* populations.** Despite ongoing cushion dieback, a low rate of recovery (1.1 % island-wide) has been recorded across the fellfield. This study identifies a second potential pathway of recovery from thinning to healthy, likely changing the island-wide estimates of recovery. Future research is required to confirm this pathway to quantify recovery rates across the island. Other transitions to be tested include: healthy to thinning, and healthy to bumpy with the reduction in plant available water (PAW).
- (ii) **Quantification of the rate of spread of short-grasslands into previously defined fellfield.** The grassland species, *Ag. magellanica* and *L. crinita*, have increased in density on the coastal slopes of the island, and it is likely that the graminoids will continue to move up-slope as the climate warms. Future monitoring requires short-grassland species to be recorded both on and off cushions.
- (iii) **Development of quantitative models for an *Azorella*-dominated short-grassland** to better understand the dynamic relationship between *A. macquariensis*, *Ag. magellanica*, the pathogens and other vascular species, in particular, the mega-herb *Pleurophyllum hookeri* Hook. (silver-leaf daisy, Asteraceae). The silver-leaf daisy is the only other species visibly susceptible to the same pathogens as *A. macquariensis*, with observations in 2017/18 suggesting that dieback in the species is increasing.
- (iv) **Estimation of quantitative thresholds** of characteristic biotic component cover (i.e. *A. macquariensis* and dieback) of an *Azorella*-centred fellfield ecosystem, to inform future listing of the ecosystem under the IUCN Red List for Ecosystems (RLE). The inherent variability of *A. macquariensis* means that setting thresholds is challenging. However, aerial images of Macquarie Island may be used to determine historical and current cover, following the successful trial in Bergstrom et al. (accepted) and integrated in a simulation approach.
- (v) **Identification of the pathogens.** Effective management and recovery actions depend on the identification of the pathogens or consortium of microbes. To-date a number of bacterial, fungal and pathogenic taxa have been identified in association with *A. macquariensis* dieback. Future research is required to demonstrate a causal link between the pathogens and disease, as per Koch's postulates or systems biology, and subsequent management technique (see Schneider and Collmer 2010).

Discussion

Based on qualitative network modelling and the construction of a state transition model, the following new, altered and confirmed understanding of Macquarie Island fellfield ecosystem has been achieved. First, under the current climate trajectory, the ACFE models clearly supported the expected loss of keystone interactions across the fellfield ecosystem as *A. macquariensis* condition continues to decline. This loss of interactions forecasts the potential for ecosystem collapse (see Valiente-Banuet et al. 2015). On the fellfield this would result in a loss of vascular plant and microarthropod diversity and abundance, and a reduction of carbon into the system. Second, in areas of advanced dieback, such as the northern sections of the island, the loss of cover and related interactions are indeed already causing localised ecosystem collapse, from an *Azorella*-dominated ecosystem to (i) a less complex gravel and bryophyte system at high elevation, and (ii) short-grassland at moderate elevation. Third, ecosystem collapse as the result of climate-driven cushion dieback is complicated by the independent change in short-grassland distribution, where at moderate elevation the encroachment of graminoid epiphytes represents the same level of threat as higher pathogen activity. Finally, the state-transition diagram identifies two potential pathways for cushion recovery. However, the rate of reinfection currently appears to be exceeding recovery, steadily removing cushion cover over time.

Drivers of change in the fellfield

The decline in condition of *A. macquariensis* under current climate conditions is hypothesised to continue through four primary mechanisms: summer plant available water (atmospheric PAW), wind, temperature and pathogen infection (indicative of warmer, more saturated winter ground conditions). While this is a simplified representation of the system, it describes the dominant hypothesised drivers and provides a representation consistent with what is observed on the island. The state-transition diagram builds on Hoffmann et al. (2019)'s causal pathway model, which hypothesises the outcome of cushion dieback on the fellfield under increasing evapotranspiration, as either increased colonisation by grasses or ablation from the system at highly exposed sites. The current state-transition diagram incorporates the importance of site maximum temperature, an inherent part of wind exposure, whereby sites that are less exposed and warmer (i.e. lower elevation) are more likely to be colonised and subsequently outcompeted by graminoids. Importantly, the potential for colonisation and out-competition of cushions by graminoids occurs regardless of the presence of cushion dieback, as demonstrated

in the ACFE models (see Box 1ii, iii). The increasingly warm temperatures may also be reducing needle ice on the fellfield, an important driver maintaining gravel turnover on the treads of the vegetation-terraces (see Selkirk-Bell and Selkirk 2013), hence the reduction of needle-ice may also facilitate colonisation of bare ground by graminoids. On the coastal slopes of Macquarie Island grass cover was found to be higher with increasing temperatures, irrespective of rabbits (Scott and Kirkpatrick 2013), thus following the eradication of rabbits in 2011 (Terauds et al. 2014) and the removal of grazing pressure, it is likely that grasslands have increased in distribution and density. While unproven, this potentially suggests that the mid-elevation fellfield may have been also been maintained as an open habitat for longer than would have been the case in the absence of rabbits. Thus the loss of *Azorella*-dominated fellfield habitat is exacerbated by the concurrent occurrence of two climate-driven but independent processes, cushion dieback and short-grassland encroachment, which may also be intensified with the removal of grazing pressure.

Potential for *A. macquariensis* recovery

The recovery and pathogenic reinfection feedback loops, implicit within the ACFE models, are visualised in the state-transition diagram. Two pathways are proposed for cushion recovery, from either black or thinning cushions (see Box 1). However, pathogenic reinfection of surviving or recovering cushions may reoccur in multiple waves, compromising the cushions ability to recover. Other systems, such as coral reefs, have also demonstrated a rapid increase in the frequency of large-scale climate-driven mortalities (e.g. coral bleaching), suggesting that the ability of species' long-term survival under current and projected climate conditions is becoming increasingly precarious (Hughes et al. 2018). The long-term persistence of *A. macquariensis* as the dominant vascular species on the fellfield of Macquarie Island is also likely to be compromised, as the regional climate is projected to maintain a similar trajectory over time (Adams 2009). Under this climate scenario it is expected that pathogen driven cushion dieback will continue, resulting in multiple waves of disease and a stepped reduction of cover (Bergstrom et al. in press). Under this foreseeable scenario, it is unlikely that the slow-growing cushion (Taylor 1955a; Bergstrom et al. 1997) will have enough time to replace itself, where disease waves persistently reduce cover over time, reducing *A. macquariensis* to a sub-dominant species or resulting in site-level population extinction.

Loss of interactions and resilience

The revised ACFE models (Fig. 5) clearly show a loss of many interactions on the fellfield during advanced dieback, where the ecosystem is simplified through the loss of one keystone species and its interactions. Complex interactions are often used as indicators of ecosystem health (Valiente-Banuet et al. 2015) and can influence species response and resilience to changing climates (Suttle et al. 2007; Gilman et al. 2010) depending on the driver of change (Losapio and Schöb 2017). Ecosystem function and its consequent health are dependent on the maintenance of a complex web of interactions, between both species and abiotic components (Tylianakis et al. 2008). In particular, keystone or foundation species and their interactions have a disproportionate effect on the ecological function of a community (Harvey et al. 2017). Consequently, the loss of keystone interactions may represent an extinction debt, where other species are able to persist for a period of time after the interactions are lost, before they too are removed from the system (Valiente-Banuet et al. 2015). The loss of interactions in ACFE in areas of advanced cushion dieback, and the negative response of dependant nodes, reveal the possibility for extinction debt on the fellfield. It is expected that on the fellfield in areas of advanced cushion dieback the diversity of vascular plants, micro-arthropods and amount of soil organic matter and associated carbon will also decline. If the cushions are unable to recover and restore their keystone function, this signals the initiation of localised ecosystem collapse.

Determining the point of ecosystem collapse is notoriously difficult, as it varies between ecological communities, and depend on the characteristics of the biotic components and interactions (Bland et al. 2018; Sato and Lindenmayer 2018). The qualitative network models used here have shown that with the loss of the dominant keystone species, *A. macquariensis*, the Macquarie Island fellfield ecosystem's character, keystone interactions and associated function are also lost. Defining a threshold for fellfield ecosystem collapse would, therefore, require the definition of *A. macquariensis* cover and dieback thresholds that are necessary to maintain keystone interactions and function. Thresholds for both cushion cover and cushion dieback are important because, as previously shown (Dickson et al. 2019), cover alone overestimates the conservation status of the species by not accounting for the future cover-loss from current dieback. This is particularly the case under low levels of recovery, as is currently occurring across the island (Chapter 2). However, despite the increasing number of techniques available with varying levels of data requirements, the identification of thresholds is complex, usually requiring detailed long-term datasets and simulation modelling (Andersen et al. 2009; Scheffer et al. 2015). This complexity is demonstrated by the Macquarie Island fellfield, as

despite being comparatively biologically simple (see Selkirk et al. 1990), the dominant vascular species *A. macquariensis* is highly variable, ranging in form from small cushions to extensive mats, dependant on-site conditions (Orchard 1989). Consequently, even setting a cover threshold is not straight-forward and is highly site dependent (Box 1). The next research step for Macquarie Island is to undertake simulation modelling in combination with *in situ* datasets to determine *A. macquariensis* thresholds for the fellfield ecosystem.

The qualitative ACFE and state-transition diagram, which describe the process of ecosystem collapse through the loss of underpinning interactions and keystone species state-transition, provide an important step in describing the risk of ecosystem collapse by clarifying and communicating assumptions (see Bland et al. 2018; Rowland et al. 2018). These models further refine state-transitions and hypothesised mechanisms of cushion and ecosystem states, which will allow more meaningful *A. macquariensis* thresholds to be set and intermediate states identified under active and advanced dieback (see Nicholson et al. 2015; Bland et al. 2018; Rowland et al. 2018). Some northern areas of the *Azorella*-dominated fellfield ecosystem (syn. sub-Antarctic Tundra) on Macquarie Island are considered locally collapsed because they are substantially different from their baseline states (Bergstrom et al. in press), having lost the majority of cushion cover (Dickson et al. 2019). Simplified linear and exponential dieback models by Dickson et al. (2019) predicted a loss of functional cover between 2.5 – 30 years depend on the starting cover in the northern, central and southern regions. The ACFE revised models reveal the consequences of this rapid removal of the keystone species and associated interactions, which support ecosystem function (biological diversity and soil development) and may predict a future localised extinction debt of dependent species. If cushion dieback continues along a similar trajectory, as expected under the current climate scenarios, the locally collapsed northern sites appear to forecast the fellfield's future state.

Conclusion

The qualitative models have formalised and clarified our current understanding and assumptions about the structure and functioning of the fellfield ecosystem on Macquarie island with *A. macquariensis* at its centre (see Bland et al. 2018; Rowland et al. 2018). Island-wide dieback of the keystone *A. macquariensis* is causing a fundamental alteration of biotic interactions, through loss of keystone interactions and subsequent biological complexity on the fellfield. This loss of complexity is likely to reduce the ecological resilience of the ecosystem to change, leading to ecosystem collapse if the rate of currently observed recovery does not

accelerate. Despite the qualitative modelling approach used here being a necessary simplification of the ecosystem, the exercise has improved our understanding of multiple processes on the fellfield and allowed exploration of the system response to different scenarios using qualitative interaction data. This understanding provides an important foundation and system-wide hypothesis about ecosystem regime change on the fellfield, which occurs across the sub-Antarctic islands and at high altitude. We demonstrate that similar to other island and high elevation (Harter et al. 2015) systems the loss of one keystone species in the fellfield, may disproportionately affect the ecological structure and consequent health of the system. If this World Heritage system is to be maintained, prioritised research and subsequent management intervention is time critical.

References

- Adams, N., 2009. Climate trends at Macquarie Island and expectations of future climate change in the sub-Antarctic. *Papers and proceedings of the Royal Society of Tasmania* 143, 1-8.
- Andersen, T., Carstensen, J., Hernandez-Garcia, E., Duarte, C.M., 2009. Ecological thresholds and regime shifts: approaches to identification. *Trends in Ecology & Evolution* 24, 49-57.
- Anthelme, F., Buendia, B., Mazoyer, C., Dangles, O., 2012. Unexpected mechanisms sustain the stress gradient hypothesis in a tropical alpine environment. *Journal of Vegetation Science* 23, 62-72.
- Ashton, D.H., Gill, A.M., 1965. Pattern and Process in a Macquarie island Feldmark. *Proceedings Of The Royal Society Of Victoria* 79, 235-248.
- Barendse, J., Chown, S.L., 2001. Abundance and seasonality of mid-altitude fellfield arthropods from Marion Island. *Polar Biology* 24, 73-82.
- Bergstrom, D.M., Bricher, P.K., Raymond, B., Terauds, A., Doley, D., McGeoch, M.A., (. . .) Ball, M.C., 2015. Rapid collapse of a sub-Antarctic alpine ecosystem: the role of climate and pathogens. *Journal of Applied Ecology* 52, 774-783.
- Bergstrom, D.M., Chown, S.L., 1999. Life at the front: history, ecology and change on southern ocean islands. *Trends in Ecology & Evolution* 14, 472-477.
- Bergstrom, D.M., Dickson, C.R., Baker, D.J., Whinam, J., Selkirk, P.M., McGeoch, M.A., in press. Ecosystem collapse on a sub-Antarctic island, In *Ecosystem Collapse and Climate Change*. eds J.G. Canadell, R.B. Jackson, p. xxx. *Ecological Studies*, Springer-Nature, xxxx.
- Bergstrom, D.M., Selkirk, P.M., Keenan, H.M., Wilson, M.E., 1997. Reproductive behaviour of ten flowering plant species on subantarctic Macquarie Island. *Opera Botanica* 132, 109-120.
- Bland, L.M., Rowland, J.A., Regan, T.J., Keith, D.A., Murray, N.J., Lester, R.E., (. . .) Nicholson, E., 2018. Developing a standardized definition of ecosystem collapse for risk assessment. *Frontiers in Ecology and the Environment* 16, 29-36.
- Bonanomi, G., Stinca, A., Chirico, G.B., Ciaschetti, G., Saracino, A., Incerti, G., 2016. Cushion plant morphology controls biogenic capability and facilitation effects of *Silene acaulis* along an elevation gradient. *Functional Ecology* 30, 1216-1226.
- Bricher, P.K., Lucieer, A., Shaw, J., Terauds, A., Bergstrom, D.M., 2013. Mapping Sub-Antarctic Cushion Plants Using Random Forests to Combine Very High Resolution Satellite Imagery and Terrain Modelling. *Plos One* 8, 1-15.

- Cahill, D.M., Rookes, J.E., Wilson, B.A., Gibson, L., McDougall, K.L., 2008. *Phytophthora cinnamomi* and Australia's biodiversity: impacts, predictions and progress towards control. Australian Journal of Botany 56, 279-310.
- Chen, I.-C., Hill, J.K., Ohlemüller, R., Roy, D.B., Thomas, C.D., 2011. Rapid Range Shifts of Species Associated with High Levels of Climate Warming. Science 333, 1024-1026.
- Dambacher, J.M., Li, H.W., Rossignol, P.A., 2003. Qualitative predictions in model ecosystems. Ecological Modelling 161, 79-93.
- Dickson, C.R., Baker, D.J., Bergstrom, D.M., Bricher, P.K., Brookes, R.H., Raymond, B., (. . .) McGeoch, M.A., 2019. Spatial variation in the ongoing and widespread decline of keystone plant species. Austral Ecology 44, 891-905.
- Gignac, L.D., 2011. Bryophytes as Predictors of Climate Change, In Bryophyte ecology and climate change. eds Z. Tuba, N.G. Slack, L.R. Stark. Cambridge University Press, ProQuest Ebook Central, <http://ebookcentral.proquest.com/lib/monash/detail.action?docID=605005>.
- Gilman, S.E., Urban, M.C., Tewksbury, J., Gilchrist, G.W., Holt, R.D., 2010. A framework for community interactions under climate change. Trends in Ecology & Evolution 25, 325-331.
- Harris, R.M.B., Beaumont, L.J., Vance, T.R., Tozer, C.R., Remenyi, T.A., Perkins-Kirkpatrick, S.E., (. . .) Bowman, D.M.J.S., 2018. Biological responses to the press and pulse of climate trends and extreme events. Nature Climate Change 8, 579-587.
- Harter, D.E.V., Irl, S.D.H., Seo, B., Steinbauer, M.J., Gillespie, R., Triantis, K.A., (. . .) Beierkuhnlein, C., 2015. Impacts of global climate change on the floras of oceanic islands – Projections, implications and current knowledge. Perspectives in Plant Ecology, Evolution and Systematics 17, 160-183.
- Harvey, E., Gounand, I., Ward, C.L., Altermatt, F., 2017. Bridging ecology and conservation: from ecological networks to ecosystem function. Journal of Applied Ecology 54, 371-379.
- Hoffmann, A.A., Rymer, P.D., Byrne, M., Ruthrof, K.X., Whinam, J., McGeoch, M., (. . .) Williams, S.E., 2019. Impacts of recent climate change on terrestrial flora and fauna: Some emerging Australian examples. Austral Ecology 44, 3-27.
- Hughes, T.P., Anderson, K.D., Connolly, S.R., Heron, S.F., Kerry, J.T., Lough, J.M., (. . .) Wilson, S.K., 2018. Spatial and temporal patterns of mass bleaching of corals in the Anthropocene. Science 359, 80-83.
- Hughes, T.P., Linares, C., Dakos, V., van de Leemput, I.A., van Nes, E.H., 2013. Living dangerously on borrowed time during slow, unrecognized regime shifts. Trends in Ecology & Evolution 28, 149-155.

- Hugo, E.A., McGeoch, M.A., Marshall, D.J., Chown, S.L., 2004. Fine scale variation in microarthropod communities inhabiting the keystone species *Azorella selago* on Marion Island. *Polar Biology* 27, 466-473.
- Jagerbrand, A.K., Bjork, R.G., Callaghan, T., Seppelt, R.D., 2011. Effects of Climate Change on Tundra Bryophytes, In *Bryophyte ecology and climate change*. eds Z. Tuba, N.G. Slack, L.R. Stark, pp. 211-236. Cambridge University Press, ProQuest Ebook Central, <http://ebookcentral.proquest.com/lib/monash/detail.action?docID=605005>.
- Keith, D.A., Rodríguez, J.P., Rodríguez-Clark, K.M., Nicholson, E., Aapala, K., Alonso, A., (. . .) Zambrano-Martínez, S., 2013. Scientific Foundations for an IUCN Red List of Ecosystems. *Plos One* 8, e62111.
- le Roux, P.C., McGeoch, M.A., 2008a. Rapid range expansion and community reorganization in response to warming. *Global Change Biology* 14, 2950-2962.
- le Roux, P.C., McGeoch, M.A., 2008b. Spatial variation in plant interactions across a severity gradient in the sub-Antarctic. *Oecologia* 155, 831-844.
- le Roux, P.C., McGeoch, M.A., 2010. Interaction intensity and importance along two stress gradients: adding shape to the stress-gradient hypothesis. *Oecologia* 162, 733-745.
- le Roux, P.C., McGeoch, M.A., Nyakatia, M.J., Chown, S.L., 2005. Effects of a short-term climate change experiment on a sub-Antarctic keystone plant species. *Global Change Biology* 11, 1628-1639.
- le Roux, P.C., Shaw, J.D., Chown, S.L., 2013. Ontogenetic shifts in plant interactions vary with environmental severity and affect population structure. *New Phytologist* 200, 241-250.
- Levins, R., 1974. Discussion paper: the qualitative analysis of partially specified systems. *Annals of the New York Academy of Sciences* 231, 123-138.
- Losapio, G., Schöb, C., 2017. Resistance of plant–plant networks to biodiversity loss and secondary extinctions following simulated environmental changes. *Functional Ecology* 31, 1145-1152.
- Marzloff, M.P., Melbourne-Thomas, J., Hamon, K.G., Hoshino, E., Jennings, S., van Putten, I.E., Pecl, G.T., 2016. Modelling marine community responses to climate-driven species redistribution to guide monitoring and adaptive ecosystem-based management. *Global Change Biology* 22, 2462-2474.
- McGeoch, M.A., le Roux, P.C., Hugo, E.A., Chown, S.L., 2006. Species and community responses to short-term climate manipulation: Microarthropods in the sub-Antarctic. *Austral Ecology* 31, 719-731.

- Melbourne-Thomas, J., Wotherspoon, S., Raymond, B., Constable, A., 2012. Comprehensive evaluation of model uncertainty in qualitative network analyses. *Ecological Monographs* 82, 505-519.
- Nicholson, E., Regan, T.J., Auld, T.D., Burns, E.L., Chisholm, L.A., English, V., (. . .) Keith, D.A., 2015. Towards consistency, rigour and compatibility of risk assessments for ecosystems and ecological communities. *Austral Ecology* 40, 347-363.
- Nyakatya, M.J., McGeoch, M.A., 2008. Temperature variation across Marion Island associated with a keystone plant species (*Azorella selago* Hook. (Apiaceae)). *Polar Biology* 31, 139-151.
- Ockendon, N., Baker, D.J., Carr, J.A., White, E.C., Almond, R.E.A., Amano, T., (. . .) Pearce-Higgins, J.W., 2014. Mechanisms underpinning climatic impacts on natural populations: altered species interactions are more important than direct effects. *Global Change Biology* 20, 2221-2229.
- Orchard, A.E., 1989. *Azorella* Lamarck (Apiaceae) on Heard and Macquarie Islands, with description of a new species, *A. macquariensis*. *Muelleria* 7, 15-20.
- Parisi, V., Menta, C., Gardi, C., Jacomini, C., Mozzanica, E., 2005. Microarthropod communities as a tool to assess soil quality and biodiversity: a new approach in Italy. *Agriculture, Ecosystems & Environment* 105, 323-333.
- Pecl, G.T., Araújo, M.B., Bell, J.D., Blanchard, J., Bonebrake, T.C., Chen, I.-C., (. . .) Williams, S.E., 2017. Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. *Science* 355, eaai9214.
- Petraitis, P., 2013. *Multiple stable states in natural ecosystems*, 1st ed. edn. Oxford : Oxford University Press, Oxford.
- R Core Team, 2019. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.
- Raath-Krüger, M.J., McGeoch, M.A., Schöb, C., Greve, M., le Roux, P.C., 2019. Positive plant–plant interactions expand the upper distributional limits of some vascular plant species. *Ecosphere* 10, e02820.
- Ramsey, D., Veltman, C., 2005. Predicting the effects of perturbations on ecological communities: what can qualitative models offer? *Journal of Animal Ecology* 74, 905-916.
- Ratajczak, Z., D'Odorico, P., Collins, S.L., Bestelmeyer, B.T., Isbell, F.I., Nippert, J.B., 2017. The interactive effects of press/pulse intensity and duration on regime shifts at multiple scales. *Ecological Monographs* 87, 198-218.

- Raymond, B., McInnes, J., Dambacher, J.M., Way, S., Bergstrom, D.M., 2011. Qualitative modelling of invasive species eradication on subantarctic Macquarie Island. *Journal of Applied Ecology* 48, 181-191.
- Rolland, V., Bergstrom, D.M., Lenne, T., Bryant, G., Chen, H., Wolfe, J., (. . .) Ball, M.C., 2015. Easy Come, Easy Go: Capillary Forces Enable Rapid Refilling of Embolized Primary Xylem Vessels. *Plant Physiology* 168, 1636-1647.
- Rowland, J.A., Nicholson, E., Murray, N.J., Keith, D.A., Lester, R.E., Bland, L.M., 2018. Selecting and applying indicators of ecosystem collapse for risk assessments. *Conservation Biology* 32, 1233-1245.
- Sato, C.F., Lindenmayer, D.B., 2018. Meeting the Global Ecosystem Collapse Challenge. *Conservation Letters* 11, e12348.
- Scheffer, M., Carpenter, S.R., 2003. Catastrophic regime shifts in ecosystems: linking theory to observation. *Trends in Ecology & Evolution* 18, 648-656.
- Scheffer, M., Carpenter, S.R., Dakos, V., Nes, E.H.v., 2015. Generic Indicators of Ecological Resilience: Inferring the Chance of a Critical Transition. *Annual Review of Ecology, Evolution, and Systematics* 46, 145-167.
- Schneider, D.J., Collmer, A., 2010. Studying Plant-Pathogen Interactions in the Genomics Era: Beyond Molecular Koch's Postulates to Systems Biology. *Annual Review of Phytopathology* 48, 457-479.
- Scott, J.J., Kirkpatrick, J.B., 2013. Changes in the cover of plant species associated with climate change and grazing pressure on the Macquarie Island coastal slopes, 1980-2009. *Polar Biology* 36, 127-136.
- Selkirk-Bell, J.M., Selkirk, P.M., 2013. Vegetation-Banked Terraces on Subantarctic Macquarie Island: a Reappraisal. *Arctic Antarctic and Alpine Research* 45, 261-274.
- Selkirk, P.M., 2012. Plateau Vegetation On Sub-Antarctic Macquarie Island. *Papers and proceedings of the Royal Society of Tasmania* 146, 71-79.
- Selkirk, P.M., Adamson, D.A., Seppelt, R.D., 1988. Terrace Types and Vegetation Dynamics On Macquarie Island. *Papers and proceedings of the Royal Society of Tasmania* 122, 59-64.
- Selkirk, P.M., Seppelt, R.D., Selkirk, D.R., 1990. Subantarctic Macquarie Island: environment and biology. Cambridge Press University Press, Cambridge.
- Smith, V.R., Steenkamp, M., 1990. Climatic change and its ecological implications at a subantarctic island. *Oecologia* 85, 14-24.

