Widespread dieback in a foundation species on a sub-Antarctic World Heritage Island: Fine scale patterns and likely drivers

Authors:

Dickson, Catherine R. ^a, Baker, David J. ^a, Bergstrom, Dana M. ^b, Brookes, Rowan H. ^c, Whinam, Jennie ^d, McGeoch, Melodie A. ^a

Author affiliations:

^a School of Biological Sciences, Monash University, Clayton 3800, VIC, Australia.

cath.dickson@monash.edu, david.baker1@monash.edu, melodie.mcgeoch@monash.edu.

^b Australian Antarctic Division, Department of Agriculture, Water and the Environment, Kingston 7050, TAS, Australia. dana.bergstrom@awe.gov.au

^c Melbourne School for Professional and Continuing Education, The University of Melbourne, Melbourne 3010, Vic, Australia. rowan.brookes@unimelb.edu.au

^d School of Technology, Environments and Design, University of Tasmania, Hobart 7001, TAS, Australia. j.whinam@utas.edu.au

Corresponding author:

Catherine R. Dickson, School of Biological Sciences, Faculty of Science, 25 Rainforest Walk, Monash University, Clayton 3800, VIC, Australia, cath.dickson@monash.edu, +61 3 9905 0023

Acknowledgements and funding statement:

We thank Dr Patricia Selkirk and Dr Grant Duffy for constructive discussions about the manuscript, and John Burgess and Rowena Hannaford for assistance with field work. We thank the handling editor and reviewers for their comments on the manuscript. This study was funded by an Australian Government, Australian Antarctic Science Program Grant (#4312) and an Australian Government Research Training Program (RTP) Scholarship, the Holsworth Wildlife Research Endowment and The Ecological Society of Australia, and the Denis and Maisie Carr Award.

Data availability statement:

The data is archived at the Australian Antarctic Data Centre, <http://dx.doi.org/doi:10.26179/5e71aba2c846a>.

The metadata is currently available, however, until manuscript is published the dataset is embargoed.

Following publication the data will be released in full.

This is the author manuscript accepted for publication and has undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the [Version of Record](#). Please cite this article as [doi: 10.1111/AEC.12958](https://doi.org/10.1111/AEC.12958)

This article is protected by copyright. All rights reserved

Dickson C. R., McGeoch M. A., Bergstrom D. M., Whinam J. & Baker D. J. (2020) Fine-scale *Azorella macquariensis* condition and site microclimate extremes data from Macquarie Island, v1. (ed Australian Antarctic Data Centre - <http://dx.doi.org/doi:10.26179/5e71aba2c846a>).

Conflict of interest disclosure:

The authors declare there are no conflicts of interest associated with this publication.

Author Manuscript

DR. CATHERINE RUTH DICKSON (Orcid ID : 0000-0002-9701-346X)

Article type : Research Article

Widespread dieback in a foundation species on a sub-Antarctic World Heritage Island: Fine scale patterns and likely drivers

Abstract

Under anthropogenic climate change, emerging diseases and pathogens are increasingly prevalent in high latitude and altitude regions that were previously protected by cold winter temperatures. Ongoing island-wide dieback of a foundation species, the cushion plant *Azorella macquariensis*, on World Heritage listed Macquarie Island provides the first sub-Antarctic example. To better understand the island-wide progression of cushion dieback and its drivers, we established and quantified plant condition classes and measured microclimate across 62 sites. We then tested whether the drivers of cushion dieback were associated with (i) water-stress: represented by vapour pressure deficit, wind exposure and gravel content, (ii) pathogen virulence: using freezing days and extreme humidity as empirically supported surrogates, or (iii) both. There was a strong north-south progression in cushion condition, with dieback most active in the centre of the island and advanced in the north. Dieback was most extensive at sites with fewer freezing days and high humidity. Natural southern refugia were explained by the significantly colder temperatures, associated with a north-south temperature gradient. It is expected that under current climate change trajectories, where Macquarie is likely to continue to become warmer and wetter, cushion dieback will remain pervasive, expanding most slowly in the south and potentially outpacing recovery. We emphasise the need for increased awareness to prevent the establishment of pathogens into and across the landscapes of newly susceptible high latitude and altitude regions. Areas of

high conservation significance need to be prioritised for management, to prevent further landscape-scale change under current climate trajectories.