- Sobocinski, K.L., Greene, C.M., Schmidt, M.W., 2018. Using a qualitative model to explore the impacts of ecosystem and anthropogenic drivers upon declining marine survival in Pacific salmon. *Environmental Conservation* 45, 278-290.
- Sonter, R.O., Semple, W.S., Lawrie, J.W., 2000. Soils, vegetation and land use, In *Soils: their properties and management*. eds P.E. Charman, B.W. Murphy, pp. 271-286. Oxford University Press, Melbourne.
- Stork, N.E., Eggleton, P., 1992. Invertebrates as determinants and indicators of soil quality. *American Journal of Alternative Agriculture* 7, 38-47.
- Suttle, K.B., Thomsen, M.A., Power, M.E., 2007. Species Interactions Reverse Grassland Responses to Changing Climate. *Science* 315, 640-642.
- Taylor, B.W., 1955a. The flora, vegetation and soils of Macquarie Island., In *ANARE Reports, Series B*, 11. pp. 1-192. Australian Antarctic Division, Melbourne.
- Taylor, B.W., 1955b. Terrace Formation on Macquarie Island. *Journal of Ecology* 43, 133-137.
- Terauds, A., Doube, J., McKinlay, J., Springer, K., 2014. Using long-term population trends of an invasive herbivore to quantify the impact of management actions in the sub-Antarctic. *Polar Biology* 37, 833-843.
- Tylianakis, J.M., Didham, R.K., Bascompte, J., Wardle, D.A., 2008. Global change and species interactions in terrestrial ecosystems. *Ecology Letters* 11, 1351-1363.
- Valiente-Banuet, A., Aizen, M.A., Alcántara, J.M., Arroyo, J., Cocucci, A., Galetti, M., (. . .) Zamora, R., 2015. Beyond species loss: the extinction of ecological interactions in a changing world. *Functional Ecology* 29, 299-307.
- Whinam, J., Abdul-Rahman, J.A., Visoiu, M., di Folco, M.B.F., Kirkpatrick, J.B., 2014. Spatial and temporal variation in damage and dieback in a threatened subantarctic cushion species. *Australian Journal of Botany* 62, 10-21.
- Wilson, B.R., Wilson, S.C., Sindel, B., Williams, L.K., Hawking, K.L., Shaw, J., (. . .) Kristiansen, P., 2019. Soil properties on sub-Antarctic Macquarie Island: Fundamental indicators of ecosystem function and potential change. *CATENA* 177, 167-179.

Appendix C

Appendix C1: Major and minor abiotic and biotic interactions within the *Azorella*-centred fellfield ecosystem (ACFE) on Macquarie Island

Table C1.1. Major and minor abiotic and biotic interactions within the *Azorella*-centred fellfield ecosystem (ACFE) on Macquarie Island under current climate conditions, determined from published literature and expert input. Major interactions are described as necessary to maintain current ecosystem function. Model abbreviations: 1: initial ACFE, (a) healthy, (b) active dieback, (c) advanced dieback. 2H: High elevation ACFE, (a) healthy, (b) advanced dieback. 2M: Moderate elevation ACFE, (a) healthy, (b) advanced dieback.

Effect of (X)	Effect on (Y)	Relationship	Comments and references
<i>Azorella</i> condition	Epiphytic <i>Agrostis</i>	Positive Major: 1 a, b, c, 2H a Minor: 2H b, 2M a, b	Epiphytic monocots are dependent on cushions under moderate to high abiotic stress (le Roux and McGeoch 2010; Bonanomi et al. 2016). As cushion cover increases, the epiphyte community increases, facilitated against abiotic effects. The closely related species <i>A. selago</i> facilitates <i>Agrostis</i> establishment (Hausmann et al. 2009), moderate ontological stages (le Roux et al. 2013) and the abundance of <i>Ag. magellanica</i> at moderate to high elevations (le Roux and McGeoch 2010; Raath-Krüger et al. 2019). However, the cushion is negatively affected by the epiphyte under warming conditions, where it creates additional shade (le Roux et al. 2005). <i>Azorella</i> does not facilitate an increase in elevation range (Raath-Krüger et al. 2019).
<i>Azorella</i> condition	Interstitial: bryophytes	Positive Major: 1 a, b, 2H a, 2M a Minor: 1 c, 2H b, 2M b	Interstitial bryophytes are dependent on cushions, however, they are at highest abundance when at low-moderate <i>Azorella</i> condition, (see Chapter 2 and Bergstrom et al. 2015)
<i>Azorella</i> condition	Bryophytes	Neutral Minor all models	As cushion health increases, neighbouring bryophytes can be suppressed and overtaken by establishing cushions (Ashton and Gill 1965). However, <i>Azorella</i> also

Effect of (X)	Effect on (Y)	Relationship	Comments and references
			maintains humidity. Response is species specific, where predominantly bryophytes do not need <i>A. macquariensis</i> to persist.
<i>Azorella</i> condition	Burrowing birds (e.g. prions, petrels)	Positive Minor all models	Antarctic prions (<i>Pachyptila desolata</i>) occasionally use cushions for structural habitat, borrowing between them on the fellfield (Brothers 1984). The ACFE is considered a minor, patchy habitat component of Antarctic prions on Macquarie Island, because of the severe exposure to harsh weather and shallow soils (see (Brothers 1984).
<i>Azorella</i> condition	Micro-arthropods	Positive Major 1 a, b, 2H a, 2M a Minor: 1 c, 2H b, 2M b	Species-specific response. However, generally <i>Azorella</i> species facilitate more suitable conditions for some species by humidity and temperatures (Barendse and Chown 2001), supporting a more abundant and diverse community than the surrounding exposed fellfield (Bergstrom et al. 2015).
<i>Azorella</i> condition	SOM (soil organic matter)	Positive Major 1 a, b, 2H a, 2M a Minor: 1 c, 2H b, 2M b	As <i>Azorella</i> species increase the soil development increases, forming its own humic layer within the cushion (Anthelme et al. 2012), increasing soil carbon (Bergstrom et al. 2015) and other macronutrients (Almeida et al. 2013).
Bryophytes	<i>Azorella</i> condition	Positive Major 1 a, b, 2H a, b, 2M a, b	As neighbouring bryophytes increase, the microclimate is ameliorated (Jagerbrand et al. 2011), facilitating <i>Azorella</i> condition. <i>Azorella</i> seedlings establish in moss beds (Ashton and Gill 1965).
Bryophytes	Epiphytic <i>Agrostis</i>	Positive Minor all models	As bryophytes increase, the immediate surrounding microclimate is ameliorated (Jagerbrand et al. 2011) and their epiphytic plants facilitated.

Effect of (X)	Effect on (Y)	Relationship	Comments and references
Burrowing birds (e.g. prions, petrels)	<i>Azorella</i> condition	Negative Minor all models	Burrows of sea birds in the southern and central plateau can cause very localised damage to plants (Taylor 1955), including <i>A. macquariensis</i> . However, ACFE is considered to be only a minor component of their habitat (Brothers 1984). While Antarctic prion may occasionally burrow in <i>A. macquariensis</i> cushions in fellfield, generally burrows are more likely between, rather than in or under cushions (see (Brothers 1984).
Epiphytic <i>Agrostis</i>	<i>Azorella</i> condition	Negative Major 1 b, c, 2M a, b Neutral Minor 1 a, 2H a,b	When <i>Azorella</i> condition is healthy in a high abiotic stress system, cushions have a neutral relationship with epiphytes, including <i>Agrostis magellanica</i> and <i>Luzula. crinita</i> . As epiphytes increase through an increase in temperature or reduction in elevation, <i>Azorella</i> condition decreases (le Roux et al. 2005). Negative impacts of epiphytes have been observed in other <i>Azorella</i> spp. (Garcia et al. 2014; Molina-Montenegro et al. 2016). While <i>Ag. magellanica</i> does not negatively affect healthy cushions on Macquarie Island, it appeared to be increasingly occupying cushions with dieback, hence facilitating the cushion's replacement in the system (Whinam et al. 2014) Relationships re-described with further analysis for 2Ma,b and 2H a,b.
Interstitial: bryophytes	<i>Azorella</i> condition	Positive Major 1 a, b, 2H a, 2M a Minor 1 c, 2H b, 2M b	A full canopy of interstitial epiphytes maintains the integrity of the <i>A. macquariensis</i> canopy (smooth, dense) resisting wind ablation (see (Bergstrom et al. 2015).
Micro-arthropods	Soil (water holding capacity)	Positive Major 1 a, b, c, 2H a, b 2M a, b	Species specific response. However, generally soil micro-arthropods are important for nutrient cycling and soil development (Parisi et al. 2005), Stork and Eggleton (1992), Smith and Steenkamp (1990).
Microclimate	<i>Azorella</i> condition	Negative Major all models	The emergence and continuation of dieback on the island is highly likely to be in response to both additive and synergistic climatic drivers, where the water-stressed

Effect of (X)	Effect on (Y)	Relationship	Comments and references
			<p>summer-growing season is increasingly the susceptibility of <i>A. macquariensis</i> to disease, while the winter is promoting the pathogen (Chapter 2):</p> <p>(i) Prior to disease outbreak, there was a decadal decrease in plant available water during the active growing season from increased temperature, wind-speed, sunshine hours, and more variable rainfall, causing high water-stress in <i>A. macquariensis</i> (Bergstrom et al. 2015). The physiology of <i>A. macquariensis</i> adjusts well to minor variability, taking up and losing water quickly (Rolland et al. 2015), however, it is unable to adapt to larger variation (Bergstrom et al. 2015). The closely related <i>A. selago</i> has also been shown to be negatively affected by drier and warmer climate conditions (le Roux et al. 2005) and populations have been observed to dieback in response to drought on islands within Îles Kerguelen (Frénot et al. 1997).</p> <p>(ii) Following disease emergence, it appears the regional climate became less water-stressed during summer, although, the increase in plant available water has yet to be tested. However, the rainfall is still increasingly variable with higher storm activity, occurring against the background of a drier atmosphere (Adams 2009), conditions that in combination with higher extreme maximum and mean growing season temperatures are still likely to be somewhat stressful to <i>A. macquariensis</i> (Ch2).</p> <p>(iii) Simultaneously the winter dormancy season (April – Sept) has become 55% wetter, albeit in larger rainfall events (Bergstrom et al. 2015), and slightly warmer (Chapter 2) conditions that are conducive to pathogens (see (Harvell et al. 2002).</p>
Microclimate	Interstitial: bryophytes	Negative Major all models	Species specific response. However, generally as evapotranspiration rates increase the interstitial bryophytes decrease (Gignac 2011). For the purpose of this model and a historically humid Macquarie Island, assume negative response. Very responsive to environment drying quickly (Jagerbrand et al. 2011), however species have well developed desiccation tolerances (Slack 2011). Precipitation shifts are most likely to cause the greatest impact (dry Antarctic valleys) (Wasley et al. 2012).

Effect of (X)	Effect on (Y)	Relationship	Comments and references
Microclimate	Bryophytes	Negative Major all models	Drought impacts on bryophytes are very species specific (Gignac 2011; Robinson et al. 2018). However, during the current microclimate with increased variability and a significant decadal reduction in PAW there was extensive bryophyte death (Bergstrom et al. 2015).
Microclimate	Epiphytic <i>Agrostis</i>	Positive Major all models	As the microclimates warm and becomes wetter (variable), epiphytes will increase under improved growing conditions (le Roux et al. 2005; le Roux and McGeoch 2008) and declining <i>A. macquariensis</i> condition (Whinam et al. 2014).
Microclimate	Micro-arthropods	Negative Major all models	Species specific response. However, generally as microclimate becomes more variable and background drying increases micro-arthropods decrease (McGeoch et al. 2006) or may change in community structure (Hugo et al. 2004).
Microclimate	Pathogens	Positive Major all models	As the annual and winter rainfall and average temperatures increase, pathogen activity increases, being advantaged by milder, wetter winters (see (Harvell et al. 2002; Garrett et al. 2016; Burgess et al. 2017). High dieback extent is recorded at sites with very high humidity and lower numbers of freezing days (Chapter 2).
Pathogen	<i>Azorella</i> condition	Negative Major all models	Dieback is currently interpreted as a pathogenic disease, expressed as a chlorosis line which moves across the cushion surface, preceding necrosis (Whinam et al. 2014; Bergstrom et al. 2015; Dickson et al. 2019).
Soil: water-holding capacity	Pathogens	Positive Major 1 a, b, c Minor 2M a, b, 2H a, b	As the soil water holding capacity increases it was assumed that the pathogen would be more likely to persist through dry periods and propagate. Assumptions were corrected following insights from the first model.
Soil: water-holding capacity	<i>Azorella</i> condition	Positive Minor all models	Topographic wetness index (TWI) and gravel content were not predictors of cushion cover on Macquarie Island (Dickson et al. 2019).

Effect of (X)	Effect on (Y)	Relationship	Comments and references
Soil: water-holding capacity	Micro-arthropods	Positive Minor all models	Species specific response. However, generally as water holding capacity increases, some species may increase as conditions are buffered from drying abiotic conditions.
Soil Organic Matter (SOM)	Soil: water-holding capacity	Positive Major all models	As the SOM increases the soil water holding capacity increases (Sonter et al. 2000).
Texture: % gravel	Soil: water-holding capacity	Negative Major all models	As the gravel content (%) increases, the soil water holding capacity decreases (Sonter et al. 2000).

References

- Adams, N., 2009. Climate trends at Macquarie Island and expectations of future climate change in the sub-Antarctic. Papers and proceedings of the Royal Society of Tasmania 143, 1-8.
- Almeida, J.P., Montufar, R., Anthelme, F., 2013. Patterns and origin of intraspecific functional variability in a tropical alpine species along an altitudinal gradient. Plant Ecology & Diversity 6, 423-433.
- Anthelme, F., Buendia, B., Mazoyer, C., Dangles, O., 2012. Unexpected mechanisms sustain the stress gradient hypothesis in a tropical alpine environment. Journal of Vegetation Science 23, 62-72.
- Ashton, D.H., Gill, A.M., 1965. Pattern and Process in a Macquarie island Feldmark. Proceedings Of The Royal Society Of Victoria 79, 235-248.
- Barendse, J., Chown, S.L., 2001. Abundance and seasonality of mid-altitude fellfield arthropods from Marion Island. Polar Biology 24, 73-82.
- Bergstrom, D.M., Bricher, P.K., Raymond, B., Terauds, A., Doley, D., McGeoch, M.A., (. . .) Ball, M.C., 2015. Rapid collapse of a sub-Antarctic alpine ecosystem: the role of climate and pathogens. Journal of Applied Ecology 52, 774-783.
- Bonanomi, G., Stinca, A., Chirico, G.B., Ciaschetti, G., Saracino, A., Incerti, G., 2016. Cushion plant morphology controls biogenic capability and facilitation effects of *Silene acaulis* along an elevation gradient. Functional Ecology 30, 1216-1226.
- Brothers, N.P., 1984. Breeding, distribution and status of burrow-nesting petrels at Macquarie Island. Wildlife Research 11, 113-131.
- Burgess, T.I., Scott, J.K., McDougall, K.L., Stukely, M.J.C., Crane, C., Dunstan, W.A., (. . .) Hardy, G.E.S.J., 2017. Current and projected global distribution of *Phytophthora cinnamomi*, one of the world's worst plant pathogens. Global Change Biology 23, 1661-1674.
- Dickson, C.R., Baker, D.J., Bergstrom, D.M., Bricher, P.K., Brookes, R.H., Raymond, B., (. . .) McGeoch, M.A., 2019. Spatial variation in the ongoing and widespread decline of keystone plant species. Austral Ecology 44, 891-905.
- Frénot, Y., Gloaguen, J., Trehen, P., 1997. Climate change in Kerguelen Islands and colonization of recently deglaciated areas by *Poa Kerguelensis* and *P. annua*. Antarctic communities: species, structure and survival, B. Battaglia, J. Valencia et DWH Walton eds., Cambridge University Press, Cambridge, 358-366.

- Garcia, R.A., Araujo, M.B., Burgess, N.D., Foden, W.B., Gutsche, A., Rahbek, C., Cabeza, M., 2014. Matching species traits to projected threats and opportunities from climate change. *Journal of Biogeography* 41, 724-735.
- Garrett, K.A., Nita, M., De Wolf, E.D., Esker, P.D., Gomez-Montano, L., Sparks, A.H., 2016. Chapter 21 - Plant Pathogens as Indicators of Climate Change, In *Climate Change* (Second Edition). ed. T.M. Letcher, pp. 325-338. Elsevier, Boston.
- Gignac, L.D., 2011. Bryophytes as Predictors of Climate Change, In *Bryophyte ecology and climate change*. eds Z. Tuba, N.G. Slack, L.R. Stark. Cambridge University Press, ProQuest Ebook Central, <http://ebookcentral.proquest.com/lib/monash/detail.action?docID=605005>.
- Harvell, C.D., Mitchell, C.E., Ward, J.R., Altizer, S., Dobson, A.P., Ostfeld, R.S., Samuel, M.D., 2002. Climate Warming and Disease Risks for Terrestrial and Marine Biota. *Science* 296, 2158-2162.
- Hausmann, N.S., Boelhouwers, J.C., McGeoch, M.A., 2009. Fine scale variability in soil frost dynamics surrounding cushions of the dominant vascular plant species (*Azorella selago*) on sub-Antarctic Marion Island. *Geografiska Annaler Series a-Physical Geography* 91A, 257-268.
- Hugo, E.A., McGeoch, M.A., Marshall, D.J., Chown, S.L., 2004. Fine scale variation in microarthropod communities inhabiting the keystone species *Azorella selago* on Marion Island. *Polar Biology* 27, 466-473.
- Jagerbrand, A.K., Bjork, R.G., Callaghan, T., Seppelt, R.D., 2011. Effects of Climate Change on Tundra Bryophytes, In *Bryophyte ecology and climate change*. eds Z. Tuba, N.G. Slack, L.R. Stark, pp. 211-236. Cambridge University Press, ProQuest Ebook Central, <http://ebookcentral.proquest.com/lib/monash/detail.action?docID=605005>.
- le Roux, P.C., McGeoch, M.A., 2008. Rapid range expansion and community reorganization in response to warming. *Global Change Biology* 14, 2950-2962.
- le Roux, P.C., McGeoch, M.A., 2010. Interaction intensity and importance along two stress gradients: adding shape to the stress-gradient hypothesis. *Oecologia* 162, 733-745.
- le Roux, P.C., McGeoch, M.A., Nyakatia, M.J., Chown, S.L., 2005. Effects of a short-term climate change experiment on a sub-Antarctic keystone plant species. *Global Change Biology* 11, 1628-1639.
- le Roux, P.C., Shaw, J.D., Chown, S.L., 2013. Ontogenetic shifts in plant interactions vary with environmental severity and affect population structure. *New Phytologist* 200, 241-250.

- McGeoch, M.A., le Roux, P.C., Hugo, E.A., Chown, S.L., 2006. Species and community responses to short-term climate manipulation: Microarthropods in the sub-Antarctic. *Austral Ecology* 31, 719-731.
- Molina-Montenegro, M.A., Oses, R., Acuna-Rodriguez, I.S., Fardella, C., Badano, E.I., Torres-Morales, P., (. . .) Torres-Diaz, C., 2016. Positive interactions by cushion plants in high mountains: fact or artifact? *Journal of Plant Ecology* 9, 117-123.
- Parisi, V., Menta, C., Gardi, C., Jacomini, C., Mozzanica, E., 2005. Microarthropod communities as a tool to assess soil quality and biodiversity: a new approach in Italy. *Agriculture, Ecosystems & Environment* 105, 323-333.
- Raath-Krüger, M.J., McGeoch, M.A., Schöb, C., Greve, M., le Roux, P.C., 2019. Positive plant–plant interactions expand the upper distributional limits of some vascular plant species. *Ecosphere* 10, e02820.
- Robinson, S.A., King, D.H., Bramley-Alves, J., Waterman, M.J., Ashcroft, M.B., Wasley, J., (. . .) Hua, Q., 2018. Rapid change in East Antarctic terrestrial vegetation in response to regional drying. *Nature Climate Change* 8, 879-884.
- Rolland, V., Bergstrom, D.M., Lenne, T., Bryant, G., Chen, H., Wolfe, J., (. . .) Ball, M.C., 2015. Easy Come, Easy Go: Capillary Forces Enable Rapid Refilling of Embolized Primary Xylem Vessels. *Plant Physiology* 168, 1636-1647.
- Slack, N.G., 2011. The Ecological Value of Bryophytes as Indicators of Climate Change, In *Bryophyte ecology and climate change*. eds Z. Tuba, N.G. Slack, L.R. Stark, pp. 3-12. Cambridge University Press, ProQuest Ebook Central.
- Smith, V.R., Steenkamp, M., 1990. Climatic change and its ecological implications at a subantarctic island. *Oecologia* 85, 14-24.
- Sonter, R.O., Semple, W.S., Lawrie, J.W., 2000. Soils, vegetation and land use, In *Soils: their properties and management*. eds P.E. Charman, B.W. Murphy, pp. 271-286. Oxford University Press, Melbourne.
- Stork, N.E., Eggleton, P., 1992. Invertebrates as determinants and indicators of soil quality. *American Journal of Alternative Agriculture* 7, 38-47.
- Taylor, B.W., 1955. The flora, vegetation and soils of Macquarie Island., In *ANARE Reports, Series B*, 11. pp. 1-192. Australian Antarctic Division, Melbourne.
- Wasley, J., Robinson, S.A., Turnbull, J.D., King, D.H., Wanek, W., Popp, M., 2012. Bryophyte species composition over moisture gradients in the Windmill Islands, East Antarctica: development of a baseline for monitoring climate change impacts. *Biodiversity* 13, 257-264.

Whinam, J., Abdul-Rahman, J.A., Visoiu, M., di Folco, M.B.F., Kirkpatrick, J.B., 2014. Spatial and temporal variation in damage and dieback in a threatened subantarctic cushion species. *Australian Journal of Botany* 62, 10-21.

Appendix C2: Relationship between *Azorella macquariensis* and monocot epiphytes

Introduction

To clarify the relationship between Epiphytic *Agrostis* (*Agrostis magellanica* and *Luzula crinita*) and *A. macquariensis*, two hypotheses were tested using data from Chapter 2 on microclimate and condition class. First, that Epiphytic *Agrostis* is positively facilitated by higher temperatures (le Roux and McGeoch 2008), and second, that there is higher cover of Epiphytic *Agrostis* on cushions at lower elevation and with more dieback (Whinam et al. 2014).

Methods

Microclimate and condition classes from Chapter 2 were used to test the above hypotheses. Microclimate temperature data was recorded 4 hourly at 62 randomly stratified sites across the extent of the Macquarie Island plateau between December 2016 and February 2018 (for full study design and methods see Chapters 1 and 2, respectively). The extreme maximum (Temp_{max}) was calculated as the mean daily temperature 95th percentile for each site. Cushion condition data (Chapter 2) included the ‘Summary Dieback’ class, the subclasses ‘Dieback with *Agrostis*’ (cushion with dieback with *Ag. magellanica* or *L. crinita*) and ‘*Agrostis*’ (healthy cushion with *Ag. magellanica* or *L. crinita*). Cover per class was calculated as the mean cover of six 1 x 2 m plots per site (see Chapter 2 for full method). For this study the class Epiphytic *Agrostis* (as used in the ACFE) was defined as the total proportion of cushion canopy occupied by *Ag. magellanica* or *L. crinita* (‘*Agrostis*’ + ‘Dieback with *Agrostis*’) at each site. The elevation for each site was defined from the 5 x 5 m Macquarie Island digital elevation model (Brolsma 2008).

The proportion of Epiphytic *Agrostis* (0,1) was modelled as a function of Temp_{max} using a beta regression model with a logit link function (betareg; (Zeileis et al. 2016). To test the relationship between Epiphytic *Agrostis* and Dieback, the proportion of Epiphytic *Agrostis* (0,1) was modelled as a function of elevation (m), Summary Dieback (%) and their interaction term, similarly using a beta regression model with a logit link function (betareg; (Zeileis et al. 2016). There was no spatial autocorrelation in either model (global Moran’s I (Bivand et al. 2017).

Results

The mean proportion of Epiphytic *Agrostis* (*Ag. magellanica* or *L. crinita*) was higher on healthy cushion cover (9.27% ± 6.74% SD), than cushion cover with dieback (7.15 ± 7.37% SD) (median values presented in Fig. C2a, Appendix C). The analysis showed that Epiphytic

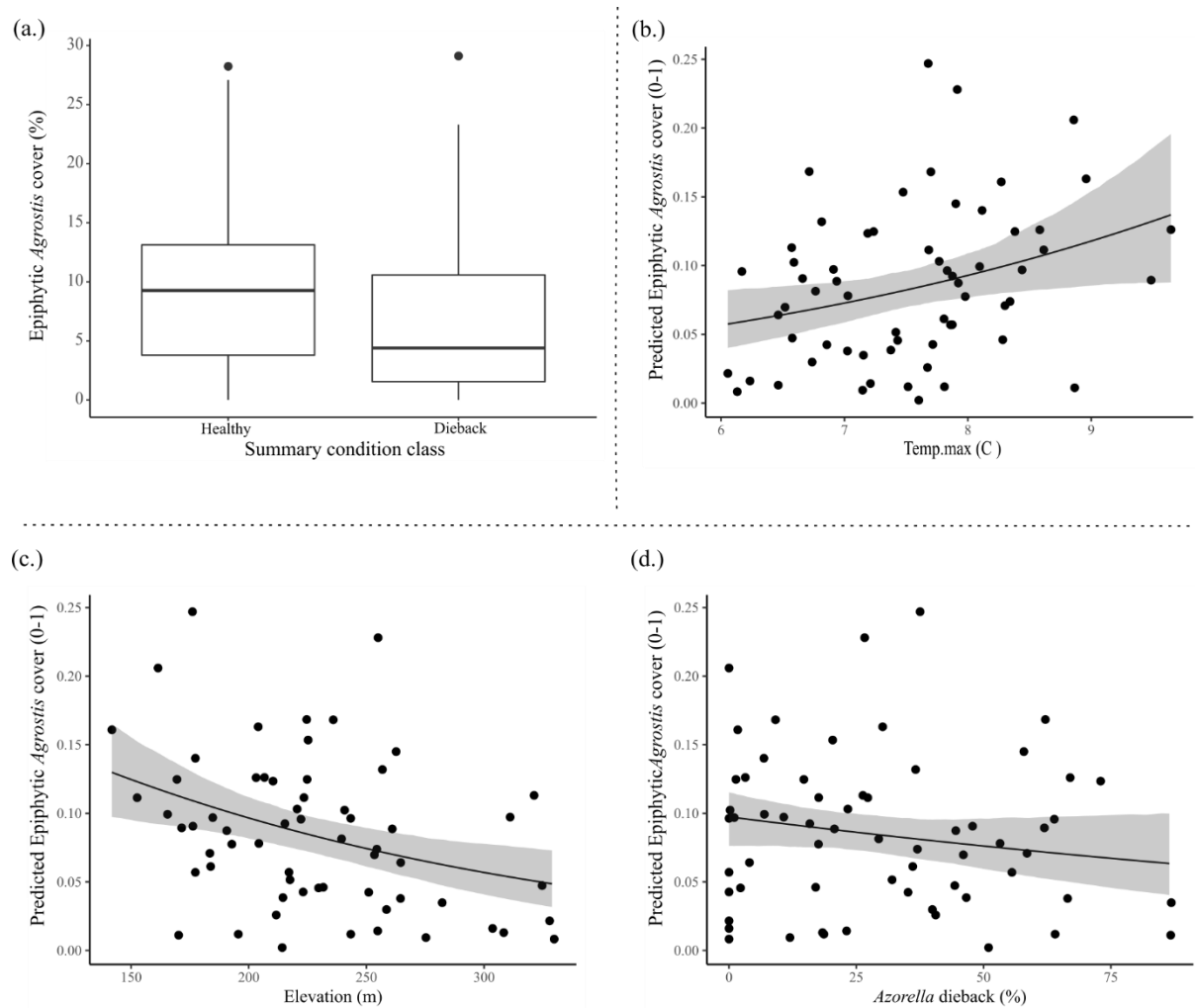


Fig. C2.1. Relationship between *Azorella macquariensis* and Epiphytic *Agrostis* (inclusive of *Agrostis magellanica* and *Luzula crinita*) under different cushion condition classes and site conditions: (a.) Proportion of Epiphytic *Agrostis* cover on healthy *A. macquariensis* and *A. macquariensis* with dieback (median boxplot, representing upper and lower quartiles, bars represent range), (b.) modelled Epiphytic *Agrostis* as a proportion of total *A. macquariensis* cover (0-1) over the extent of Temp_{max} (mean daily 95th percentile temperature); (c. - d.) separately modelled Epiphytic *Agrostis* as a proportion of total *A. macquariensis* cover (0-1) of all condition classes over the extent of (c.) elevation (m) and (d.) dieback (%). Figures b. – d. are all significant relationships ($p < 0.05$) over-laid with the total recorded cover of Epiphytic *Agrostis* (%) on *A. macquariensis* of any condition class.

Agrostis cover was significantly higher under higher temperatures (Est.coef = 0.27 ± 0.10 se, $z = 2.5$, $p = 0.01$, Pseudo- $R^2 = 0.08$; Fig. C2b, Appendix C). Epiphytic *Agrostis* was significantly more abundant at lower elevation (Est.coef = -0.01 ± 0.003 se, $z = -3.70$, $p < 0.001$; Fig C2c., Appendix C), which corresponds the negative temperature lapse rate of $0.7^\circ\text{C} \cdot 100\text{m}^{-1}$ on Macquarie Island (Chapter 2, (Tweedie and Bergstrom 2000). Epiphytes were found to have a higher cover on cushions with less dieback (Est.coef = -0.04 ± 0.02 se, $z = -2.15$, $p = 0.03$; Fig. C2d., Appendix C). There was no significant interaction between elevation and dieback.

Discussion

While there was not the capacity within the dataset to test whether the cover of *Agrostis magellanica* on and off cushions co-varied with elevation change, the above analysis provided useful insights. The results imply that a change in elevation or temperature changes the relationship between *A. macquariensis* and Epiphytic *Agrostis*, where cushions at lower and slightly warmer elevations have a higher cover of epiphytes. The relationship between the closely related species *A. selago* and Epiphytic *Agrostis* has been shown to change over a stress gradient, where *Ag. magellanica* becomes increasingly facilitated with higher elevation, before the relationship curve plateaus (le Roux and McGeoch 2010). This relationship is also likely to occur on Macquarie Island, where Epiphytic *Agrostis* is more dependent on *A. macquariensis* for survival and density under high-stress high elevations, while having an increasingly neutral and competitive relationship at the slightly warmer moderate elevations.

The establishment of Epiphytic *Agrostis* was not facilitated by cushion dieback. Surprisingly, there was a significant but weak negative relationship with dieback identified, reflecting the reduction of epiphytes on cushions with dieback. Likewise, there was no evidence for the feedback loop of Epiphytic *Agrostis* increasing dieback through higher epiphyte cover.

References

- Bivand, R., Altman, M., Anselin, L., Assunção, R., Berke, O., Bernat, A., (. . .) Yu, D., 2017. Package ‘spdep’: Spatial Dependence: Weighting Schemes, Statistics and Models. Version 0.7-4. . CRAN, <https://CRAN.R-project.org/package=spdep>.
- Brolsma, H., 2008. Macquarie Island AIRSAR DEM (Digital Elevation Model). <http://data.aad.gov.au/aadc/metadata/>.
- le Roux, P.C., McGeoch, M.A., 2008. Rapid range expansion and community reorganization in response to warming. *Global Change Biology* 14, 2950-2962.
- le Roux, P.C., McGeoch, M.A., 2010. Interaction intensity and importance along two stress gradients: adding shape to the stress-gradient hypothesis. *Oecologia* 162, 733-745.
- Tweedie, C.E., Bergstrom, D.M., 2000. A climate change scenario for surface air temperature at subantarctic Macquarie Island (ed.), In *Antarctic Ecosystems: Models for Wider Understanding*. eds W. Davison, C. Howard-Jones, P. Broady, pp. 272-281. Canterbury University Press, Canterbury.
- Whinam, J., Abdul-Rahman, J.A., Visoiu, M., di Folco, M.B.F., Kirkpatrick, J.B., 2014. Spatial and temporal variation in damage and dieback in a threatened subantarctic cushion species. *Australian Journal of Botany* 62, 10-21.
- Zeileis, A., Cribari-Neto, F., Gruen, B., Kosmidis, I., Simas, A.B., Rocha, A.V., Zeileis, M.A., 2016. betareg: Beta Regression. Version 3.1-0, <https://CRAN.R-project.org/package=betareg>

Chapter 4

Conservation options for a sub-Antarctic keystone species threatened by climate change

Introduction

The threat of anthropogenic climate change to natural systems is increasingly apparent, both as sustained climate change and as increasingly frequent extreme climate events (Harris et al. 2018). In response to the novel climate, species distributions are changing (Pech et al. 2017), population health is decreasing (Hoberg and Brooks 2015), and an increasing number of large-scale ecological collapses are occurring (Harris et al. 2018; Lindenmayer and Sato 2018; Hoffmann et al. 2019). For biodiversity on islands, climate change and the associated indirect threats, such as novel diseases, are considered to be the highest emerging threat, with nearly half of all threatened island endemics vulnerable to climate change (Russell and Kueffer 2019). While not always formally recognised, >99% of threatened species are sensitive to one or more climate threat (Delach et al. 2019).

To address the direct and indirect effects of climate change there have been several generalised management frameworks, strategies and reviews written since 2010 for managing species and ecosystems (e.g. Conroy et al. 2011; Watson et al. 2012; Gillson et al. 2013; Shoo et al. 2013; Kueffer and Kaiser-Bunbury 2014). These frameworks commonly follow five broad objectives, (i) increase protected area extent, (ii) improve representation and replication within the protected area, (iii) integrate within policy, (iv) improve management and restoration techniques, and (v) consider high intervention or novel management techniques. While objectives i-iv are well accepted and commonly implemented recovery actions, research shows that conservation practitioners are hesitant to implement novel actions because of the risk of the unknown and perceived comparative lack of effectiveness (Hagerman and Satterfield 2013; Hoeggner and Hughes 2019). However, it is increasingly clear that to effectively address novel threats and make lasting change, we need to implement 'high intervention' management actions with inherently more associated uncertainty (Hoegh-Guldberg et al. 2008; Hoeggner and Hughes 2019; Prober et al. 2019).

Australian threatened species recovery plans increasingly recognise the threat of climate change, however, recovery actions are rarely linked to addressing that threat (Hoeggner and Hughes 2019). In the United States of America, conservation practitioners agree (97%) that high intervention actions, such as assisted migration, will need to be implemented to effectively address climate change threats (Hagerman and Satterfield 2013). However, in most cases, traditional management actions were still prioritised more highly, as they are seen to be more effective and less risky (Hagerman and Satterfield 2013). Similarly, in Australia, recovery

plans primarily recommended well accepted, comparatively passive and low intervention recovery actions, most of which lack the boldness to prevent extinction under a novel climate (Hoeppner and Hughes 2019). The general perception that climate change is a future long-term rather than current threat, may drive the lack of prioritisation of high intervention actions, as it is believed that there is time to address the knowledge gaps before needing to act (Hoeppner and Hughes 2019).

Structured decision making (StDM) provides one method to address uncertainty and identify effective conservation management solutions for novel climate threats. It has been used successfully for threatened species management and for addressing changing species distributions (Gregory et al. 2013; Panfylova et al. 2019; Robinson et al. 2019). Uncertainty is often given as the reason for delaying management actions while additional research or data is gathered to clarify the solution, however, in many cases it only refines the knowledge and does not change the final recommended management action (Cook et al. 2013). The cost of inaction while research takes place also needs to be considered, as during this time the threat can continue to intensify (Gregory et al. 2013). StDM is an iterative process that engages technical experts, policymakers, conservation managers and stakeholders in an exchange of information to develop targeted objectives. The process helps to expose and explore the full range of potential management actions, the consequences of those actions, and the associated trade-offs from different perspectives (Gregory et al. 2012). It also allows decision-makers/conservation practitioners to step outside of their own experience, which often unintentionally limits the considered management solutions, to explore the full range of possibilities, including the consequences of ‘business as usual’ (Gregory et al. 2013).

The ongoing island-wide dieback of the dominant keystone species, *Azorella macquariensis* Orchard (Apiaceae, Macquarie cushions, see Fig. 2 of the General Introduction), and bryophytes of the surrounding fellfield on sub-Antarctic Macquarie Island (Whinam et al. 2014; Bergstrom et al. 2015; Dickson et al. 2019) represents a complex management problem driven by climate change. It will require the consideration of increasingly high intervention recovery actions to maintain the species and ecosystem in which it plays a key role. Cushion dieback, first observed in 2008/09, is hypothesised to be driven by short-term climate pulses (e.g. increasingly stormier climate, larger rainfall events, longer periods between rainfall, increased wind speed and sunshine hours) and long-term climate presses (e.g. higher maximum temperatures, annual rainfall, drier atmosphere) that have simultaneously weakened *A. macquariensis* during the growing season and provided more conducive conditions for the

pathogen during the cushions' dormant winter period (Ch2, (Bergstrom et al. 2015; Bergstrom et al. in press). The loss of cushion cover resulted in the rapid national listing of *A. macquariensis* as critically endangered in 2010 (Threatened Species Scientific Committee, TSSC 2010a). The management response from the multi-agency taskforce was swift, establishing a clear baseline of knowledge, quarantine policy, and undertaking low-intervention management actions to preserve the genetic material of the species (Bergstrom et al. 2015). However, one decade after island-wide cushion dieback was first recorded, it continues to affect almost a third of all cushion cover (Dickson et al. 2019) and is causing localised ecological collapse in the north of the island (Chapter 3, Bergstrom et al. in press). To address dieback and maintain fellfield ecosystem function bolder actions are required. These will necessitate a greater level of intervention, invariably carrying a higher risk of unknown biotic responses.

Complex management decision-making has previously been applied on Macquarie Island to eradicate multiple vertebrate pests impacting the island's biodiversity, which although ultimately very successful, resulted in some unanticipated negative intermediary outcomes (see Bergstrom et al. 2009; Terauds et al. 2014; Springer 2016). Specifically, following the eradication of feral cats (*Felis catus* L.) in 2001, there was a substantial increase in the European rabbit (*Oryctolagus cuniculus* L.) population (Bergstrom et al. 2009). The large increase in rabbit numbers resulted in a trophic cascade, with severe grazing impacts and erosion occurring across the island, particularly on coastal slopes important for seabird nesting (Bergstrom et al. 2009). This outcome emphasised the importance of holistically considering all potential management options and outcomes prior to implementation (see Raymond et al. 2011), thus ensuring that management is best able to respond to uncertain biotic responses (Bergstrom et al. 2009).

Therefore, with multiple lines of new evidence emerging since the national 'Conservation Advice' was endorsed in 2010 for *A. macquariensis*, and in the face of its ongoing rapid decline, here I apply a Structured-Decision Making (StDM) framework (Gregory et al. 2012) to explicitly identify the full range of recovery actions available to address uncertainty associated with managing threatened species vulnerable to climate change (see Gregory et al. 2013). As part of this process the aims of the chapter are to (i) show the advance in understanding achieved by the research presented in this thesis, and (ii) based on this and other evidence-based advances over the last decade, I discuss the range of policy and recovery solutions possible. I draw on techniques applied in similar Australian and international contexts, and

provide prioritised recommendations for recovery actions for *A. macquariensis* and the associated fellfield ecosystem.

Methods

This study focuses on the first four of the six step StDM process (Fig. 1.), building the scientific evidence-base for a range of management options in a consultative process. This can then be subsequently evaluated by conservation practitioners for implementation within the current management context. First, the decision context is clarified (Fig. 1.i.), summarizing the current values, trends and threats to *A. macquariensis* and the associated fellfield ecosystem, focussing on the enhanced understanding from the research presented in this thesis and published literature from the last decade. Second, over-arching conservation vision, sub-objectives and their associated performance measures for the species and the ecosystem are defined (Fig. 1.ii.). Third, a ‘*recovery action matrix*’ is developed of current and potential management actions from literature and expert input (Fig. 1.iii), which is visualised as a continuum of the ability to affect long-term change against the risk of unexpected outcomes (Fig. 1.iv.). The biological consequence and risk of each high intervention management action is then identified and linked to associated research objectives to mitigate those risks, where necessary.

(i) Clarification of the decision context

The current decision context (Fig. 1.i.) was determined from published literature, unpublished research presented in this thesis and grey literature, including the state and federal conservation advice. The ecological and cultural values of the species and fellfield, their conservation status, population and ecosystem trends, and threats to their conservation status were synthesised, highlighting new knowledge about the species and the ecosystem. The synthesised knowledge was used to revise and update the causal pathway model Hoffmann et al. (2019) and to describe the current understanding of drivers of *A. macquariensis* dieback and their consequences.

(ii) Definition of the conservation vision, management objectives, and desired outcomes

Despite conservation objectives being generally seen as very clear to conservation managers involved in day-to-day recovery of the species, conservation or recovery objectives can often remain comparatively ambiguous to other stakeholders, with unarticulated performance measures (Gregory et al. 2013). The process of clearly defining objectives is important to

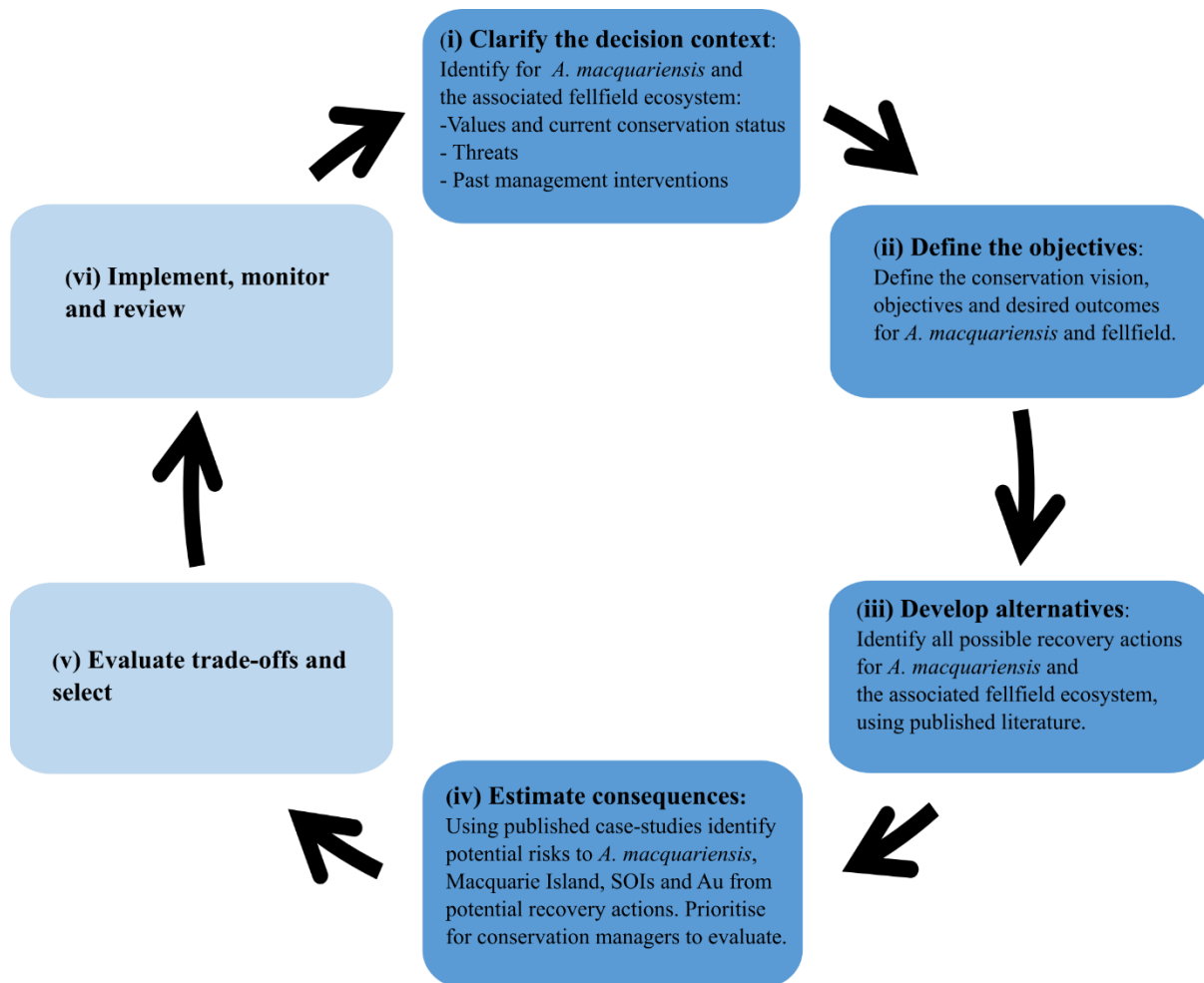


Fig. 1. Structured decision making (StDM) framework (Gregory et al. 2012) used for complex decision-making that involves multiple sources of uncertainty. This study completed steps i – iv to define the full range of potential alternative recovery actions and estimates the consequences for the critically endangered *Azorella macquariensis* and associated fellfield ecosystem on Macquarie Island using published case studies and the results presented in previous chapters of this thesis. The outcome of applying this framework are discussed and tabulated for future evaluation and implementation by conservation managers within the current management context of Macquarie Island (steps v and vi). Abbreviations include: Southern Ocean Islands (SOI) and Australia (Au).

(i) initiate the discussion about the objectives and formalise the balance between scientific or technical information and value judgements, (ii) explore all dimensions of management at the start of the process and avoid the biases of focussing on one traditional area of management, and (iii) raise the key uncertainties about climate change responses or management techniques for discussion that need to be considered during the planning process (Gregory et al. 2013).

Management objectives were defined in the Tasmanian Threatened Species Listing Statement (Tasmanian Threatened Species, TSS 2012, pg 5.) as:

- “*determine and address the cause of decline;*
- *monitor and describe the nature of the decline and any recovery of Azorella macquariensis and associated feldmark species;*
- *expand and maintain a representative ex situ conservation holding of seed and living plants.*”

However, while these objectives have set a direction for previous recovery efforts, they contain ambiguity about the values of the species and ecosystem to be conserved, and hence do not provide a clear vision for the system. Consequently, a new draft conservation vision, conservation objectives, and their associated performance measures for the purpose of this study were defined based on the values identified in the decision context (Fig. 1.ii.).

(iii) Develop alternatives – identification of all possible conservation interventions

To determine the range of alternate management and research priorities (Fig. 1.iii.), I reviewed published, unpublished and grey literature on *A. macquariensis* and related species. Specifically, relevant ongoing or incomplete recovery actions and research from the Tasmanian Threatened Species Listing Statement (TSS 2012) and the federal *Environment Protection and Biodiversity Conservation (EPBC) Act 1999* Conservation Advice (TSSC 2010b) were incorporated into the recommended management actions. For clarity, fine-scale management actions or research priorities were grouped into categories (see Appendix D1). The status of all previous recovery actions and research were classified as (a) complete, to be maintained, (b) implemented, requires refinement following research outcomes, (c) attempted, requires additional research, (d) not yet attempted, and (e) no longer relevant.

(iv) Consideration of potential risks and the likelihood of success of interventions

A recovery action matrix was produced to illustrate the relationship between the ability to affect long-term change for the species and/or the fellfield ecosystem (x-axis) against the risk of the

unexpected outcomes (y-axis; uncertainty/estimate consequences see Fig. 1.iv). The level of management intervention required to complete the action was simultaneously shown on the x-axis, where actions were considered ‘passive’ if they do not physically impact the species or the ecosystem (following Hoepfner and Hughes 2019). The potential recovery actions are outlined in Table 2, defining the (i) objective of the action and (ii) potential risks to be considered or mitigated.

Initial stakeholder review and prioritisation of conservation vision, actions and research (i – iv)

The conservation vision and objectives for the species and the fellfield, draft recovery actions, research priorities, and recovery action matrix were discussed at a workshop of relevant experts. Experts present at the workshop were from Monash University and five government agencies encompassed expertise in *Azorella* ecology and biology, Macquarie Island ecology, plant physiology, reserve management and threatened species recovery (see thesis acknowledgements).

Recovery actions and associated research were subsequently prioritised based on the objectives that were established for both *A. macquariensis* and the associated fellfield ecosystem and the scientific knowledge available.

Results and discussion

(i) Clarification of the decision context – current status of A. macquariensis and the fellfield ecosystem and its management

The current context within which decisions about *A. macquariensis* and the fellfield ecosystem need to be made is that a threatened, keystone species endemic to Macquarie Island continues to decline in condition (see Dickson et al. 2019). Dieback continues to affect almost a third of cushion cover island-wide, a decade after it was first observed (Dickson et al. 2019), ranging from more advanced dieback in the north to healthier cushions in the south (Chapter 2). Both the morphology and current plant condition is highly variable across the island (Dickson et al. 2019, Chapter 2), making it challenging to identify typical populations to prioritise for protection, and define cushion cover and dieback thresholds to trigger management response (Chapter 3). Current declines in the dominant cushion condition are leading to complete loss

of vascular plant biomass from some northern fellfield sites (Bergstrom et al. in press; Chapter 3) and thus there is an associated loss of soil carbon, microarthropod diversity (Bergstrom et al. 2015), vascular plant diversity and abundance (see le Roux and McGeoch 2010; Raath-Krüger et al. 2019) and iconic vegetation terraces (Selkirk 2012). Windy sites may be denuded of diseased cushions within three years, while those cushions at moderate elevation are increasingly likely to be outcompeted by graminoids (Chapter 3, Fig. 2). Low levels of recovery ($1.1 \pm \text{SD } 0.4\%$) occur island-wide, however, multiple waves of dieback have been observed to occur on the same site and same cushion (Chapter 3, (Dickson et al. 2019; Bergstrom et al. in press), resulting in the pervasive erosion of cushion cover (Chapter 3). While the rate of loss is still unclear (Chapter 3), over time it is expected that *A. macquariensis* will either become a sub-dominant species or in very exposed areas removed entirely. The full description of the value and trends of *A. macquariensis* are thoroughly described in Chapters 1 to 3 of this thesis.

The iconic tundra-like fellfield ecosystem on Macquarie Island is not listed under the *EPBC Act 1999* or the International Union for Conservation of Nature (IUCN)'s Red List of Ecosystems (RLE). This is despite the on-going cushion dieback threatening the fellfield's ecological character and function across the island, which has already resulted in localised ecosystem collapse at some northern sites (Chapter 3; Bergstrom et al. in press). The fellfield dominates the extensive windswept alpine plateau of Macquarie Island (> 200 m asl, approximately 50% of the area) (Selkirk 2012). This highly patterned ecosystem contains some of the most well-defined and spectacular global examples of vegetation-banked terraces, dominated by *A. macquariensis* and associated bryophytes (Taylor 1955b; Selkirk 1998; Selkirk-Bell and Selkirk 2013), which are considered a key geo-conservation feature of the island (Comfort 2014). These patterned features form part of the superlative wild beauty (Criterion vii) and geo-conservation features (Criterion viii) for which Macquarie Island was awarded World Heritage status in 1997 (Parks and Wildlife Service 2006). The listing of the fellfield ecosystem under the RLE and *EPBC Act 1999* is considered a management priority, to improve recognition and strategic management for the ecosystem (see Bland et al. 2019).

Threats to the species and associated ecosystem (a. – d.)

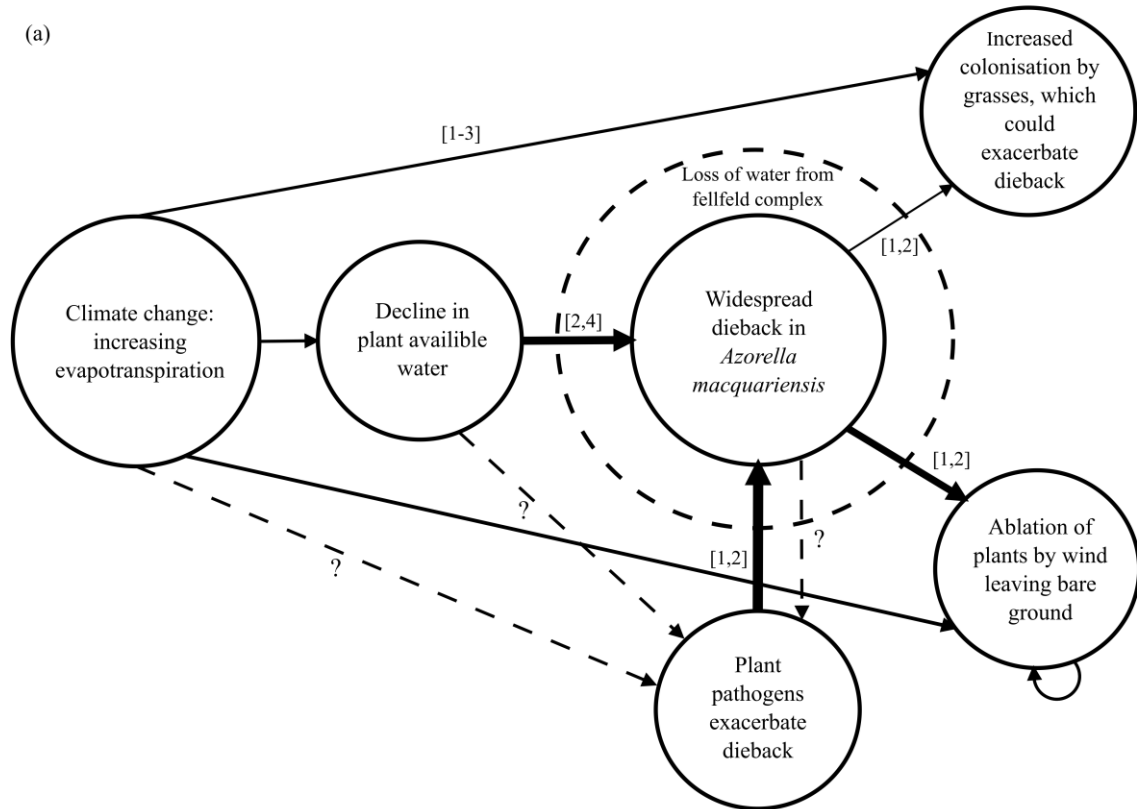
The highest threat to *A. macquariensis* and the associated fellfield ecosystem is the ongoing cushion dieback in response to a change in the regional climate (TSSC 2010b; TSS 2012; Whinam et al. 2014; Bergstrom et al. 2015). Macquarie Island has comparatively few direct current human impacts (Bergstrom and Chown 1999), with a rationalised walking track network to reduce trampling on the fellfield (Parks and Wildlife Service 2006) and no

mammalian pests following the success of the Macquarie Island Pest Eradication Program (MIPEP) in 2014 (Springer 2016). The three extant weed species (Williams et al. 2019) and three exotic pest species (Frénot et al. 2005) currently represent a low threat to *A. macquariensis* (see d. introduced species). Consequently focus is placed on the direct and indirect effects of climate change (sections a. – c.), described in the context of the revised causal pathway model and the disease triangle. The revised causal pathway model (Fig. 2) first developed by Hoffmann et al. (2019) describes the current understanding of the drivers of *A. macquariensis* dieback, emphasising the additive and synergistic nature of the direct and indirect effects of climate (Chapter 2).

a. Threat: Climate

For disease or pathogen outbreaks to occur two or three of the axes of a disease triangle need to change, expressed as (i) an increasingly weakened host, (ii) a more conducive environment and/or (iii) increased pathogen virulence (Garrett et al. 2016). The oceanic sub-Antarctic Macquarie Island is historically very climatically stable, misty (annual mean relative humidity, 89%), windy (annual mean wind speed, 9.3 ms^{-1}) and cold (month max. temp. Jan $8.4 - 4.7^{\circ}\text{C}$) (Selkirk et al. 1990). *Azorella macquariensis* is well adapted to this windy wet climate, and it quickly takes up available atmospheric water, but conversely rapidly loses water (Rolland et al. 2015). However, since 1970 there has been significant change in climate, both as (i) a sustained change (press), including a drier atmosphere (Adams 2009), increased sunshine hours (Bergstrom et al. 2015), increased extreme maximum and mean maximum temperature, primarily in the summer growing season months (Chapter 2), and (ii) more novel episodic (pulse) events, including increased storm activity, driving higher winds and more variable weather patterns (Adams 2009) and a 55% increase in winter rainfall that occurs in larger events (Bergstrom et al. 2015). This resulted in a significant increase in the evapotranspiration rate and associated deficit in plant available water for 17 summer growing seasons pre-2008, substantially weakening *A. macquariensis* immediately prior to the disease outbreak (Bergstrom et al. 2015). The water-stress has seemingly lessened post-2010, indicated by cushions regaining turgidity (Bergstrom et al. in press) (water stress levels still to be tested), and there is a much higher saturation of the soil during winter, the important summer growing season (October – March) is still

(a)



(b)

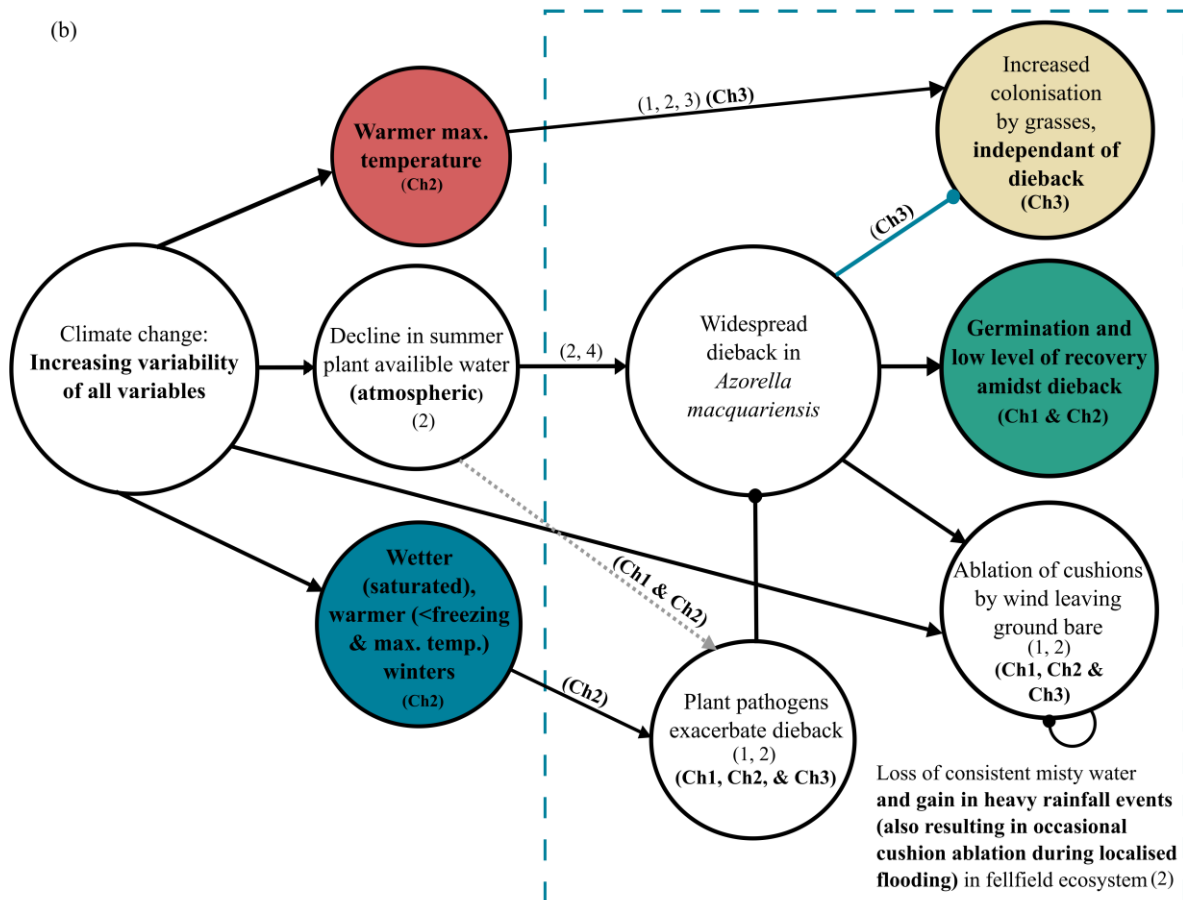


Fig. 2. The simplified causal pathway model of direct and indirect drivers of *Azorella macquariensis* (Macquarie cushions) dieback on the Macquarie Island fellfield, as described by (a) Hoffmann et al. (2019), and (b) updated following increased understanding from this thesis. The updated model (b) depicts (i) the direct weakening effect of climate change on the cushion, in drought conditions pre-2010, which lessened post-2010, and (ii) the indirect effect of climate change creating both a more conducive environment for pathogens, causing cushion dieback and facilitating the independent grass colonisation of cushions. The three right-hand nodes describe the hypothesised outcome for cushions under a changing climate. A change or increase in understanding from Hoffmann et al. (2019) is indicated by bold text, coloured nodes or coloured interaction lines, including (i) cushion dieback is facilitated under the increasingly wet winters, at sites with less freezing days and warming maximum temperatures, while water-stress is not directly related to dieback extent in the models, (ii) with warming maximum temperatures cushions are expected to become increasingly colonised by grasses, independent of dieback, and (iii) background levels of germination and recovery from dieback are occurring at low levels across the fellfield. Interactions are directional, positive (\rightarrow), negative ($-\bullet$) and removed from model (...). The feedback loop represents the acceleration of ablation with the loss of cushion surface integrity. Numbers associated with nodes and interactions refer to literature that discusses or has provided evidence for the process: (1) Whinam et al. (2014); (2) Bergstrom et al. (2015); (3) le Roux and McGeoch (2008); (4) le Roux et al. (2005); (Ch1) thesis Chapter 1, Dickson et al. (2019) ; (Ch2) thesis Chapter 2; (Ch3) thesis Chapter 3.

significantly warmer (Chapter 2) and has higher rainfall variability (Bergstrom et al. 2015). This increase in warmth and higher variability of rainfall, with the associated reduction in misty precipitation, is resulting in less atmospheric water, which may still be causing stress in *A. macquariensis* from a reduction in plant available water (Fig. 2).

b. Threat: Pathogen response

During the winter cushion dormancy period (April – September), when leaves senesce, the island is increasingly warm (Chapter 2) with much higher rainfall than experienced historically (pre-1960) and that now occurs in larger events (Bergstrom et al. 2015) (Fig. 2.). In other systems, warmer and wetter trending conditions have been shown conducive to disease or pathogens (Harvell et al. 2002). Here, I showed that dieback extent was negatively related to freezing days and positively related to very high relative humidity (Chapter 2), both variables associated with pathogens (see Garrett et al. 2016; Burgess et al. 2017). Extensive and comparatively healthy southern cushion populations persist in conditions suggestive of a natural refugium, because the south is significantly colder with more freezing days (Chapter 2). In contrast, microclimate (Chapter 2) and topographic (Dickson et al. 2019) modelling found that variables representative of water-stress were not important for determining dieback extent. Consequently, the direct relationship between pathogen activity and a deficit in plant available water is no longer supported in the models (Fig. 2). Despite this, weakened *A. macquariensis* condition is still considered an important precursor to pathogenic infection, as shown in the disease triangle (see Chapter 2). The possibility of the final axis of the disease triangle, increased pathogen virulence and the implied pathogen identification, requires extensive further research (see Table 3).

The iconic mega-herb *Pleurophyllum hookeri* Buchanan (silver-leaf daisy, Asteraceae) is the only other species seemingly affected by the same dieback as *A. macquariensis*, although juveniles (<10cm) are not affected (Whinam et al. 2014). Where *A. macquariensis* and adult *P. hookeri* occur together, the radiating dieback kills both species, clearly visible from the chlorosis line on the cushion. Other *Azorella macquariensis* epiphytes and surrounding vascular plants are not affected by the passing of the chlorosis line. During 2017 *P. hookeri* was present at a third of all surveyed *A. macquariensis* sites (n = 30 of 90) across the island's plateau, of which a third (n = 11) had low levels of pathogen dieback (<10% of *P. hookeri* cover) (Dickson et al. 2018, updated 2018a). While *P. hookeri* dieback occurred across the island, in 2018 large areas of *P. hookeri* dieback (100 x 100 m) occurred in association with cushion dieback east of Mount Hamilton, around Mount Eitel and *P. hookeri* dieback

independent of cushions on the Bauer Bay Track (pers. obs). Dieback appears to be increasing over time, with higher amounts observed in 2019 (M. Visoiu pers. comm. 2019). Despite these two species being from different families, with different forms and growth rates (Bergstrom et al. 1997), they are the only plant species on the island to both have a large well-defined taproot and undergo winter senescence, before new leaves emerge in September. However, note that dieback also occurred in cushion canopies where the taproot was not visually affected by lesions (Whinam et al. 2014). Further research is required to establish the extent of dieback in *P. hookeri* populations and to confirm whether it is the same pathogens driving dieback as in *A. macquariensis*. The only other dicot species with a similar taproot *Stilbocarpa polaris* (Hombr. & Jacquinot ex Hook.f.) A.Gray (Macquarie Island cabbage, Araliaceae) syn. *Azorella polaris* G.M.Plunkett & A.N.Nicolas (Plunkett and Nicolas 2017) is currently unaffected by the dieback. This is despite some co-occurrence of the species at moderate elevation where dieback is present.

c. Threat: Short-grassland response to climate

The fellfield is traditionally highly exposed and species-poor (Selkirk et al. 1990). In this environment *Azorella* species facilitate greater diversity and cover of vascular plants, by ameliorating the harsh conditions (e.g. le Roux and McGeoch 2010). However, as sub-Antarctic maximum temperatures increase under regional climate change, there has been a movement of vascular plants upslope of $3.4 \pm 0.8 \text{ m yr}^{-1}$ (le Roux and McGeoch 2008). Of the major sub-Antarctic Islands, Macquarie Island has one of the lowest maximum elevations, with plant species already occurring its the full extent (433 m asl), providing no capacity for *A. macquariensis* to move upslope as temperatures warm (Baker et al. unpublished). Dominant short-grassland species, *Agrostis magellanica* Lam. (Poaceae) and *Luzula crinita* Hook. (Juncaceae), have increased in cover on the Macquarie Island coastal escarpments simultaneously with a rise in maximum temperatures (Scott and Kirkpatrick 2013), suggesting this may also be occurring across the island at similar elevations (Chapter 3). On the fellfield the dominant epiphytes of *A. macquariensis* (*Ag. magellanica* and *L. crinita*) increase in cover with higher maximum temperatures or alternatively with a reduction in elevation, while cushion dieback reduces epiphyte cover (Chapter 3; Fig. 2). Additionally, under warming temperatures it is likely that needle ice, which maintains and turns over gravel treads on the iconic vegetation terraces (see Selkirk-Bell and Selkirk 2013), is also decreasing, potentially allowing grass to establish and flatten the landscape. This, together with qualitative modelling, suggests that short-grassland species threaten to colonise and outcompete moderate elevation

A. macquariensis populations as maximum temperatures rise, irrespective of dieback (Chapter 3; Fig. 2). However, the change in the distribution and density of grassland species in response to warmer temperatures is complicated by the eradication of rabbits and removal of grazing pressure in 2011 (see Terauds et al. 2014). While it is known that *Ag. magellanica* and *L. crinita* were increasing in density irrespective of rabbits on coastal slopes (Scott and Kirkpatrick 2013), it is also possible that rabbits were maintaining a more open structure at moderate elevation on the fellfield than previously observed. Therefore, although vascular species respond variably to rabbit eradication on different sub-Antarctic islands (Chapuis et al. 2004), on the warmer and wetter Macquarie Island, the removal of grazing pressure may also be driving the redistribution of short-grasslands and subsequent out-competition of *A. macquariensis*.

d. Threat: Introduced species

The introduction and establishment of new alien plants, vertebrates, invertebrates, and pathogens onto Macquarie Island represents a potential additional threat to *A. macquariensis* if they establish (TSSC 2010b; TSS 2012), as they do on many sub-Antarctic islands (Frénét et al. 2005). Currently, thorough ongoing quarantine procedures are in place to prevent incursions, monitoring the movement of personnel and equipment on and off-island (Parks and Wildlife Service 2006). There are three well-established extant weed species (*Poa annua* L., *Cerastium fontanum* Baumg., and *Stellaria media* L.) on the island (Williams et al. 2019). However, all three weeds represent a very low threat to *A. macquariensis* on the fellfield predominantly occupying different habitats. Despite both *P. annua* and *C. fontanum* occurring island-wide, including as sparse individuals on the fellfield, their highest densities occur at low to moderate elevation, primarily in disturbed sites (see Scott and Kirkpatrick 2008; Williams et al. 2016; Sindel et al. 2018). *S. media* has a more limited distribution, occurring along the island's watercourses at predominantly low to moderate elevation, and radiating from points of historical disturbance in the northern third of the island (Williams et al. 2019). Historically the European rabbit caused minor, localised mechanical damage to *A. macquariensis* affecting < 10% of cushion canopies in or near short-grasslands (Whinam et al. 2014), however, the threat is no longer present following the successful eradication of rabbits in 2011 (Terauds et al. 2014). With the completion of the Macquarie Island Pest Eradication Program, the island was declared mammalian pest-free in 2014 (Springer 2016), leaving only three extant exotic birds (common starling *Sturnus vulgaris* L., common redpoll *Acanthis flammea* L., and Palearctic mallard *Anas platyrhynchos* L.) (Frénét et al. 2005). Similar to the weed species, the exotic birds represent a limited threat to *A. macquariensis* on the fellfield, preferentially

occupying the short-grasslands, coastal escarpments, and platforms (Selkirk et al. 1990). Therefore, overall there is minimal threat from extant invasive alien species.

Leaf expulsion, putative anomaly

During the 2017/2018 Austral summer *A. macquariensis* was observed to be expelling a small number of leaves from cushions island-wide (Fig. 3a-c). The expelled leaves appeared to be the first leaves to emerge post-senescence in spring 2018, because they were consistently located on the outside of the new seasons growth, above the previous seasons leaves (Fig. 3d-f). This observation was considered an anomaly, as the cushions are well known to retain their annually senesced leaves within their canopy, where they break down and form humic mulch, while new leaves grow at the tips of the branchlets in the new spring season (Taylor 1955a; Ashton and Gill 1965; Bergstrom et al. 2015). Similarly the expulsion of leaves had not been recorded in the previous summer season, nor within the memory of experienced Macquarie Island botanists (D. Bergstrom, P. Selkirk, J. Whinam, pers. comm. 2018). However, it had been previously observed once before in the mid-2000s, following a large snow fall (J. Shaw, pers. comm., Nov. 2019). While no recordings of leaf expulsion were made during the 2018/2019 summer, it was again observed along the length of Macquarie Island in October 2019 (A. Turbett, Tasmanian Parks and Wildlife Service, pers. comm., October 2019). Despite the loss of leaves, leaf expulsion did not disrupt the integrity of the canopy nor make the cushions apparently more susceptible to ablation. Leaf expulsion was recorded from 58.8% ($n = 48$ of 82) of the *A. macquariensis* sites assessed in this thesis, from both large and small (< 100 mm diameter) cushions, and occurred the length and breadth of the island (unpub. data). It was predominantly recorded in healthy cushions, although on closer inspection cushions with dieback were also observed to occasionally expel leaves. Leaf samples were taken from six sites, from cushions that were expelling leaves and those that were not, however, on closer inspection nearly all cushions were expelling at least a few leaves. There was no visual difference between the plants.

Plants often enter early senescence and experience leaf abscission (detachment) in response to drought or severe water stress (Munné-Bosch and Alegre 2004). While early senescence of the total canopy under drought conditions was shown in experimental manipulation of *A. selago* (le Roux et al. 2005), no leaves were expelled (M.A. McGeoch, pers. comm, November 2019), nor is *A. macquariensis* entering early senescence. Alpine plants are also known to have



Fig. 3. Healthy *Azorella macquariensis* (Macquarie cushions) showing unusual dead leaf expulsion from the cushion canopy (a. – c.) during the 2017/2018 Austral summer. The arrow indicates a high concentration of expelled leaves (a.), while expelled leaves (brown) are spread across or emerging from the canopy of cushions b. and c., respectively. Close-up images of sampled cushion rosettes and leaves (e. – g.), showing the putative first leaf from the current season senesced (brown), and soon to be shed, on the outer edge of the new growth.

varying freezing tolerances at different times of the growing season (Sierra-Almeida et al. 2009), and are increasingly susceptible to lethal leaf spring freezing events with the earlier snowmelt in alpine ecosystems under climate change (Wheeler et al. 2014). While Macquarie Island rarely maintains snow cover for more than a week (Selkirk et al. 1990), it is plausible that a chance heavy snow fall, subsequent melt and freeze, timed simultaneously with the first leaf emergence of *A. macquariensis* in spring, could result in the early leaves' abscission and subsequent expulsion. However, the driver of leaf expulsion or abscission has not yet been tested. It is possible that this is either a new response to a changing climate, or that it has previously periodically occurred but not been noted, given *A. macquariensis* was not of previous conservation concern. Future research is needed to clarify the cause of the leaf expulsion and the regularity at which it occurs.

Past interventions to address the threats

Following the observation of island-wide dieback in 2008/09 (Whinam et al. 2014; Bergstrom et al. 2015) *A. macquariensis* was listed as nationally critically endangered in 2010 (TSSC 2010a) and endangered in Tasmania in 2009 (TSS 2012). Island-wide dieback surveys were conducted and monitoring programs were subsequently established (Bricher et al. 2013; Bergstrom 2013, updated 2014; Shaw and Terauds 2013, updated 2016; Whinam et al. 2014; Bergstrom et al. 2015). The research and monitoring created a baseline knowledge of *A. macquariensis* physiology (Bergstrom et al. 2015; Rolland et al. 2015), distribution (Bricher et al. 2013), condition (Selkirk 2012; Whinam et al. 2014; Bergstrom et al. 2015; Dickson et al. 2019), microclimates (Chapter 2) and state-transition of cushion condition (Chapter 3). Recovery actions successfully banked the seed, established an isolated *ex situ* population on North Head on Macquarie Island (Perrins and Tapson 2014; Tapson 2014), defined three special management areas (SMAs) that limit access to high quality cushion populations and implemented quarantine procedures to stop the inter-island spread of disease (Bergstrom et al. 2015). However, despite targeted germination and pathology research, *A. macquariensis* germination cues and pathogens remain unidentified (Bergstrom et al. 2015) and the dieback is ongoing and pervasive (Dickson et al. 2019).

(ii) Definition of the conservation vision, management objectives, and desired outcomes

The recommended conservation vision defined in this study is ‘Conserve *Azorella macquariensis* and ecological function of the fellfield ecosystem across Macquarie Island’, and is composed of three sub-objectives (i) maintain cover and abundance of *A. macquariensis*, (ii) maintain genetic diversity of *A. macquariensis*, and (iii) maintain fellfield ecosystem function (Table 1). Each of the three sub-objectives have high level performance measures identified to guide the development of alternative recovery actions.

(iii) Develop alternatives – identification of all possible conservation interventions, and (iv) estimate consequences

Fifteen recovery actions were identified from the literature as either priorities to maintain or for consideration for future implementation (Table 2, Fig. 4). Eleven actions were previously recommended under the national Conservation Advice (TSSC 2010b) and Tasmanian State Listing Statement (TSS 2012) and are considered to be important to include within the recommended future actions (Actions 1 – 11, Table 2, Table S1). Four of the fifteen recommended recovery actions were developed from relevant published Australian and international case studies (Actions 12 – 15, Table 2). Recovery actions that have been successfully implemented or been attempted since 2009 were overwhelmingly passive (6 of 15) and low risk (8 of 15), and while they provided important policy and biosecurity structure, they do not have the ability to maintain ecosystem function (Fig. 4). The implementation of primarily passive and low intervention recovery actions to-date primarily reflects the necessity to develop baseline knowledge and policy in the comparatively short time-frame since the island-wide *A. macquariensis* dieback was first detected (10 years). Those active interventions implemented focussed on securing *ex situ* *A. macquariensis* collections to preserve the species, while none has the capacity to maintain ecosystem function (Fig. 4). Previously recommended and predominantly implemented actions under the state and federal conservation advice relating to monitoring, baseline research, developing germination and propagation techniques, or identifying the putative pathogens were considered research for this study (Table 3).

Invariably the newly recommended or yet to be attempted actions have a higher risk of unexpected outcomes (Fig. 4), with additional risks to be considered or mitigated (Table 2). However, they also have the highest potential to effect lasting change and maintain ecosystem function. The following sections discuss (a.) existing recovery actions that should be retained and refined with recent research outcomes to secure *A. macquariensis ex situ* and prevent

Table 1. Conservation vision and the management objectives and management performance measures in line with this desired outcome for the critically endangered *Azorella macquariensis* and the associated fellfield ecosystem on Macquarie Island (MI).

High level conservation vision	
Conserve <i>Azorella macquariensis</i> and ecological function of the fellfield ecosystem across Macquarie Island	
Objectives	Performance measures
Maintain cover and abundance of <i>A. macquariensis</i>	<ul style="list-style-type: none"> • Current (2020) distribution and cover maintained, natural regeneration occurring. • No cushion dieback within high value conservation areas (special management areas, SMAs). • Former northern distribution restored with pathogen-resistant cushions. • No new introductions of exotic plants, animals or pathogens on MI.
Maintain genetic diversity of <i>A. macquariensis</i>	<ul style="list-style-type: none"> • Seed bank maintained and supplemented to reach target of >10,000 seeds, allowing seed to be used for recovery actions. • Isolated North Head (MI) <i>ex situ</i> population maintained (>50 individuals). • Genetically diverse <i>ex situ</i> population germinated, propagated and maintained off MI.
Maintain fellfield ecosystem function	<ul style="list-style-type: none"> • Iconic vegetation terraces (geo-conservation features) maintained in landscape. • Keystone / landscape engineer role of plant species maintained on the fellfield: <ul style="list-style-type: none"> • Biotic diversity (i.e. “<i>habitat complexity, connectivity, and community diversity</i>”) maintained. • Maintenance of soil organic carbon in the fellfield ecosystem. • Locally collapsed areas of fellfield restored with pathogen-resistant species.

Table 2. Recommended *Azorella macquariensis* and fellfield recovery actions on Macquarie Island (MI). * indicates that action is not dependant on the suggested research, but will benefit from the increased knowledge. Sources for management actions as listed: National Conservation Advice for *A. macquariensis* (EPBC), and Tasmanian Threatened Species Listing Statement (TSS). Abbreviations include: Australian Antarctic Division (AAD), Australia (Au), Environmental Protection and Biodiversity Conservation Act 1999 (EPBC Act 1999), thesis chapter (Ch), Australian Department of Environment and Energy (DoEE), Tasmanian Department of Primary Industry, Parks, Water, Environment (DPIPWE), International Union for Conservation of Nature (IUCN) Red List of Ecosystems (RLE), Royal Tasmanian Botanical Gardens (RTBG), Special Management Areas (SMAs), Southern Ocean Islands (SOI), Tasmanian Parks and Wildlife Service (TasPWS).

Intervention option	Values protected	Objectives	Risks to be considered and/or mitigated	Required research & policy	Source	Recommended Implementation Priority
Existing actions to be maintained						
1. Cooperation of stakeholders	Species, ecosystem	<ul style="list-style-type: none"> Sharing of knowledge and resources between key stakeholders (DPIPWE, TasPWS, AAD, DoEE, RTBG & research institutions). 	<ul style="list-style-type: none"> Cooperation not achieved. 	<ul style="list-style-type: none"> NA 	EPBC, TSS	High, ongoing
2. Education of stakeholders, and wider public	Species, ecosystem	<ul style="list-style-type: none"> Increased awareness of fellfield change by expeditioners, Antarctic and global science community, and the general community. 	<ul style="list-style-type: none"> Education does not reach the required audience. 	<ul style="list-style-type: none"> NA 	EPBC, TSS	High, ongoing
3. Biosecurity – off (inter) island	Species, ecosystem	<ul style="list-style-type: none"> Prevention of pathogen spread to other SOI or mainland Australia (science and tourism). No biological material taken off island without appropriate biosecurity practices. 	<ul style="list-style-type: none"> Not all pathways identified. 	<ul style="list-style-type: none"> *Ai-v 	EPBC, TSS	High, ongoing

Intervention option	Values protected	Objectives	Risks to be considered and/or mitigated	Required research & policy	Source	Recommended Implementation Priority
		<ul style="list-style-type: none"> Maintain strict biosecurity procedures to prevent new biological threats from arriving on the island. 				
4. Maintain seed bank	Species	<ul style="list-style-type: none"> Long-term maintenance of viable seed (>10,000 seeds) to preserve genetic diversity, to be made available for use in research and conservation actions. 	<ul style="list-style-type: none"> Funding resources not continued, seed bank not maintained, and genetic material lost. 	<ul style="list-style-type: none"> NA 	EPBC, TSS	High, ongoing
5. Maintain <i>ex situ</i> population on MI	Species	<ul style="list-style-type: none"> Long-term conservation of genetic diversity (>50 individuals) and production of seed for future conservation use through the maintenance of the isolated North Head <i>ex situ</i> population. 	<ul style="list-style-type: none"> Pathogenic infection of isolated population. Resources required to support system discontinued. 	<ul style="list-style-type: none"> NA 	EPBC, TSS	High, ongoing
Actions to be strengthened or refined						
6. Biosecurity - on island (Special management areas, SMA)	Species, ecosystem	<ul style="list-style-type: none"> Prevention/slowing of disease spread to highest conservation value populations on MI through the use of restricted access SMAs and associated hygiene protocols. 	<ul style="list-style-type: none"> Ineffective, spread continues. 	<ul style="list-style-type: none"> Refine SMAs using identified variables (Ch2) *Ai-vi. 	EPBC, TSS	High, ongoing

Intervention option	Values protected	Objectives	Risks to be considered and/or mitigated	Required research & policy	Source	Recommended Implementation Priority
		<ul style="list-style-type: none"> Minimise physical damage to <i>A. macquariensis</i> throughout its distribution. 				
7. Establishment of <i>ex situ</i> population (Tas, Au)	Species	<ul style="list-style-type: none"> Long-term conservation of genetic material as a RTBG living collection, until species can be secured on MI. 	<ul style="list-style-type: none"> Introduction of pathogen to mainland, if using translocated individuals. Extensive quarantine needed. Continued inability to maintain an <i>ex situ</i> population. 	<ul style="list-style-type: none"> Bi-ii *Ai,ii,iv,v. 	EPBC, TSS	High
8. National Recovery Plan or updated Conservation Advice for <i>A. macquariensis</i>	Species, ecosystem	<ul style="list-style-type: none"> National Recovery Plan or updated EPBC Conservation Advice approved for <i>A. macquariensis</i> to inform strategic management decisions. 		<ul style="list-style-type: none"> *A – F Updated EPBC Conservation Advice Recovery Plan 	EPBC, TSS	Moderate
Actions not yet attempted						
9. Listing of Fellfield under IUCN Red List of Ecosystems and EPBC Act 1999	Ecosystem, species	<ul style="list-style-type: none"> List fellfield ecosystem under IUCN RLE and EPBC Act to increase recognition and strategic management actions as matter of National Environmental Significance (under EPBC Act 1999) 		<ul style="list-style-type: none"> *Ai-vii, *Ci-ix, focus on vi. *Di-ii 	EPBC, TSS	Moderate

Intervention option	Values protected	Objectives	Risks to be considered and/or mitigated	Required research & policy	Source	Recommended Implementation Priority
10.Assisted migration of <i>A. macquariensis</i> to SOI	Species	<ul style="list-style-type: none"> Conservation of <i>A. macquariensis ex situ</i> using translocated individuals to a similar environment on a sub-Antarctic island, until species is secure on MI or the Australian mainland. 	<ul style="list-style-type: none"> Cannot germinate/propagate the species. Introduction of pathogen to other SOIs (if using translocated MI individuals). Extensive quarantine needed. Potential for hybridisation with <i>A. selago</i> (wind pollinated). Not politically achievable. Population doesn't establish or becomes competitive. 	<ul style="list-style-type: none"> Ai-iv Bi,ii Translocation plan 	EPBC	Low
11.Propagation & restoration with resistant phenotypes	Species, ecosystem	<ul style="list-style-type: none"> Re-establish collapsed <i>A. macquariensis</i> populations with pathogen resistant individuals to secure the species and ecosystem function. 	<ul style="list-style-type: none"> Resource intensive. No phenotype or genotype resistant to disease. Species cannot be germinated and/or propagated. 	<ul style="list-style-type: none"> Ei Ai-ii Bi-ii 	~TSS	High
12.Pathogen resistance through genetic modification	Species, ecosystem	<ul style="list-style-type: none"> Develop pathogen resistance in <i>A. macquariensis</i> using genomic editing techniques and re-establish collapsed populations, to secure the species and ecosystem function. 	<ul style="list-style-type: none"> Resource intensive. <i>A. macquariensis</i> genome not current described. Effectivity of technology is compromised when target genes are unknown. Genomic editing techniques unsuccessful. Biotic interactions negatively altered or competitive individual 	<ul style="list-style-type: none"> Ei-ii Ai-ii Bi-ii 		Low

Intervention option	Values protected	Objectives	Risks to be considered and/or mitigated	Required research & policy	Source	Recommended Implementation Priority
			produced and ecological niche changed. <ul style="list-style-type: none"> • Cannot propagate or establish new genetically modified individuals. 			
13.Pathogen control (chemical application)	Species, ecosystem	<ul style="list-style-type: none"> • Remove the pathogen threat from MI to retain the species and ecosystem function. • Prioritise the highest <i>A. macquariensis</i> conservation value areas for treatment first. 	<ul style="list-style-type: none"> • Control treatment cannot be effectively identified. • Off-target damage may occur: broad-scale chemical application may negatively affect MI microbes, changing the community. • It is likely to be an on-going application. • Expensive. • Cannot germination or propagate <i>A. macquariensis</i> for trials. 	<ul style="list-style-type: none"> • Ai-ii • Bi-ii • Fi-ii 		High
14.Assisted migration of <i>A. selago</i> to MI	Ecosystem	<ul style="list-style-type: none"> • Restore and maintain fellfield ecosystem function and iconic terraces with more morphologically robust and closely related species, <i>A. selago</i>. 	<ul style="list-style-type: none"> • Hybridisation with <i>A. macquariensis</i>. • <i>A. selago</i> is also susceptible to pathogens. • Does not establish or fill same ecological niche. • Species cannot be germinated and/or propagated. 	<ul style="list-style-type: none"> • Ai-iii • Bi-ii • Translocation plan 		Moderate
15.Assisted migration of South American <i>Azorella</i> sp. to MI	Ecosystem	<ul style="list-style-type: none"> • Restore and maintain fellfield ecosystem function and iconic terraces with a morphologically similar 	<ul style="list-style-type: none"> • Hybridisation with <i>A. macquariensis</i>. • South American species are also susceptible to pathogens. 	<ul style="list-style-type: none"> • Ai,ii,vi,vii. • Translocation plan 		Moderate

Intervention option	Values protected	Objectives	Risks to be considered and/or mitigated	Required research & policy	Source	Recommended Implementation Priority
		species, which are well known for their antibacterial properties.	<ul style="list-style-type: none"> • Cannot be established on MI. • Does not fill same ecological niche. 			

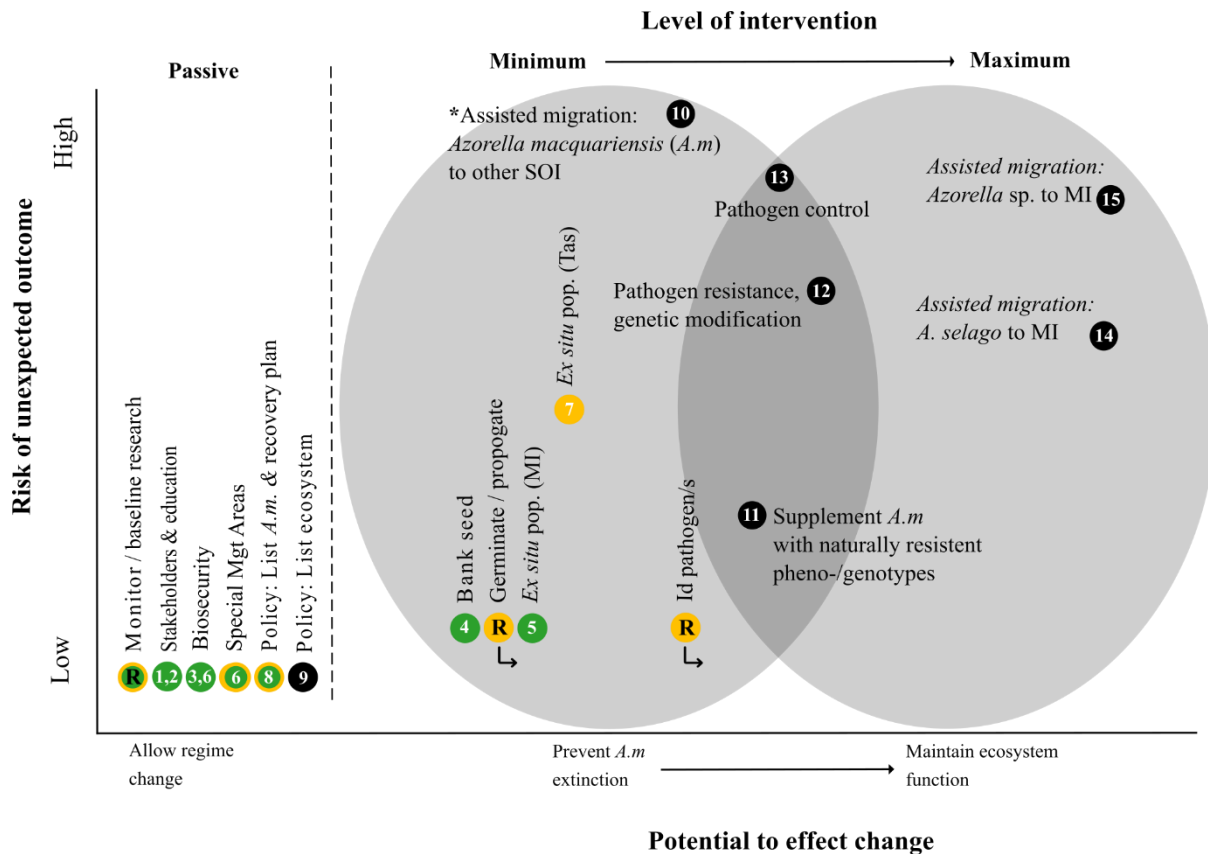


Fig. 4. Recommended recovery actions for *Azorella macquariensis* (*A.m*) and the Macquarie Island (MI) fellfield, presented as the level of intervention required and the consequent potential to effect change, against the risk of negative outcomes (uncertainty). Action status: existing action, to be maintained (●); implemented, requires refinement following research outcomes (●); attempted, requires additional research (●); not yet attempted (●); research action contributes to all actions to the right (→). R indicates actions that are termed research in Table 3; numbers 1 – 15 refer to recommended management actions in Table 2 (not in order of importance); and, * acknowledges that additional international political will (decision support) is required, which would increase the level of intervention to maximum. Ovals indicate independent objective of action, overlap indicates ability to address both objectives. Abbreviations include: population (pop), Southern Ocean Island (SOI) and Tasmania, Australia (Tas).

further spread of the disease. Focus is then given to (b.) the yet to be attempted recovery actions that have the highest potential to affect long-term change and maintain ecosystem function, describing similar successful case studies and risks to be considered before implementation.

a. Existing recovery actions to be maintained or refined (low risk):

To effectively recover this species and prevent further spread of the disease off Macquarie Island, maintaining a cooperative taskforce of stakeholders (**Action 1**) that (i) work to maintain rigorous biosecurity (**Actions 3 and 6**, Table 2, Fig. 4), (ii) educate Macquarie Island expeditioners, tourists and the general public about the island-wide dieback (**Action 2**, Table 2, Fig. 4), and (iii) momentum for the recovery of the species and the ecosystem, remains important as a well-accepted and effective recovery actions (see Mawdsley et al. 2009).

The preservation of genetic material *ex situ*, both in a seedbank (**Action 4**, Table 2, Fig. 4) and in *ex situ* populations or seed orchards (**Action 5 and 7**, Table 2, Fig. 4) are well accepted threatened flora recovery actions (Mawdsley et al. 2009; Broadhurst and Coates 2017; Monks et al. 2019). The continued, unmitigated decline of *A. macquariensis* emphasises the importance of maintaining *ex situ* collections to provide the ability to restore future populations, once the germination cues and propagation techniques are determined. Following extensive effort, 4110 viable seeds from 365 individuals were banked by the Royal Tasmanian Botanical Gardens (RTBG), as part of the Australian Seed Bank Partnership (Perrins and Wood 2019). However, future work is required to increase the amount of banked seed to the ideal 10-20,000 seeds, particularly as this seed will be needed for future conservation research and recovery actions. Preliminary germination trials of *A. macquariensis* at RTBG and Royal Botanic Gardens Kew (Kew, England) has been unsuccessful, similarly the species could not be propagated or maintained as an *ex situ* population of translocated individuals from Macquarie Island on mainland Australia (L. Perrins RTBG, pers. comm., October 2019). Dedicated expertise and resources is required at both RTBG and Kew to address the germination and propagation knowledge gaps. Consequently, the ongoing maintenance of the *ex situ* ‘seed-orchard’ (54 potted and watered individuals) on the isolated Macquarie Island headland, away from naturally occurring cushions and dieback (Perrins and Wood 2019), remains vitally important as a source of seed and genetic material for future conservation actions (**Action 5**) (see Broadhurst and Coates 2017). The seed-orchard is particularly important while continued research is still needed to successfully establish and maintain an *ex situ* population on the Australian mainland (**Action 7**, Table 2, Fig. 4).

Following a decade of research, monitoring programs (Table 3), special management areas (SMAs, **Action 6**, Table 2, Fig. 4) and policy documents (**Action 8**, Table 2, Fig. 4) need to be updated. For example, a clear monitoring program needs to be identified, that occurs biennially, including both dieback and cushion cover variables to identify loss of cushion cover from the system (Dickson et al. 2019). Further, to determine the rate of change of *A. macquariensis* populations and the associated abiotic conditions on the fellfield, refined cushion condition classes, associated grassland cover and microclimate data need to be included in the current monitoring program (see Box 1, Chapter 3). Future work is required to determine whether current scale of microclimate data (27 m²) is the appropriate resolution. The three current SMAs (reduced from 10, **Action 6**) were designated to prevent disturbance to the most extensive and highest conservation value sites for *A. macquariensis* (TSS 2012). Surveys in 2017 confirmed that sites within the SMAs (n = 4 of 90) still contained some of the healthiest and most extensive populations island-wide (Dickson et al. 2018, updated 2018a). It is recommended that with the identification of dieback correlates, freezing days and extreme humidity (Chapter 2), the SMAs boundaries are refined and additional locations that may serve as cushion refugia from dieback are identified. The use of special management areas (exclusion zones) and hygiene procedures is still considered the most effective management tool for addressing or slowing the spread of disease on a landscape-scale (Monks et al. 2019).

The federal and state conservation advice for *A. macquariensis* were rapidly prepared following the identification of island-wide dieback in 2008/2009 (TSSC 2010b; TSS 2012). However, the advice is now considerably out-of-date following the large increase in scientific knowledge about cushion dieback, and the response of the associated fellfield ecosystem to regional climate change (**Action 8**, Table 2, Fig. 4). National recovery plans are considered the main tool for threatened species recovery, identifying the biological understanding of the species, key threatening processes, required recovery actions and associated budget (Stewart et al. 2018), with the aim of improving the conservation status of a species (Bottrill et al. 2011). While a national recovery plan for the cushion plant is recommended (TSS 2012), the value of single species plans are being increasingly questioned (Bottrill et al. 2011), especially given the extensive preparation time required. Therefore, given the shared objectives of *A. macquariensis* stakeholders it is recommended to update the current *EPBC Act 1999* Conservation Advice, providing a current but succinct document to guide management, with the application of specific, measurable, achievable, realistic and timely (SMART) objectives and prioritised actions (**Action 8**, Table 2, Fig. 4).

Table 3. Recommended *Azorella macquariensis* and fellfield research priorities, * indicates that action is not dependant, but will benefit from the suggested research. Thesis chapters with additional rationale indicated by ‘Ch’. Abbreviations include: Macquarie Island (MI), Southern Ocean Islands (SOI).

Research topic	Values protected	Objectives	Required research	Associated recovery actions
A Identification of pathogen/s	Species, ecosystem	<ul style="list-style-type: none"> Identify pathogen/s and test other flora species’ susceptibility under different environmental conditions to enable appropriate management actions on MI and across the sub-Antarctic. 	i. Pathogen/s or consortium of microbes identified (Ch3). ii. Confirmation of causality (Koch’s postulates) (Ch3). iii. Susceptibility of <i>A. selago</i> to the pathogen/s. iv. Susceptibility of other SOI flora to the pathogens. v. Increased understanding of why only <i>A. macquariensis</i> & <i>Pleurophyllum hookeri</i> are susceptible on MI. vi. Susceptibility of other <i>Azorella</i> species to the pathogens. vii. Refine understanding about physiological and environmental drivers of disease.	*3, *6, *7, *8, *9, 10, 11, 12, 13, 14, 15.
B Germination and propagation	Species, ecosystem	<ul style="list-style-type: none"> Successfully germinate and propagate <i>A. macquariensis</i> for <i>ex situ</i> cultivation, population supplementation and translocation. 	i. Germination cues. ii. Propagation techniques.	7, *8, 10, 11, 12, 13, 14.
C Population monitoring	Species, ecosystem	<ul style="list-style-type: none"> Identify the rate of decline and potential recovery in <i>A. macquariensis</i> condition and the associated fellfield ecosystem. Quantify the rate of spread of the short-grassland upslope under current climate conditions. 	i. Biennial monitoring undertaken to identify current population trends, including total cover and detailed condition classes (Ch2) to identify rate of decline and recovery of <i>A. macquariensis</i> (Ch3). ii. Test hypothesised cushion condition state-transition paths (Ch3).	*8, *9

Research topic	Values protected	Objectives	Required research	Associated recovery actions
			<ul style="list-style-type: none"> iii. Quantification of change in <i>A. macquariensis</i> cover since 2010 using aerial analysis and image analysis (Bergstrom et al. in press). iv. Model spread of disease and predicted rate of change under future climate models. v. Quantify rate of short-grassland encroachment into the historical distribution of the fellfield (Ch3). vi. Development of qualitative <i>Azorella</i>-dominated short-grassland model (Ch3). vii. Estimation of quantitative ecosystem thresholds (Ch3). viii. Baseline research to improve ecological understanding of <i>A. macquariensis</i>, i.e. pollination rates, seed production, growth, time to maturity. ix. Clarification of the importance of refined soil properties (e.g. soil texture, soil organic matter, fine particles) and water holding capacity in relation to <i>A. macquariensis</i> root architecture. 	
D Microclimate monitoring	Species, ecosystem	<ul style="list-style-type: none"> • Identify changes in microclimate conditions on MI to provide an advanced warning of future disease trends. 	<ul style="list-style-type: none"> i. Biennial island-wide microclimate modelling (Ch2). ii. Test the importance of microclimate scale. Is the current 27 m² resolution appropriate or does it need to be refined 1 m². 	*8, *9
E Identification and development of resistant traits	Species, ecosystem	<ul style="list-style-type: none"> • Identify phenotypic and/or genotypic traits in <i>A. macquariensis</i> resistant to disease for use in future population supplementation. 	<ul style="list-style-type: none"> i. Identify phenotypic or genotypic traits resistant to both disease and water-stress in <i>A. macquariensis</i>, <i>A. selago</i> and <i>P. hookeri</i>. 	*8, 11, 12

Research topic	Values protected	Objectives	Required research	Associated recovery actions
			ii. Develop genetic resistance to disease in affected species through genomic editing techniques.	
F Pathogen control (fungal/chemical treatment)	Species, ecosystem	<ul style="list-style-type: none"> Determine the appropriate treatment and safe application rate for <i>A. macquariensis</i> and <i>P. hookeri</i> dieback to protect the areas of highest conservation value. 	i. Robust application trials, identifying effect on focal pathogen/s and the naturally occurring soil and plant microbes of MI. ii. Rigorous trial of treatment on surrounding flora.	*8, 13

Increased scientific knowledge about the decline of the dominant keystone cushion plant and associated fellfield ecosystem also provides the ability to adequately assess the Macquarie Island fellfield under the IUCN Red-list of Ecosystems (RLE; **Action 9**, Table 2, Fig. 4). Other ecosystems have also been RLE-listed based on a similar pathogen (*Phytophthora cinnamomi*) threat that is changing the structure of the community and the limited geographic distribution of the community (see Barrett and Yates 2015). RLE provides an important management tool that systematically classifies the ecosystem against defined criteria, importantly ecosystems classified as critically endangered or endangered are also considered ‘matters of national environmental significance (NES)’ under the *EPBC Act 1999* (Bland et al. 2019). RLE-listing would provide the remote Macquarie Island fellfield with increased recognition as a matter of NES, ensuring that it was considered a management priority within policy documents, with the potential to increase strategic implementation of management objectives and heighten public awareness (see Bland et al. 2019).

b. Potential recovery actions to be considered, yet to be attempted (moderate to high risk, Actions 10 - 15)

Action 10: Assisted migration of A. macquariensis to Southern Ocean Island (objective: species)

Translocation of species threatened by intractable threats (such as climate change or novel pathogens) to local or regional refugia are increasingly used to enable the species’ persistence (Mawdsley et al. 2009; Monks et al. 2019). Translocations outside of the indigenous range of the species are considered ‘assisted migration’ (Hoegh-Guldberg et al. 2008), although to-date assisted migrations have rarely been implemented in Australia (Silcock et al. 2019). The assisted migration of endemic *A. macquariensis* to another Southern Ocean Island (SOI) with similar site conditions may represent the only opportunity to maintain an *ex situ* population off Macquarie Island (**Action 10**, Table 2, Fig. 4), as *A. macquariensis* cannot be currently maintained on the Australian mainland despite specifically designed housing at the RTBG (L. Perrins RTBG, pers. comm., October 2019). To ensure that the assisted migration was successful a translocation plan that identifies key features of the host site, risks to mitigated and ongoing management actions needed should be prepared (see Commander et al. 2018; Silcock et al. 2019). In the sub-Antarctic those sites suitable would likely correspond with the distribution of sister species, *A. selago* Hook (see Huntley 1972), of which only Heard and McDonald Islands occur within Australian territory.

However, the assisted migration of *A. macquariensis* to other SOIs currently carries a high risk of (i) inadvertently bringing the pathogens to the host site with translocated individuals from Macquarie Island, and (ii) the potential of hybridisation between the wind-pollinated *A. macquariensis* and *A. selago* (see Hoegh-Guldberg et al. 2008). Currently the pathogens causing cushion dieback are unknown, as is the susceptibility of other SOIs species to the pathogen, including the closely related *A. selago*. These knowledge gaps are considered a high research priority (Table 3). Despite the current and anticipated continued decline in cushion cover with projected climate change (Chapter 2), similar to other species affected by pathogens, *A. macquariensis* is unlikely to be extirpated by the pathogen across the extent of its range (see pathogen ‘trade-off theory’ Alizon et al. 2009)), rather reduced to an understory species with low cover (Bergstrom et al. in press). Using the decision framework for assisted migrations under climate change of Hoegh-Guldberg et al. (2008), the comparatively low likelihood of island-wide *A. macquariensis* extinction, current risks, and the logistical and political challenge working between SOIs, mean that *A. macquariensis* is not currently recommended for assisted migration. However, assisted migration for *A. macquariensis* should be revisited if the likelihood of island-wide extinction increases over time.

Action 11: Propagation and restoration with resistant A. macquariensis phenotypes/genotypes (objectives: species and ecosystem function)

The lowest risk recovery action with the potential to maintain both *A. macquariensis* and fellfield ecosystem function is the identification and breeding of pathogen ‘field resistance’ in cushions for future restoration of collapsed sites (**Action 11**, Table 2, Fig. 4). Cushion and stem necrosis following the chlorosis line affects cushions to differing extents, ranging from complete rosette death (condition ‘black’) to a proportion of rosette or leaf death (‘thinning’) (Chapter 2 and 3). The necrosis of leaves or proportion of leaves may be caused by programmed cell death, a defence action seen in other plant species in response to Oomycete pathogens (Wang et al. 2019). While the variation of leaf loss may be explained by field resistance (individual or population tolerance) to disease through varying genetic characteristics or other localised environmental conditions (see Cahill et al. 2008). Cushions are highly variable across populations, both in plastic traits (i.e. form and leaf area) and the likely fixed traits (spine and stomatal density) (Dickson et al. 2018, updated 2018b). However, the relationship between morphological traits and dieback has not yet been tested. Despite showing no spatial genetic structure, *A. macquariensis* contains some genetic differentiation between populations, and has

a higher genetic diversity than sister species *A. selago* on Marion Island (Chau et al. 2019), providing some potential for genotypic disease resistance to occur.

Selective breeding for disease resistance is well implemented in cultivated crops, livestock and managed fisheries (e.g. Butcher et al. 1984; Nelson et al. 2017; Elaswad and Dunham 2018), however, it has also been used with varying levels of success in some wild populations (see Santos et al. 2015). For example, breeding resistance to Dutch Elm disease (current primary pathogen *Ophiostoma novo-ulmi*) is the most effective method to ensure European elm (*Elmus* sp.) persistence, although this has required intensive research over a 90 year period in multiple countries to adapt to and manage the changing focal pathogens (Martín et al. 2019). In Australia *P. cinnamomi* resistance in clonal *Eucalyptus marginata* seedlings has been developed from selective breeding of field resistant individuals, which is now used as the basis of a seed orchard for eventual use at restoration sites (Stukely et al. 2007). Currently the mechanisms for the *P. cinnamomi* resistance in the *E. marginata* clones is not well understood, nor has field resistance been developed for any of the many other species affected by the pathogen (Cahill et al. 2008). Despite this, identifying and breeding genetic resistance to *P. cinnamomi* is still considered an important area for future research, to improve the conservation outlook for susceptible species (Cahill et al. 2008; Sena et al. 2018). Similarly, despite the challenges identifying *A. macquariensis* genetic resistance, this provides a valuable area to consider for future research, providing the possibility to both sustain *A. macquariensis* and therefore maintain the associated fellfield ecosystem function. It is recognised that this will require substantial research effort to not only identify resistant genotypes, but also simultaneously identify germination and propagation techniques (Table 3).

Action 12. Pathogen resistance through genetic modification (objectives: species and ecosystem function)

Recent advances in genomic editing technologies provide the potential to address intractable conservation threats, such as developing control methods for invasive organisms or pathogens (Johnson et al. 2016; Piaggio et al. 2017) and genetic resistance to plant pathogens in natural systems (Sena et al. 2018). Genomic editing technologies (i.e.. clustered regularly interspaced short palindromic repeats, CRISPR-Cas9), provide an efficient method to target genes, eliminating the time needed for trials with resistance breeding (Yin and Qiu 2019). This technology has been successfully used to create resistance in crop species including, rice to rice bacterial blight (*Xanthomonas oryzae* pv. *oryzae*, Li et al. 2012), citrus species to citrus canker (*Xanthomonas citri* subsp. *citri*, Peng et al. 2017) and wheat to powdery mildew

(*Blumeria graminis* f. sp. *tritici*, Zhang et al. 2017). However, this technology requires that the full host genome has been described and that molecular information about the target gene is available (Yin and Qiu 2019), which similar to many non-commercial species, is not available for *A. macquariensis*. While providing new potential solutions, conservation concerns have been raised about the ethics of such technologies that have the ability to rapidly facilitate evolutionary processes, fundamentally changing a species and its biotic interactions (Webber et al. 2015) and the conservation effectivity of the technology when the target gene/s are unknown (Kardos and Shafer 2018). The development of *A. macquariensis* genetic resistance to the current pathogen using genomic editing (**Action 12**, Table 2, Fig. 4) would require considerable research, as the cushion's genome would have to be described, pathogens and target genes identified, similarly it also assumes that *A. macquariensis* can be readily propagated and maintained *ex situ*. It is therefore not considered a high priority for implementation. However, as capabilities in the genomic editing technology field rapidly develop, this action should be reassessed over time with the progression of propagation techniques.

Action 13. Pathogen control (fungicide/chemical application) (objective: species and ecosystem function)

Chemical control of invasive pathogens in natural ecosystems is considered an important management tool for protecting high-value areas or individuals (**Action 13**, Table 2, Fig. 4). However, it is considered currently unfeasible at a broad-scale because of the associated costs and off-target environmental and health concerns (Martín et al. 2019; Monks et al. 2019). Potassium phosphonate (phosphite) has been used to successfully reduce the susceptibility of threatened species to *Phytophthora cinnamomi*, and thereby reducing the associated impact on diversity and structure of a critically endangered ecosystem in Western Australia (Barrett and Yates 2015; Barrett and Rathbone 2018). However, the ongoing aerial application is expensive, with frequent reapplications necessary, and therefore is only considered as a viable option for high-value natural areas (Barrett and Rathbone 2018). Similarly, *P. cinnamomi* was successfully contained and eradicated from small areas using a combination of resource-intensive techniques, fungicide, host removal and fumigation (Dunstan et al. 2010). The highly intensive nature of pathogen control or eradication means the managers need to be judicious with its use (Monks et al. 2019). On Macquarie Island cushion dieback occurs island-wide (128 km²), however, prioritisation of the highest conservation value sites for pathogen control is highly recommended, focussing on the *Azorella* special management areas (SMAs) in the south

of the island. Similar to ongoing research on controlling *P. cinnamomi*, rigorous trials are required to both identify control techniques and the potential for off-target damage to Macquarie Island ecological (including microbial or fungal) communities. To progress this recovery action, the identification of the *A. macquariensis* pathogens and germination and propagation techniques are simultaneously required (Table 3).

Actions 14. and 15. Assisted migration of A. selago or South American Azorella species to MI (objective: ecosystem function)

The on-going *A. macquariensis* dieback is persistently removing cover and biomass of this keystone species from the fellfield, resulting in localised ecosystem collapse in northern areas and loss of iconic terrace formations associated with the species (Chapter 3; Bergstrom et al. in press). Currently the pathogens remain unidentified (Bergstrom et al. 2015) and the other associated management actions require further research, suggesting that dieback may continue unabated into the near future. To maintain ecosystem function, and thereby maintain the iconic terrace structures and biotic diversity on the fellfield, translocating an analogous species to fill the same ecological niche is a conceivable option (**Actions 14 and 15**, Table 2, Fig. 4). The creation of a hybrid novel ecosystem, which while primarily valuing ecosystem function, aims to maintain historical ecosystem components and processes wherever possible (Higgs 2017). Ecological replacements or functional analogues have been used to successfully restore biotic interactions and fulfil keystone roles, for plants by using the pollen fossil record to identify and restore locally extinct species (Wood et al. 2017) and for animals, in high-profile rewilding projects (Griffiths et al. 2011; Wood et al. 2017; Seddon and Armstrong 2019). The assisted migration of an ecological replacement species into comparatively intact natural ecosystems, such as the World Heritage Macquarie Island, is likely to be controversial (see Seddon and Armstrong 2019). However, Macquarie Island has experienced vegetation change in the past, with large fluctuations of rabbits resulting in grazing pressure and erosion across the island (see Terauds et al. 2014). The highest associated risks of using an ecological replacement to maintain ecosystem function are the (i) unanticipated ecological effects, where the species occupies a different ecological niche, resulting in negative effects on the recipient site and outcompeting native species, (ii) introduction of another novel pathogen, or (iii) inability of the ecological replacement to establish (Seddon and Armstrong 2019). However, if other recovery actions prove unviable, the alternative is to not intervene, which under the current climate trajectory will result in the pervasive erosion of *A. macquariensis* cover from ongoing

dieback, either removing it from the landscape or reducing it to a non-dominant species depending on site conditions (see Dickson et al. 2019, Chapter 3).

Two potential ecological replacement species are the morphologically more robust sub-Antarctic *A. selago* and a South American species, such as *A. compacta* Phil. (Ilareta). Both cushions, *A. selago* (McGeoch et al. 2008; le Roux and McGeoch 2010) and *A. compacta* (Anthelme et al. 2017) are similarly considered keystone species, facilitating biotic diversity and concentrating resources. *Azorella selago* is also known from terraces on Heard and Îles Kerguelen, albeit not as well developed as on Macquarie Island (Selkirk-Bell and Selkirk 2013). It is unknown whether these species would be similarly susceptible to the pathogens. However, the close phylogenetic relatedness between *A. macquariensis* and *A. selago*, which are the only members of the Cirrhosae clade (Plunkett and Nicolas 2017) and both formerly described within *A. selago* (Orchard 1989), suggests that *A. selago* is also likely to be susceptible to the pathogen. *Azorella compacta* (clade Laretia; Plunkett and Nicolas 2017) is one of many South American *Azorella* and *Mulinum* species that are well known source of diterpenoids used in natural and pharmaceutical medicines (Bórquez et al. 2016), including for their antibacterial properties (Wächter et al. 1999). The more distant level of phylogenetic relatedness and the high presence of diterpenoids may potentially provide *A. compacta* with some resistance to the pathogen, and provide a potential species to be investigated for use as an ecological replacement on Macquarie Island.

All suggested assisted migration projects should be regarded as long-term commitments that require the co-operation of multiple government agencies (including international) in remote locations, with biological challenges. While *A. compacta* can be readily germinated and is sold as seed to the general public, *A. selago* (as is the case with *A. macquariensis*) cannot currently be germinated, as the ripening and germination cues remain unknown (Frénét and Gloaguen 1994). Despite some variability, all three *Azorella* species are slow growing. The growth rate of *A. macquariensis* has been estimated at 6.4 mm.yr⁻¹ (Taylor 1955a), with very slow phenology (Bergstrom et al. 1997). *A. selago* grows radially < 56 mm.yr⁻¹ (Frénét et al. 1993; le Roux and McGeoch 2004), while *A. compacta* grew only 17 mm.14 months⁻¹ (Kleier et al. 2015). These growth rates indicate that they would likely require extensive time to establish and reinstate the historical level of cover required to restore ecosystem function and thus would need to be managed over the long-term. The logistical challenge of undertaking assisted migrations on remote SOIs highlights the importance of creating a successful self-sustaining population with the required number of propagules. To capture > 95% of the genetic diversity

within a population, successful translocations require > 50 individuals, with the secondary goal of >1000 individuals within several generations (Weeks et al. 2011). Furthermore, a review of Australian translocations indicates that for translocations to be successful with active recruitment, a sufficient number of individuals is a necessity (ideally > 1000), suggesting that if this number is unachievable then the action should be reconsidered (Silcock et al. 2019).

While the assisted migration of another *Azorella* species to Macquarie Island has merit as one of the few ways to maintain fellfield ecosystem function and is recommended for consideration, careful planning needs to be undertaken. This includes formal translocation plans (see Commander et al. 2018; Silcock et al. 2019), and trials assess *A. selago* and *A. compacta* for their susceptibility to the pathogen and suitability for the Macquarie Island fellfield ecosystem.

The way forward – urgency of simultaneously implementing research with bold actions

One decade after island-wide dieback was first identified in the keystone species *A. macquariensis*, dieback remains pervasive (Dickson et al. 2019) and is causing localised ecosystem collapse (Chapter 3). This decline in species condition, and by extension reduction of ecosystem function, is occurring despite a substantial increase in understanding about the drivers of dieback (Fig. 2) and the previously implemented management and policy actions (Fig. 4). While the continuation of existing passive and low-risk recovery actions is considered a high priority to sustain management momentum and protect *ex situ* genetic material, they do not address the threat of ongoing island-wide dieback. Under the current climate projection, the currently implemented actions or a ‘business as usual’ approach, will likely result in island-wide fellfield regime change over the long-term, based on the current trajectory of dieback (Chapter 2, Chapter 3). Bolder actions are required to address cushion dieback and maintain the Macquarie Island fellfield ecosystem function under the novel climate threat (see Hoeppepner and Hughes 2019).

A diverse range of recovery actions were identified that have the potential to secure *A. macquariensis ex situ* populations and maintain ecosystem function (Table 2). These actions were given a prioritisation level for implementation and were recommended for consideration by conservation managers within the current management context. However, all actions with the ability to affect change required key research gaps to be addressed before they can be fully implemented (Table 2, cross-referencing Table 3). The most urgent research priorities were

considered to be the identification of the pathogen (Table 3.A), and *A. macquariensis* germination and propagation techniques (Table 3.B), as they are required to implement the highest number of recovery actions able to effect lasting change. While beyond the scope of this study, the monitoring and review of recovery actions is a critical component of StDM (Fig. 1.vi) and adaptive management, particularly when implementing recovery actions with some level of uncertainty (Gregory et al. 2013). Consequently, ongoing *A. macquariensis* population (Table 3.C) and microclimate (Table 3.D) monitoring and associated research is considered critical, to improve understanding of the cushion and fellfield response to ongoing climate change and implement recovery actions.

The iconic patterned *Azorella*-dominated fellfield ecosystem is an evocative landscape of the windswept World Heritage Macquarie Island, containing some of the best global examples of vegetation-terraces. The island-wide dieback of the endemic *A. macquariensis* likely signals the start of an island-wide fellfield regime change over the long-term, and represents the first species to respond to climate change on a landscape-scale in the sub-Antarctic (Chapter 2). To preserve the function of the fellfield ecosystem, as currently described, there is an urgent need to begin research, to identify the pathogen and propagate *A. macquariensis*. However, it is important to ensure that recovery actions and research are undertaken simultaneously, and that research, or lack thereof, to address uncertainty is not used as a justification for inaction (see Hoeppe and Hughes 2019). The *Azorella* multi-agency taskforce has a strong history of working together collaboratively, simultaneously undertaking a rapid management and research response (Bergstrom et al. 2015). This ability of multiple government and research institutions to rapidly respond together provides optimism for the identification of future solutions and timely implementation, to conserve *A. macquariensis* and the fellfield ecosystem under future climate change projections.

References

- Adams, N., 2009. Climate trends at Macquarie Island and expectations of future climate change in the sub-Antarctic. *Papers and proceedings of the Royal Society of Tasmania* 143, 1-8.
- Alizon, S., Hurford, A., Mideo, N., Van Baalen, M., 2009. Virulence evolution and the trade-off hypothesis: history, current state of affairs and the future. *Journal of Evolutionary Biology* 22, 245-259.
- Anthelme, F., Meneses, R.I., Huaman Valero, N.N., Pozo, P., Dangles, O., 2017. Fine nurse variations explain discrepancies in the stress-interaction relationship in alpine regions. *Oikos* 126, 1173-1183.
- Ashton, D.H., Gill, A.M., 1965. Pattern and Process in a Macquarie island Feldmark. *Proceedings Of The Royal Society Of Victoria* 79, 235-248.
- Baker, D.J., Dickson, C.R., Bergstrom, D.M., Whinam, J., McGeoch, M.A., unpublished. Are microrefugia likely to exist as conservation features for cold-adapted species across the sub-Antarctic islands? xx xx, xx.
- Barrett, S., Rathbone, D., 2018. Long-term phosphite application maintains species assemblages, richness and structure of plant communities invaded by *Phytophthora cinnamomi*. *Austral Ecology* 43, 360-374.
- Barrett, S., Yates, C.J., 2015. Risks to a mountain summit ecosystem with endemic biota in southwestern Australia. *Austral Ecology* 40, 423-432.
- Bergstrom, D.M., 2013, updated 2014. Macquarie Is. *Azorella* dieback 5 m x 5 m quadrats 2008-2012, ed. Australian Antarctic Data Centre - CAASM Metadata., <http://dx.doi.org/10.4225/15/50FF1931B92C1>.
- Bergstrom, D.M., Bricher, P.K., Raymond, B., Terauds, A., Doley, D., McGeoch, M.A., (. . .) Ball, M.C., 2015. Rapid collapse of a sub-Antarctic alpine ecosystem: the role of climate and pathogens. *Journal of Applied Ecology* 52, 774-783.
- Bergstrom, D.M., Chown, S.L., 1999. Life at the front: history, ecology and change on southern ocean islands. *Trends in Ecology & Evolution* 14, 472-477.
- Bergstrom, D.M., Dickson, C.R., Baker, D.J., Whinam, J., Selkirk, P.M., McGeoch, M.A., in press. Ecosystem collapse on a sub-Antarctic island, In *Ecosystem Collapse and Climate Change*. eds J.G. Canadell, R.B. Jackson, p. xxx. Ecological Studies, Springer-Nature, xxxx.
- Bergstrom, D.M., Lucieer, A., Kiefer, K., Wasley, J., Belbin, L., Pedersen, T.K., Chown, S.L., 2009. Indirect effects of invasive species removal devastate World Heritage Island. *Journal of Applied Ecology* 46, 73-81.

- Bergstrom, D.M., Selkirk, P.M., Keenan, H.M., Wilson, M.E., 1997. Reproductive behaviour of ten flowering plant species on subantarctic Macquarie Island. *Opera Botanica* 132, 109-120.
- Bland, L.M., Nicholson, E., Miller, R.M., Andrade, A., Carré, A., Etter, A., (. . .) Keith, D.A., 2019. Impacts of the IUCN Red List of Ecosystems on conservation policy and practice. *Conservation Letters* 0, e12666.
- Bórquez, J., Bartolucci, N.L., Echiburú-Chau, C., Winterhalter, P., Vallejos, J., Jerz, G., Simirgiotis, M.J., 2016. Isolation of cytotoxic diterpenoids from the Chilean medicinal plant *Azorella compacta* Phil from the Atacama Desert by high-speed counter-current chromatography. *Journal of the Science of Food and Agriculture* 96, 2832-2838.
- Bottrill, M.C., Walsh, J.C., Watson, J.E.M., Joseph, L.N., Ortega-Argueta, A., Possingham, H.P., 2011. Does recovery planning improve the status of threatened species? *Biological Conservation* 144, 1595-1601.
- Bricher, P.K., Lucieer, A., Shaw, J., Terauds, A., Bergstrom, D.M., 2013. Mapping Sub-Antarctic Cushion Plants Using Random Forests to Combine Very High Resolution Satellite Imagery and Terrain Modelling. *Plos One* 8, 1-15.
- Broadhurst, L., Coates, D., 2017. Plant conservation in Australia: Current directions and future challenges. *Plant Diversity* 39, 348-356.
- Burgess, T.I., Scott, J.K., McDougall, K.L., Stukely, M.J.C., Crane, C., Dunstan, W.A., (. . .) Hardy, G.E.S.J., 2017. Current and projected global distribution of *Phytophthora cinnamomi*, one of the world's worst plant pathogens. *Global Change Biology* 23, 1661-1674.
- Butcher, T.B., Stukely, M.J.C., Chester, G.W., 1984. Genetic variation in resistance of *Pinus radiata* to *Phytophthora cinnamomi*. *Forest Ecology and Management* 8, 197-220.
- Cahill, D.M., Rookes, J.E., Wilson, B.A., Gibson, L., McDougall, K.L., 2008. *Phytophthora cinnamomi* and Australia's biodiversity: impacts, predictions and progress towards control. *Australian Journal of Botany* 56, 279-310.
- Chapuis, J.L., Frénot, Y., Lebouvier, M., 2004. Recovery of native plant communities after eradication of rabbits from the subantarctic Kerguelen Islands, and influence of climate change. *Biological Conservation* 117, 167-179.
- Chau, J.H., Born, C., McGeoch, M.A., Bergstrom, D., Shaw, J., Terauds, A., (. . .) Jansen van Vuuren, B., 2019. The influence of landscape, climate and history on spatial genetic patterns in keystone plants (*Azorella*) on sub-Antarctic islands. *Molecular Ecology* 28, 3291-3305.

- Comfort, M.D., 2014. Macquarie Island World Heritage Area Geoconservation Strategy, In Nature Conservation Report Series 14/2. Resource Management and Conservation Division, Department of Primary Industries Parks Water and Environment, Hobart.
- Commander, L.E., Coates, D., Broadhurst, L., Offord, C.A., Makinson, R.O., Matthes, M., 2018. Guidelines for the translocation of threatened plants in Australia. Third Edition. Australian Network for Plant Conservation, Canberra.
- Conroy, M.J., Runge, M.C., Nichols, J.D., Stodola, K.W., Cooper, R.J., 2011. Conservation in the face of climate change: The roles of alternative models, monitoring, and adaptation in confronting and reducing uncertainty. *Biological Conservation* 144, 1204-1213.
- Cook, C.N., Mascia, M.B., Schwartz, M.W., Possingham, H.P., Fuller, R.A., 2013. Achieving Conservation Science that Bridges the Knowledge–Action Boundary. *Conservation Biology* 27, 669-678.
- Delach, A., Caldas, A., Edson, K., Krehbiel, R., Murray, S., Theoharides, K., (. . .) Miller, J.R.B., 2019. Agency plans are inadequate to conserve US endangered species under climate change. *bioRxiv*, 647396.
- Dickson, C.R., Baker, D.J., Bergstrom, D.M., Bricher, P.K., Brookes, R.H., Raymond, B., (. . .) McGeoch, M.A., 2019. Spatial variation in the ongoing and widespread decline of keystone plant species. *Austral Ecology* 44, 891-905.
- Dickson, C.R., Baker, D.J., Bergstrom, D.M., Whinam, J., McGeoch, M.A., 2018, updated 2018a. *Azorella macquariensis* condition and site topographic values, ed. Australian Antarctic Data Centre - CAASM Metadata., <http://dx.doi.org/doi:10.26179/5bf382d899d95>.
- Dickson, C.R., Bergstrom, D.M., Whinam, J., McGeoch, M.A., 2018, updated 2018b. *Azorella macquariensis* leaf trait database, ed. Australian Antarctic Data Centre - CAASM Metadata., <http://dx.doi.org/doi:10.26179/5bf37ba81fd4e>.
- Dunstan, W.A., Rudman, T., Shearer, B.L., Moore, N.A., Paap, T., Calver, M.C., (. . .) Hardy, G.E.S.J., 2010. Containment and spot eradication of a highly destructive, invasive plant pathogen (*Phytophthora cinnamomi*) in natural ecosystems. *Biological Invasions* 12, 913-925.
- Elaswad, A., Dunham, R., 2018. Disease reduction in aquaculture with genetic and genomic technology: current and future approaches. *Reviews in Aquaculture* 10, 876-898.
- Frénét, Y., Chown, S.L., Whinam, J., Selkirk, P.M., Convey, P., Skotnicki, M., Bergstrom, D.M., 2005. Biological invasions in the Antarctic: extent, impacts and implications. *Biological Reviews* 80, 45-72.

- Frénôt, Y., Gloaguen, J.C., 1994. Reproductive-performance of native and alien colonizing phanerogams on a glacier foreland, Iles Kerguelen. *Polar Biology* 14, 473-481.
- Frénôt, Y., Gloaguen, J.C., Picot, G., Bougere, J., Benjamin, D., 1993. *Azorella selago* Hook - used to estimate glacier fluctuations and climatic history in the Kerguelen Islands over the last 2 centuries. *Oecologia* 95, 140-144.
- Garrett, K.A., Nita, M., De Wolf, E.D., Esker, P.D., Gomez-Montano, L., Sparks, A.H., 2016. Chapter 21 - Plant Pathogens as Indicators of Climate Change, In *Climate Change* (Second Edition). ed. T.M. Letcher, pp. 325-338. Elsevier, Boston.
- Gillson, L., Dawson, T.P., Jack, S., McGeoch, M.A., 2013. Accommodating climate change contingencies in conservation strategy. *Trends in Ecology & Evolution* 28, 135-142.
- Gregory, R., Arvai, J., Gerber, L.R., 2013. Structuring Decisions for Managing Threatened and Endangered Species in a Changing Climate. *Conservation Biology* 27, 1212-1221.
- Gregory, R., Failing, L., Harston, G., Long, G., McDaniels, T., Ohlson, D., 2012. Structured decision making: A practical guide to environmental management choices. Wiley-Blackwell, Chichester, West Sussex.
- Griffiths, Christine J., Hansen, Dennis M., Jones, Carl G., Zuël, N., Harris, S., 2011. Resurrecting Extinct Interactions with Extant Substitutes. *Current Biology* 21, 762-765.
- Hagerman, S.M., Satterfield, T., 2013. Entangled judgments: Expert preferences for adapting biodiversity conservation to climate change. *Journal of Environmental Management* 129, 555-563.
- Harris, R.M.B., Beaumont, L.J., Vance, T.R., Tozer, C.R., Remenyi, T.A., Perkins-Kirkpatrick, S.E., (. . .) Bowman, D.M.J.S., 2018. Biological responses to the press and pulse of climate trends and extreme events. *Nature Climate Change* 8, 579-587.
- Harvell, C.D., Mitchell, C.E., Ward, J.R., Altizer, S., Dobson, A.P., Ostfeld, R.S., Samuel, M.D., 2002. Climate Warming and Disease Risks for Terrestrial and Marine Biota. *Science* 296, 2158-2162.
- Higgs, E., 2017. Novel and designed ecosystems. *Restoration Ecology* 25, 8-13.
- Hoberg, E.P., Brooks, D.R., 2015. Evolution in action: climate change, biodiversity dynamics and emerging infectious disease. *Philosophical Transactions of the Royal Society B: Biological Sciences* 370, 20130553.
- Hoegh-Guldberg, O., Hughes, L., McIntyre, S., Lindenmayer, D.B., Parmesan, C., Possingham, H.P., Thomas, C.D., 2008. Assisted Colonization and Rapid Climate Change. *Science* 321, 345-346.

- Hoepfner, J.M., Hughes, L., 2019. Climate readiness of recovery plans for threatened Australian species. *Conservation Biology* 33, 534-542.
- Hoffmann, A.A., Rymer, P.D., Byrne, M., Ruthrof, K.X., Whinam, J., McGeoch, M., (. . .) Williams, S.E., 2019. Impacts of recent climate change on terrestrial flora and fauna: Some emerging Australian examples. *Austral Ecology* 44, 3-27.
- Huntley, B.J., 1972. Notes on the ecology of *Azorella selago* Hook. f. *Journal of South African Botany* 38, 103-114.
- Johnson, J.A., Altwegg, R., Evans, D.M., Ewen, J.G., Gordon, I.J., Pettorelli, N., Young, J.K., 2016. Is there a future for genome-editing technologies in conservation? *Animal Conservation* 19, 97-101.
- Kardos, M., Shafer, A.B.A., 2018. The Peril of Gene-Targeted Conservation. *Trends in Ecology & Evolution* 33, 827-839.
- Kleier, C., Trenary, T., Graham, E.A., Stenzel, W., Rundel, P.W., 2015. Size class structure, growth rates, and orientation of the central Andean cushion *Azorella compacta*. *Peerj* 3, 1-14.
- Kueffer, C., Kaiser-Bunbury, C.N., 2014. Reconciling conflicting perspectives for biodiversity conservation in the Anthropocene. *Frontiers in Ecology and the Environment* 12, 131-137.
- le Roux, P.C., McGeoch, M.A., 2004. The use of size as an estimator of age in the subantarctic cushion plant, *Azorella selago* (Apiaceae). *Arctic Antarctic and Alpine Research* 36, 509-517.
- le Roux, P.C., McGeoch, M.A., 2008. Rapid range expansion and community reorganization in response to warming. *Global Change Biology* 14, 2950-2962.
- le Roux, P.C., McGeoch, M.A., 2010. Interaction intensity and importance along two stress gradients: adding shape to the stress-gradient hypothesis. *Oecologia* 162, 733-745.
- le Roux, P.C., McGeoch, M.A., Nyakatia, M.J., Chown, S.L., 2005. Effects of a short-term climate change experiment on a sub-Antarctic keystone plant species. *Global Change Biology* 11, 1628-1639.
- Li, T., Liu, B., Spalding, M.H., Weeks, D.P., Yang, B., 2012. High-efficiency TALEN-based gene editing produces disease-resistant rice. *Nature Biotechnology* 30, 390-392.
- Lindenmayer, D.B., Sato, C., 2018. Hidden collapse is driven by fire and logging in a socioecological forest ecosystem. *Proceedings of the National Academy of Sciences* 115, 5181-5186.

- Martín, J.A., Sobrino-Plata, J., Rodríguez-Calcerrada, J., Collada, C., Gil, L., 2019. Breeding and scientific advances in the fight against Dutch elm disease: Will they allow the use of elms in forest restoration? *New Forests* 50, 183-215.
- Mawdsley, J.R., O'Malley, R., Ojima, D.S., 2009. A Review of Climate-Change Adaptation Strategies for Wildlife Management and Biodiversity Conservation. *Conservation Biology* 23, 1080-1089.
- McGeoch, M.A., Le Roux, P.C., Hugo, E.A., Nyakatya, M.J., 2008. Spatial Variation in the Terrestrial Biotic System, In *The Prince Edward Islands: land-sea interactions in a changing ecosystem*. eds S. Chown, P.W. Froneman, pp. 245-276. African Sun Media, Stellenbosch, South Africa.
- Monks, L., Barrett, S., Beecham, B., Byrne, M., Chant, A., Coates, D., (. . .) Yates, C., 2019. Recovery of threatened plant species and their habitats in the biodiversity hotspot of the Southwest Australian Floristic Region. *Plant Diversity* 41, 59-74.
- Munné-Bosch, S., Alegre, L., 2004. Die and let live: leaf senescence contributes to plant survival under drought stress. *Functional Plant Biology* 31, 203-216.
- Nelson, R., Wiesner-Hanks, T., Wissner, R., Balint-Kurti, P., 2017. Navigating complexity to breed disease-resistant crops. *Nature Reviews Genetics* 19, 21-33.
- Orchard, A.E., 1989. *Azorella* Lamarck (Apiaceae) on Heard and Macquarie Islands, with description of a new species, *A. macquariensis*. *Muelleria* 7, 15-20.
- Panfylova, J., Ewen, J.G., Armstrong, D.P., 2019. Making structured decisions for reintroduced populations in the face of uncertainty. *Conservation Science and Practice* 1, e90.
- Parks and Wildlife Service, 2006. Macquarie Island Nature Reserve and World Heritage Area Management Plan, ed. Parks and Wildlife Service, Department of Tourism, Arts and the Environment, p. 189, Hobart, Australia.
- Pecl, G.T., Araújo, M.B., Bell, J.D., Blanchard, J., Bonebrake, T.C., Chen, I.-C., (. . .) Williams, S.E., 2017. Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. *Science* 355, eaai9214.
- Peng, A., Chen, S., Lei, T., Xu, L., He, Y., Wu, L., (. . .) Zou, X., 2017. Engineering canker-resistant plants through CRISPR/Cas9-targeted editing of the susceptibility gene CsLOB1 promoter in citrus. *Plant Biotechnology Journal* 15, 1509-1519.
- Perrins, L., Tapson, N., 2014. Conservation on a remote island: Safeguarding the Macquarie Island cushion plant (*Azorella macquariensis*). *Australasian Plant Conservation: Journal of the Australian Network for Plant Conservation* 22, 20-21.

- Perrins, L., Wood, J., 2019. News from the Australian Seed Bank Partnership: seed collecting way down south. *Australasian Plant Conservation* 28, 28-30.
- Piaggio, A.J., Segelbacher, G., Seddon, P.J., Alphey, L., Bennett, E.L., Carlson, R.H., (. . .) Wheeler, K., 2017. Is It Time for Synthetic Biodiversity Conservation? *Trends in Ecology & Evolution* 32, 97-107.
- Plunkett, G.M., Nicolas, A.N., 2017. Assessing *Azorella* (Apiaceae) and its allies: Phylogenetics and a new classification. *Brittonia* 69, 31-61.
- Prober, S.M., Doerr, V.A.J., Broadhurst, L.M., Williams, K.J., Dickson, F., 2019. Shifting the conservation paradigm: a synthesis of options for renovating nature under climate change. *Ecological Monographs* 89, e01333.
- Raath-Krüger, M.J., McGeoch, M.A., Schöb, C., Greve, M., le Roux, P.C., 2019. Positive plant–plant interactions expand the upper distributional limits of some vascular plant species. *Ecosphere* 10, e02820.
- Raymond, B., McInnes, J., Dambacher, J.M., Way, S., Bergstrom, D.M., 2011. Qualitative modelling of invasive species eradication on subantarctic Macquarie Island. *Journal of Applied Ecology* 48, 181-191.
- Robinson, L.M., Marzloff, M.P., van Putten, I., Pecl, G., Jennings, S., Nicol, S., (. . .) Frusher, S., 2019. Structured Decision-Making Identifies Effective Strategies and Potential Barriers for Ecosystem-Based Management of a Range-Extending Species in a Global Marine Hotspot. *Ecosystems*.
- Rolland, V., Bergstrom, D.M., Lenne, T., Bryant, G., Chen, H., Wolfe, J., (. . .) Ball, M.C., 2015. Easy Come, Easy Go: Capillary Forces Enable Rapid Refilling of Embolized Primary Xylem Vessels. *Plant Physiology* 168, 1636-1647.
- Russell, J.C., Kueffer, C., 2019. Island Biodiversity in the Anthropocene. *Annual Review of Environment and Resources* 44, 31-60.
- Santos, C., Machado, H., Correia, I., Gomes, F., Gomes-Laranjo, J., Costa, R., 2015. Phenotyping *Castanea* hybrids for *Phytophthora cinnamomi* resistance. *Plant Pathology* 64, 901-910.
- Scott, J.J., Kirkpatrick, J.B., 2008. Rabbits, landslips and vegetation change on the coastal slopes of subantarctic Macquarie Island, 1980-2007: implications for management. *Polar Biology* 31, 409-419.
- Scott, J.J., Kirkpatrick, J.B., 2013. Changes in the cover of plant species associated with climate change and grazing pressure on the Macquarie Island coastal slopes, 1980-2009. *Polar Biology* 36, 127-136.

- Seddon, P.J., Armstrong, D.P., 2019. The role of translocation in rewilding, In Rewilding. eds N. Pettorelli, S.M. Durant, J.T. du Toit, pp. 303-324. Cambridge University Press, Cambridge.
- Selkirk-Bell, J.M., Selkirk, P.M., 2013. Vegetation-Banked Terraces on Subantarctic Macquarie Island: a Reappraisal. *Arctic Antarctic and Alpine Research* 45, 261-274.
- Selkirk, J.M., 1998. Active vegetation-banked terraces on Macquarie island. *Zeitschrift Fur Geomorphologie* 42, 483-496.
- Selkirk, P.M., 2012. Plateau Vegetation On Sub-Antarctic Macquarie Island. *Papers and proceedings of the Royal Society of Tasmania* 146, 71-79.
- Selkirk, P.M., Seppelt, R.D., Selkirk, D.R., 1990. Subantarctic Macquarie Island: environment and biology. Cambridge Press University Press, Cambridge.
- Sena, K., Crocker, E., Vincelli, P., Barton, C., 2018. *Phytophthora cinnamomi* as a driver of forest change: Implications for conservation and management. *Forest Ecology and Management* 409, 799-807.
- Shaw, J., Terauds, A., 2013, updated 2016. Macquarie Island *Azorella* presence/absence data. From island wide plant survey 2010-11. Australian Antarctic Data Centre - CAASM Metadata., <http://dx.doi.org/doi:10.4225/15/57AAB3B6AFAEB>.
- Shoo, L.P., Hoffmann, A.A., Garnett, S., Pressey, R.L., Williams, Y.M., Taylor, M., (. . .) Williams, S.E., 2013. Making decisions to conserve species under climate change. *Climatic Change* 119, 239-246.
- Sierra-Almeida, A., Cavieres, L.A., Bravo, L.A., 2009. Freezing resistance varies within the growing season and with elevation in high-Andean species of central Chile. *New Phytologist* 182, 461-469.
- Silcock, J.L., Simmons, C.L., Monks, L., Dillon, R., Reiter, N., Jusaitis, M., (. . .) Coates, D.J., 2019. Threatened plant translocation in Australia: A review. *Biological Conservation* 236, 211-222.
- Sindel, B.M., Kristiansen, P.E., Wilson, S.C., Shaw, J.D., Williams, L.K., 2018. Managing invasive plants on sub-Antarctic Macquarie Island. *The Rangeland Journal* 39, 537-549.
- Springer, K., 2016. Methodology and challenges of a complex multi-species eradication in the sub-Antarctic and immediate effects of invasive species removal. *New Zealand Journal of Ecology* 40, 273-278.
- Stewart, B.A., Ford, B.M., Van Helden, B.E., Roberts, J.D., Close, P.G., Speldewinde, P.C., 2018. Incorporating climate change into recovery planning for threatened vertebrate species in southwestern Australia. *Biodiversity and Conservation* 27, 147-165.

- Stukely, M.J.C., Crane, C.E., McComb, J.A., Bennett, I.J., 2007. Field survival and growth of clonal, micropropagated *Eucalyptus marginata* selected for resistance to *Phytophthora cinnamomi*. *Forest Ecology and Management* 238, 330-334.
- Tapson, N., 2014. *Azorella macquariensis*: Battling for survival in the subantarctic. *Australasian Plant Conservation: Journal of the Australian Network for Plant Conservation* 23, 25-26.
- Taylor, B.W., 1955a. The flora, vegetation and soils of Macquarie Island., In ANARE Reports, Series B, 11. pp. 1-192. Australian Antarctic Division, Melbourne.
- Taylor, B.W., 1955b. Terrace Formation on Macquarie Island. *Journal of Ecology* 43, 133-137.
- Terauds, A., Doube, J., McKinlay, J., Springer, K., 2014. Using long-term population trends of an invasive herbivore to quantify the impact of management actions in the sub-Antarctic. *Polar Biology* 37, 833-843.
- TSS, 2012. Listing Statement for *Azorella macquariensis* (macquarie cushions). , ed. P. Department of Primary Industries, Water and Environment, Hobart, Tasmania. <https://dpiwve.tas.gov.au/Documents/Azorella-macquariensis-listing-statement.pdf>.
- TSSC, 2010a. Advice to the Minister for Environment Protection, Heritage and the Arts from the Threatened Species Scientific Committee (the Committee) on amendment to the list of threatened species under the Environmental Protection and Biodiversity Conservation Act 1999 (EPBC Act): *Azorella macquariensis* (Macquarie Cushions), ed. Department of Environment Protection, Heritage and the Arts, Canberra. <http://www.environment.gov.au/biodiversity/threatened/species/pubs/21846-listing-advice.pdf>.
- TSSC, 2010b. Approved conservation advice for *Azorella macquariensis* (Macquarie Cushions), ed. Department of Environment Protection, Heritage and the Arts, Canberra. <http://www.environment.gov.au/biodiversity/threatened/species/pubs/21846-conservation-advice.pdf>.
- Wächter, G.A., Matooq, G., Hoffmann, J.J., Maiese, W.M., Singh, M.P., Montenegro, G., Timmermann, B.N., 1999. Antibacterial Diterpenoid Acids from *Azorella compacta*. *Journal of Natural Products* 62, 1319-1321.
- Wang, Y., Tyler, B.M., Wang, Y., 2019. Defense and Counterdefense During Plant-Pathogenic Oomycete Infection. *Annual Review of Microbiology* 73, 667-696.
- Watson, J.E.M., Rao, M., Ai-Li, K., Yan, X., 2012. Climate Change Adaptation Planning for Biodiversity Conservation: A Review. *Advances in Climate Change Research* 3, 1-11.

- Webber, B.L., Raghu, S., Edwards, O.R., 2015. Opinion: Is CRISPR-based gene drive a biocontrol silver bullet or global conservation threat? *Proceedings of the National Academy of Sciences of the United States of America* 112, 10565-10567.
- Weeks, A.R., Sgro, C.M., Young, A.G., Frankham, R., Mitchell, N.J., Miller, K.A., (. . .) Hoffmann, A.A., 2011. Assessing the benefits and risks of translocations in changing environments: a genetic perspective. *Evolutionary Applications* 4, 709-725.
- Wheeler, J.A., Hoch, G., Cortés, A.J., Sedlacek, J., Wipf, S., Rixen, C., 2014. Increased spring freezing vulnerability for alpine shrubs under early snowmelt. *Oecologia* 175, 219-229.
- Whinam, J., Abdul-Rahman, J.A., Visoiu, M., di Folco, M.B.F., Kirkpatrick, J.B., 2014. Spatial and temporal variation in damage and dieback in a threatened subantarctic cushion species. *Australian Journal of Botany* 62, 10-21.
- Williams, L.K., Fergus, A.J., Shaw, J.D., Terauds, A., Kristiansen, P., Wilson, S.C., (. . .) Sindel, B.M., 2019. Quantifying site and species factors to inform the feasibility of eradication of alien plants from Southern Ocean Islands: *Stellaria media* on Macquarie Island. *Biological Invasions* 21, 993–1005.
- Williams, L.K., Kristiansen, P., Sindel, B.M., Wilson, S.C., Shaw, J.D., 2016. Quantifying the seed bank of an invasive grass in the sub-Antarctic: seed density, depth, persistence and viability. *Biological Invasions* 18, 2093-2106.
- Wood, J.R., Alcover, J.A., Blackburn, T.M., Bover, P., Duncan, R.P., Hume, J.P., (. . .) Wilmschurst, J.M., 2017. Island extinctions: processes, patterns, and potential for ecosystem restoration. *Environmental Conservation* 44, 348-358.
- Yin, K., Qiu, J.-L., 2019. Genome editing for plant disease resistance: applications and perspectives. *Philosophical Transactions of the Royal Society B: Biological Sciences* 374, 20180322.
- Zhang, Y., Bai, Y., Wu, G., Zou, S., Chen, Y., Gao, C., Tang, D., 2017. Simultaneous modification of three homoeologs of TaEDR1 by genome editing enhances powdery mildew resistance in wheat. *The Plant Journal* 91, 714-724.

Appendix D: Recommended recovery action status for *Azorella macquariensis* and the associated fellfield ecosystem on Macquarie Island.

Table D1.1 Recovery actions and status for *Azorella macquariensis* from the National Conservation Advice (EPBC) (TSSC 2010b) and the Tasmanian Threatened Species (TSS) Listing Statement (TSS 2012) categorised under the related recommended recovery actions from this study.

Recovery Action	National Conservation Listing Category	Source	Status
1. Education of stakeholders, and wider public			
<ul style="list-style-type: none"> Raise awareness of Macquarie Cushions with expeditioners on Macquarie Island through site visits, signage, and posters/information brochures. 	Community Information/Consultation	EPBC	Existing, to be maintained
2. Cooperation of stakeholders			
<ul style="list-style-type: none"> Maintain a co-operative program between the divisions of the Department of Primary Industries, Parks, Water and Environment, the Australian Antarctic Division and other research institutions to facilitate the conservation of the species. 		TSS	Existing, to be maintained
3. Biosecurity – off (inter) island			
<ul style="list-style-type: none"> Implement biosecurity controls to minimise the risk of spread of any pathogen that may be implicated in the dieback, from Macquarie to other subantarctic islands or to Tasmania 	Diseases and Alien Species	EPBC, TSS	Existing, to be maintained
<ul style="list-style-type: none"> Continue stringent biosecurity controls to prevent the introduction of alien species to Macquarie Island. 	Diseases and Alien Species	EPBC, TSS	Existing, to be maintained
4. Maintain seed bank			
<ul style="list-style-type: none"> Continue to undertake appropriate seed collection and storage. 	Recovery enabled	EPBC, TSS	Existing, to be maintained
5. Maintain isolated <i>ex situ</i> population on MI			
<ul style="list-style-type: none"> Supplement the collection of seed for long-term storage at the Tasmanian Seed Conservation Centre including establishing a seed orchard on Macquarie Island to overcome seed collection difficulties. 		TSS	Existing, to be maintained
6. Biosecurity – on island (special management areas, SMA)			
<ul style="list-style-type: none"> Develop and implement suitable hygiene protocols to protect known sites from further outbreaks of dieback. 	Diseases and Alien Species	EPBC	Existing, to be maintained

Recovery Action	National Conservation Listing Category	Source	Status
<ul style="list-style-type: none"> Minimise inappropriate disturbance in areas where Macquarie Cushions occurs. Determine the cause of the decline and implement appropriate control measures where possible. 	Habitat Loss, Disturbance and Modification	EPBC TSS	Existing, to be maintained To be refined
7. Establishment of <i>ex situ</i> population (Tas, Au)			
<ul style="list-style-type: none"> Continue to maintain live plants in cultivation. Establish a suitable facility to securely maintain <i>Azorella macquariensis</i> plants at the Royal Tasmanian Botanical Gardens. 	Recovery enabled	EPBC TSS	To be refined To be refined
8. Listing of Fellfield under IUCN Red List of Ecosystems and EPBC Act 1999			
<ul style="list-style-type: none"> Pursue the listing of the fellmark community on Macquarie Island under State and National legislation. 		TSS	Not yet attempted
9. National recovery plans for <i>A. macquariensis</i> and the fellfield ecosystem			
Develop a recovery plan.		TSS	Not yet attempted
10. 'Assisted migration' of <i>A. macquariensis</i> to SOI			
<ul style="list-style-type: none"> Investigate options for establishing additional populations. Implement national translocation protocols (Commander et al. 2018) if establishing additional populations is considered necessary and feasible. 	Recovery enabled Recovery enabled	EPBC EPBC	Not yet attempted Not yet attempted
11. Propagation & restoration of resistant phenotypes			
<ul style="list-style-type: none"> Develop potential <i>in situ</i> adaptation measures. 		TSS	Not yet attempted
12. Pathogen resistance through genetic modification			
13. Pathogen control (fungicide/chemical application)			
14. Assisted migration of <i>A. selago</i> to MI			
15. Assisted migration of suitable South American <i>Azorella sp.</i> to MI			

Recovery Action	National Conservation Listing Category	Source	Status
Actions included within research by this study			
• Monitor known populations to identify key threats.	Habitat Loss, Disturbance and Modification	EPBC	To be refined
• Monitor the progress of recovery, including the effectiveness of management actions and the need to adapt them if necessary.	Habitat Loss, Disturbance and Modification	EPBC	To be refined
• Monitor the impact on <i>Azorella macquariensis</i> over time and associated changes in the feldmark ecosystem		TSS	To be refined
• Monitor the progress of the dieback across the island and manage areas with low levels of dieback to minimise potential adverse impacts		TSS	To be refined
• Develop techniques to improve the condition of <i>ex situ</i> holdings and to propagate the species through tissue culture		TSS	To be refined
Actions complete or no longer applicable			
• Continue to implement the Macquarie Island pest eradication plan for the control and eradication of rabbits, rats and mice in the region.	Rabbit and rodent impacts	EPBC	Complete
• Where appropriate, manage rabbit and rodent impacts at important/significant sites through exclusion fencing or other barriers.	Rabbit and rodent impacts	EPBC	No longer applicable

General Discussion

The impact of climate change on biological systems is complex, varying depending on the species and combination of interacting drivers, and often results in an unexpected biological response (Parmesan and Hanley 2015). The resultant threats can appear intractable, operating on a landscape-scale with no clear solution. The ongoing island-wide dieback of *Azorella macquariensis* Orchard (Apiaceae, Macquarie cushions) on sub-Antarctic Macquarie Island in response to both direct and indirect climate threats is one such example, as demonstrated in my thesis. I show that similar to other systems, island-wide cushion dieback is not driven by one clear variable, but instead occurs in response to additive and compound climate drivers. Cushion dieback emerged immediately after an extensive period of high water-stress during the summer growing seasons that weakened *A. macquariensis* (Bergstrom et al. 2015). The current cushion dieback is now driven by an increasingly warm, winter saturated, and variable system. I used qualitative network modelling to illustrate the keystone interactions provided by *A. macquariensis* in the fellfield ecosystem and showed why the loss of this species from the fellfield will result in ecosystem collapse. Addressing landscape-scale pathogen- or drought-driven dieback in natural systems is particularly complex, with limited progress made over multiple decades, primarily through the development of increased resistance and containment, rather than eradication (Cahill et al. 2008; Garrett et al. 2016). I show that this may also be the case for *A. macquariensis*. As despite the previous decade of research and management actions resulting in an enhanced understanding of climate drivers of pathogen dieback and the complex interactions between *A. macquariensis* and the fellfield, dieback remains pervasive. Below I discuss the outcomes of my thesis, the need for bolder higher-intervention actions and the broader implications for dominant foundation species in high latitude and altitude regions.

High latitude regions have some of the fastest global warming rates (Field et al. 2014), and together with high altitude regions, are increasingly susceptible to novel pathogens with the associated reduction in extreme cold temperatures (Pauchard et al. 2016). The island-wide dieback of *A. macquariensis* and potential for island-wide ecosystem collapse is the first landscape-scale response to climate change and novel pathogens in the sub-Antarctic. However, large-scale dieback, or potentially early senescence, of *A. selago* in response to drought-like conditions was observed on several islands in Îles Kerguelen (Frénét et al. 1997), providing the first indication of the southern ocean islands' vegetation susceptibility to climate change. Outside of the sub-Antarctic, there are an increasing number of examples of novel pathogens in high altitude or latitude regions. For example, the damaging effects of the pathogen

Phytophthora cinnamomi have recently been found in new regions of alpine Australia (Green 2016), and it is expected to expand further into alpine regions globally with the reduction of extreme cold weather (Burgess et al. 2017). The increased susceptibility of high altitude or latitude sites to pathogens, combined with the increased mobility of people between countries and regions (Anderson et al. 2004), suggest that landscape-scale pathogen-driven dieback, similar to that described in this thesis on Macquarie Island, is increasingly likely.

It is unclear whether the pathogen/s on Macquarie Island are native or introduced. Previously the yellow chlorosis lines (that proceed necrosis) had only been observed in several isolated *A. macquariensis* cushions in the 1986-87, 1989-90 (Whinam et al. 2014) and 1998/99 Austral summers, before emerging island-wide in 2008/2009 (Bergstrom et al. 2015). Future research to identify the pathogen will hopefully clarify this, confirming whether it was (i) indigenous and previously latent on Macquarie Island, and potentially more widely present across the southern ocean islands, or (ii) introduced with scientists or managers prior to 1986, spread by biotic or abiotic vectors, and then ‘activated’ island-wide by regional climate change. Regardless, it emphasises the devastating consequence of these comparatively intractable threats once established. There is a need for much greater recognition by the scientific community, land managers and general public about the ease to which pathogens can be moved, the consequences, and the value of thorough hygiene procedures between sites, regions, and countries. Macquarie Island has proven to be the sentinel for both the southern ocean islands and more widely high altitude regions (see (Bergstrom and Chown 1999). Providing a clear example of the rapid rate that a novel pathogen can reduce the cover of a dominant foundation species, and demonstrates the susceptibility of islands with low topographic complexity and very little functional redundancy (see (Harter et al. 2015). The comparatively biotically simple Macquarie Island, with relatively few external impacts, provides a good opportunity to determine effective recovery actions to restore ecosystem function within collapsed areas of the fellfield (see (Bergstrom and Chown 1999).

Despite the complexity and often perceived intractable nature of many climate change driven threats, management decisions still need to be made (Hoepfner and Hughes 2019). If no decision is made and ‘business as usual’ management is continued, under projected climate change vulnerable ecosystems will likely continue along the same trajectory, ultimately resulting in ecosystem collapse. Globally, ecosystem collapse has substantial consequences for both biodiversity and human health through the reduction of ecosystem services, including provisioning (e.g. food, water), regulating (e.g. climate, flood, disease regulation), supporting

(e.g. soil formation, nutrient cycling) and cultural (e.g. aesthetic) services (van der Geest et al. 2019). This potential for loss of ecosystem services further supports the importance of the early detection of ecosystem decline, and the early implementation of intervention actions wherever possible. To effectively address climate change threats to vulnerable species and ecosystems, conservation managers will increasingly need to use high intervention management actions, which have a higher level of associated uncertainty and require the implementation of adaptive management (Hoeppner and Hughes 2019; Prober et al. 2019). Structured decision making (StDM) provides one decision framework to help managers make complex decisions (Gregory et al. 2013) and has been successfully used in threatened species management to address climate change pressures (Gregory et al. 2013; Robinson et al. 2019). StDM encourages managers to identify all potential solutions, including those outside their direct experience, to expose and explore the consequences of the solutions and the ‘trade-offs’ from different perspectives (Gregory et al. 2013). In this thesis, I used the first four steps of the StDM process to clarify the current conservation context for *A. macquariensis* and the associated fellfield ecosystem and then discussed the full range of recovery options available to maintain ecosystem function. The potential recovery actions I suggest, such as assisted migration or alleviating natural stressors (e.g. pathogen), are predominantly described as ‘climate-targeted’ options that ‘build adaptive capacity’ within the renovating climate change typology (Prober et al. 2019). The need for these types of actions within the typology recognises that to maintain fellfield ecosystem function under projected climate change, management actions will have to be increasingly high-intervention (see (Prober et al. 2019)).

The conservation value of abundant species and their contribution to ecosystem services is regularly under-estimated (Baker et al. 2019) until dramatic declines from large-scale threats are identified (Degrassi et al. 2019). This is particularly true for foundation species, described as dominant primary producers that characterise the system, facilitate the diversity of the surrounding species, and stabilise ecosystem processes (i.e. modulates fluxes in energy and nutrients) (Ellison 2019). Previously *A. macquariensis* has been described as a keystone species, including within this thesis. However, going forward it is suggested to change the terminology to foundation species, fitting the above description. *Azorella macquariensis* defines the structure of fellfield on Macquarie Island as the dominant vascular plant (Selkirk 2012), changing the biological diversity in and around it, and importantly also stabilising ecosystem processes by concentrating resources (Bergstrom et al. 2015), and comparable to other *Azorella* species, stabilising microclimate (see (Badano and Cavieres 2006; Nyakatya

and McGeoch 2008). Despite research on the iconic vegetation terraces and floristic diversity of the fellfield (i.e. Selkirk 2012; Selkirk-Bell and Selkirk 2013), similar to other foundation species, *A. macquariensis* only became a species of conservation and research interest following the initiation of island-wide dieback in 2008/09. It is also similarly threatened by complex threats, such as non-native species (pathogens) and climate change, which are invariably more cost-effective and successful to manage before they become established (see (Degrassi et al. 2019)).

In my thesis I have addressed the four components of the conceptual framework for the management of a foundation species, *A. macquariensis*, on the Macquarie Island fellfield ecosystem (see (Degrassi et al. 2019)). **(1) Provide evidence of the species as a foundation species:** *Azorella macquariensis* is the dominant vascular plant of the Macquarie Island fellfield, albeit highly variable in cover (Selkirk 2012; Dickson et al. 2019). It facilitates a greater diversity of microarthropods (Bergstrom et al. 2015) and similar to other *Azorella* species, facilitates the diversity (le Roux et al. 2013; Raath-Krüger et al. 2019) and abundance (Chapter 3) of vascular plants and reduces the extreme microclimate temperatures within the cushion (Taylor 1955). *Azorella macquariensis* is also a major component of the iconic vegetation terraces, that characterise the patterned fellfield ecosystem and represent the most extensive, well-developed vegetation terraces globally (Selkirk-Bell and Selkirk 2013). Hence, *A. macquariensis* contributes substantially to the ‘sense of place’, representative of wild landscapes across the island. **(2) Quantify ecosystem services:** *A. macquariensis* provides keystone interactions within the fellfield ecosystem, increasing soil organic carbon (Bergstrom et al. 2015) in a carbon poor ecosystem (Wilson et al. 2019), and concentrates nutrients similar to other *Azorella* species (see (Badano et al. 2006) facilitating biotic diversity. These keystone interactions are lost under advanced cushion dieback that removes cover from the system, resulting in localised ecosystem collapse (Chapter 3). **(3) Long-term comprehensive monitoring strategies:** this thesis refined the requirements for effective monitoring, with the development of refined cushion condition classes and use of microclimate data. The inclusion of these refined variables will allow the early identification of declining habitat condition, and the ability to quantify the rate of change of the fellfield ecosystem. Priorities for the long-term monitoring are outlined in Chapters 1-4. **(4) Conservation management:** The *A. macquariensis* cover-loss models (Chapter 1) show that under a worst case scenario, dependant on the spread of dieback and starting cover, *A. macquariensis* could be lost from the ecosystem within 30 years, resulting in the ecological collapse of the fellfield ecosystem

(Chapter 3). Chapter 4 synthesises the knowledge gained in this thesis with other research and international case studies, to provide a wide range of potential recovery actions for implementation, and emphasises the associated research required.

Conclusion

In conclusion, my thesis has shown that *A. macquariensis* dieback is pervasive, and is now a feature of the system (Fig. 1.i.a) that is potentially resulting in irreversible change (Fig. 1.i.b). I have identified multiple additive drivers of cushion dieback that are similarly associated with disease in other ecosystems (Fig. 1.ii.a), and have clear interactions (Fig. 1.ii.b). Macquarie Island has an increasingly conducive environment for pathogen activity, with an increasingly variable climate, which is 50 % wetter during the winter season (Bergstrom et al. 2015) and has significantly warmer maximum temperatures (Chapter 3). Natural cold refugia exist in the south of the island (Fig. 1.iii), which represents the best-case scenario for the species if recovery currently remains at very low levels. However, the low level of cushion recovery in combination with multiple feedback loops, represented as additional ‘waves’ of dieback and the natural movement of grasslands upslope, suggests that under current climate projections the situation for *A. macquariensis* and the fellfield ecosystem will continue to worsen (Fig. 1.iv). If we want to maintain the Macquarie Island fellfield and its ecosystem function, as currently described, then we need to integrate the knowledge gained (Fig. 1.v.a) to act rapidly. Recovery actions need to be bolder with higher levels of intervention and simultaneously integrated with research, to identify the pathogen/s and propagation techniques (Fig. 1.v.b). The experience of *A. macquariensis* dieback from an unknown climate-driven pathogen on Macquarie Island demonstrates the importance of (i) monitoring and developing an in-depth understanding of foundation species across the sub-Antarctic and Antarctic peninsula prior to the emergence of large-scale threats, to increase the likelihood of successful management through early intervention, and (ii) that rigorous inter-island quarantine procedures remain a very high priority to ensure that this disease is not inadvertently spread across the southern ocean islands or further afield.

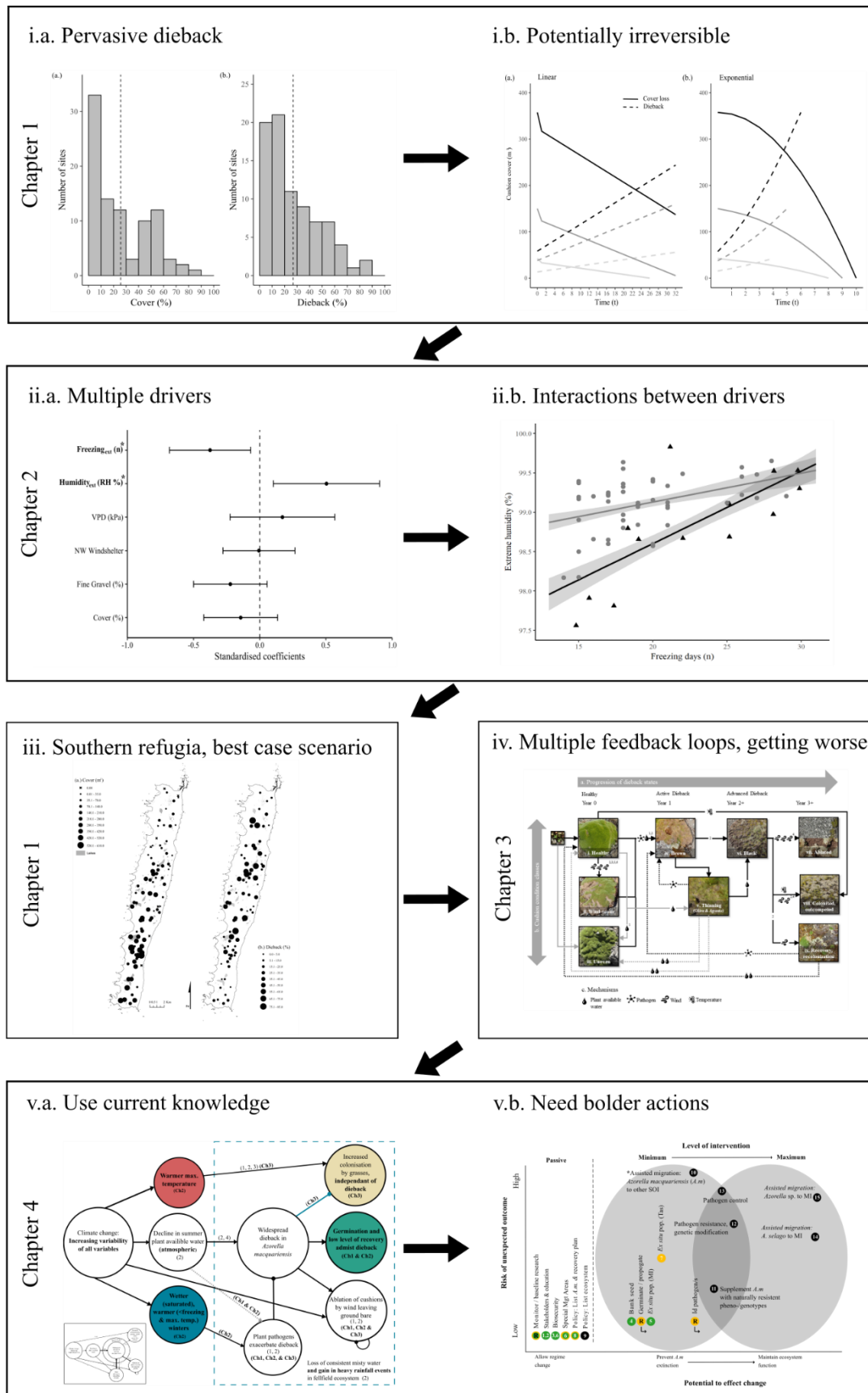


Fig. 1. Key findings of this thesis and relationships between thesis chapters, depicted on panels one (i.) through to five (v.).

References

- Anderson, P.K., Cunningham, A.A., Patel, N.G., Morales, F.J., Epstein, P.R., Daszak, P., 2004. Emerging infectious diseases of plants: pathogen pollution, climate change and agrotechnology drivers. *Trends in Ecology & Evolution* 19, 535-544.
- Badano, E.I., Cavieres, L.A., 2006. Impacts of ecosystem engineers on community attributes: effects of cushion plants at different elevations of the Chilean Andes. *Diversity and Distributions* 12, 388-396.
- Badano, E.I., Jones, C.G., Cavieres, L.A., Wright, J.P., 2006. Assessing impacts of ecosystem engineers on community organization: a general approach illustrated by effects of a high-Andean cushion plant. *Oikos* 115, 369-385.
- Baker, D.J., Garnett, S.T., O'Connor, J., Ehmke, G., Clarke, R.H., Woinarski, J.C.Z., McGeoch, M.A., 2019. Conserving the abundance of nonthreatened species. *Conservation Biology* 33, 319-328.
- Bergstrom, D.M., Bricher, P.K., Raymond, B., Terauds, A., Doley, D., McGeoch, M.A., (. . .) Ball, M.C., 2015. Rapid collapse of a sub-Antarctic alpine ecosystem: the role of climate and pathogens. *Journal of Applied Ecology* 52, 774-783.
- Bergstrom, D.M., Chown, S.L., 1999. Life at the front: history, ecology and change on southern ocean islands. *Trends in Ecology & Evolution* 14, 472-477.
- Burgess, T.I., Scott, J.K., McDougall, K.L., Stukely, M.J.C., Crane, C., Dunstan, W.A., (. . .) Hardy, G.E.S.J., 2017. Current and projected global distribution of *Phytophthora cinnamomi*, one of the world's worst plant pathogens. *Global Change Biology* 23, 1661-1674.
- Cahill, D.M., Rookes, J.E., Wilson, B.A., Gibson, L., McDougall, K.L., 2008. *Phytophthora cinnamomi* and Australia's biodiversity: impacts, predictions and progress towards control. *Australian Journal of Botany* 56, 279-310.
- Degrassi, A.L., Brantley, S., Levine, C.R., Mohan, J., Record, S., Tomback, D.F., Ellison, A.M., 2019. Loss of foundation species revisited: conceptual framework with lessons learned from eastern hemlock and whitebark pine. *Ecosphere* 10, e02917.
- Dickson, C.R., Baker, D.J., Bergstrom, D.M., Bricher, P.K., Brookes, R.H., Raymond, B., (. . .) McGeoch, M.A., 2019. Spatial variation in the ongoing and widespread decline of keystone plant species. *Austral Ecology* 44, 891-905.
- Ellison, A.M., 2019. Foundation Species, Non-trophic Interactions, and the Value of Being Common. *iScience* 13, 254-268.

- Field, C.B., Barros, V.R., Mach, K.J., Mastrandrea, M.D., Aalst, M.v., Adger, W.N., (. . .) Yohe, G.W., 2014. Technical Summary, In *Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part A: Global and Sectoral Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change.* eds C.B. Field, V.R. Barros, D.J. Dokken, K.J. Mach, M.D. Mastrandrea, T.E. Bilir, (. . .) L.L. White, pp. 35-94. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.
- Frénôt, Y., Gloaguen, J., Trehen, P., 1997. Climate change in Kerguelen Islands and colonization of recently deglaciated areas by *Poa Kerguelensis* and *P. annua*. Antarctic communities: species, structure and survival, B. Battaglia, J. Valencia et DWH Walton eds., Cambridge University Press, Cambridge, 358-366.
- Garrett, K.A., Nita, M., De Wolf, E.D., Esker, P.D., Gomez-Montano, L., Sparks, A.H., 2016. Chapter 21 - Plant Pathogens as Indicators of Climate Change, In *Climate Change (Second Edition)*. ed. T.M. Letcher, pp. 325-338. Elsevier, Boston.
- Green, K., 2016. Dieback of *Nematolepis ovatifolia* (Rutaceae), an endemic shrub in the alpine-subalpine heaths of the Snowy Mountains, is facilitated by climate change. *Cunninghamia* 16, 1-9.
- Gregory, R., Arvai, J., Gerber, L.R., 2013. Structuring Decisions for Managing Threatened and Endangered Species in a Changing Climate. *Conservation Biology* 27, 1212-1221.
- Harter, D.E.V., Irl, S.D.H., Seo, B., Steinbauer, M.J., Gillespie, R., Triantis, K.A., (. . .) Beierkuhnlein, C., 2015. Impacts of global climate change on the floras of oceanic islands – Projections, implications and current knowledge. *Perspectives in Plant Ecology, Evolution and Systematics* 17, 160-183.
- Hoeggner, J.M., Hughes, L., 2019. Climate readiness of recovery plans for threatened Australian species. *Conservation Biology* 33, 534-542.
- le Roux, P.C., Shaw, J.D., Chown, S.L., 2013. Ontogenetic shifts in plant interactions vary with environmental severity and affect population structure. *New Phytologist* 200, 241-250.
- Nyakatya, M.J., McGeoch, M.A., 2008. Temperature variation across Marion Island associated with a keystone plant species (*Azorella selago* Hook. (Apiaceae)). *Polar Biology* 31, 139-151.
- Parmesan, C., Hanley, M.E., 2015. Plants and climate change: complexities and surprises. *Annals of Botany* 116, 849-864.
- Pauchard, A., Milbau, A., Albiñ, A., Alexander, J., Burgess, T., Daehler, C., (. . .) Kueffer, C., 2016. Non-native and native organisms moving into high elevation and high latitude

- ecosystems in an era of climate change: new challenges for ecology and conservation. *Biological Invasions* 18, 345-353.
- Prober, S.M., Doerr, V.A.J., Broadhurst, L.M., Williams, K.J., Dickson, F., 2019. Shifting the conservation paradigm: a synthesis of options for renovating nature under climate change. *Ecological Monographs* 89, e01333.
- Raath-Krüger, M.J., McGeoch, M.A., Schöb, C., Greve, M., le Roux, P.C., 2019. Positive plant–plant interactions expand the upper distributional limits of some vascular plant species. *Ecosphere* 10, e02820.
- Robinson, L.M., Marzloff, M.P., van Putten, I., Pecl, G., Jennings, S., Nicol, S., (. . .) Frusher, S., 2019. Structured Decision-Making Identifies Effective Strategies and Potential Barriers for Ecosystem-Based Management of a Range-Extending Species in a Global Marine Hotspot. *Ecosystems*.
- Selkirk-Bell, J.M., Selkirk, P.M., 2013. Vegetation-Banked Terraces on Subantarctic Macquarie Island: a Reappraisal. *Arctic Antarctic and Alpine Research* 45, 261-274.
- Selkirk, P.M., 2012. Plateau Vegetation On Sub-Antarctic Macquarie Island. *Papers and proceedings of the Royal Society of Tasmania* 146, 71-79.
- Taylor, B.W., 1955. The flora, vegetation and soils of Macquarie Island., In *ANARE Reports, Series B*, 11. pp. 1-192. Australian Antarctic Division, Melbourne.
- van der Geest, K., de Sherbinin, A., Kienberger, S., Zommers, Z., Sitati, A., Roberts, E., James, R., 2019. The Impacts of Climate Change on Ecosystem Services and Resulting Losses and Damages to People and Society, In *Loss and Damage from Climate Change: Concepts, Methods and Policy Options*. eds R. Mechler, L.M. Bouwer, T. Schinko, S. Surminski, J. Linnerooth-Bayer, pp. 221-236. Springer International Publishing, Cham.
- Whinam, J., Abdul-Rahman, J.A., Visoiu, M., di Folco, M.B.F., Kirkpatrick, J.B., 2014. Spatial and temporal variation in damage and dieback in a threatened subantarctic cushion species. *Australian Journal of Botany* 62, 10-21.
- Wilson, B.R., Wilson, S.C., Sindel, B., Williams, L.K., Hawking, K.L., Shaw, J., (. . .) Kristiansen, P., 2019. Soil properties on sub-Antarctic Macquarie Island: Fundamental indicators of ecosystem function and potential change. *CATENA* 177, 167-179.