Keywords

Azorella, sub-Antarctic, climate change, pathogen, microclimate

Introduction

Natural World Heritage Sites (NWHS), inscribed for beauty and biological diversity, are increasingly threatened by the loss of dominant vegetation from intensifying human pressures (Allan et al. 2017). Instances of loss are occurring globally, including at NWHS sites with high levels of protection, due to pressures from pests and diseases emerging with climate change (Allan et al. 2017). Impacts from emerging diseases and pathogens are anticipated to continue to increase (Harvell et al. 2002; Hoberg and Brooks 2015). Under rapidly changing climate conditions, plants are maladapted to the threat of novel pathogens and can have little or no evolved resistance to them (Stenlid and Oliva 2016). In both agricultural and natural systems landscape-scale plant mortalities have often been associated with warmer and wetter conditions, where less extreme minimum temperatures and leaf surface wetness are increasing the prevalence of plant diseases and pests (Anderson et al. 2004; Garrett et al. 2016; Harvell et al. 2002). For example *Xylella fastidiosa* (Proteobacteria), a plant pathogen from the Americas with a broad host range, is predicted to expand further through Europe, and potentially globally, under future climate conditions (Sicard et al. 2018). Similarly, and despite being well protected, North American NWHS are considered to have the highest threat of dominant vegetation loss from an increase of Mountain pine beetle (*Dendroctonus ponderosae*) populations during years with higher minimum temperatures and reduced precipitation (Preisler et al. 2012). The negative consequences of these increasing pathogen and pest footprints are likely to be severe for biodiversity (Harvell et al. 2002) and ecosystem services (Boyd et al. 2013).

Higher elevation and latitude sites are particularly susceptible to novel pathogens as historically cold climates become warmer and experience fewer extreme cold events (Pauchard et al. 2016). The increasingly mild winter conditions and lack of extreme cold events allows for higher pathogen survival in several plant species, suggesting disease severity is likely to increase in the future (see Harvell et al. 2002). In these regions, cold-adapted plant species may be increasingly susceptible to disease under higher temperatures

and changing disease communities (Cohen et al. 2019). For example, in response to climate change crop pathogens have moved on average $2.7 \pm 0.8 \text{ km yr}^{-1}$ poleward since 1960, increasing their global footprint and threatening future food security (Bebber et al. 2013). In natural systems, 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 active island-wide pathogenic dieback of the dominant alpine species *Azorella macquariensis* Orchard (Apiaceae, Macquarie cushions) on the natural World Heritage site (NWHS) of Macquarie Island (Bergstrom et al. 2015; Whinam et al. 2014) is now the first occurrence of landscape-scale dieback and large-scale loss of vegetation cover in the sub-Antarctic (Fig. 1). The trigger for *A. macquariensis* dieback was hypothesised to be a reduction in plant available water over 17 summer growing seasons, facilitating a secondary pathogenic infection of weakened plants (Bergstrom et al. 2015). A wide range of microbes with pathogenic potential have been identified in association with *A. macquariensis*, and to date the most likely disease causing agent is considered to be a fungus in the genus *Rosellinia* (Bergstrom et al. 2015). However, the relationship between climate conditions, pathogen associated symptoms and cushion plant decline remains poorly understood. It is also unclear whether ongoing dieback is driven by conditions that; (i) continue to place the plant under water stress during the summer growing season; (ii) are conducive to pathogens during winter, which coincide with *A. macquariensis* dormancy; or (iii) promote a combination of these 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 apparently not well adapted to the increased evapotranspiration rates on the island and increased variability in climate (Bergstrom et al. 2015). If water stress alone is driving dieback, this suggests that the highest proportion of dieback would be found in areas of highest abiotic ‘stress’ on the island. Topographic modelling (i.e. using topography as a proxy for local climate conditions) of *A. macquariensis* dieback showed latitude (N-S location on island) to be a significant predictor of plant condition. However, it shed little additional light on the possible microscale conditions associated with spatially highly variable patterns of plant decline (Dickson et al. 2019).

Plant distribution and condition responds to fine-scale climate 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 and progression of disease (see Bland et al. 2018; Sato

and Lindenmayer 2018). Similarly, the fine-scale response of plants to climate (Körner and Hiltbrunner 2018) means 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 (Lembrechts et al. 2019). 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). 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 current dieback progression at a landscape scale and determine future management recommendations, here we test if there is a relationship between fine-scale plant location 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 with 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 by Dickson et al. (2019), here we use microclimate and fine-scale cushion condition classes to further tease apart these putative drivers of dieback. The implications of the results are discussed in the context of the future persistence and management of this critically endangered foundation species under projected climate change.

Methods

Study system

Macquarie Island (54°30'S, 158°55'E) is an oceanic sub-Antarctic island covering 123.9 km² (c. 34 km long, c. 5 km wide) (Fig. 2), with an undulating alpine plateau at 200 and 433 m asl. (Selkirk et al. 1990). Historically the local climate has been cool (av. 4.8°C), misty (relative humidity, RH 89%, rainfall 895 mm yr⁻¹) and windy (9.3 ms⁻¹), with very low daily variation (Selkirk et al. 1990). However, significant change in the regional climate have occurred since the 1970s, including an increase in sunshine hours and the average wind speeds (Bergstrom et al. 2015), and also more frequent and stronger cyclonic events (Adams 2009). The average temperature increased by 0.6°C up until the late 1990s (Tweedie and Bergstrom 2000), however, the mean warming trend became increasingly ambiguous from the 1980s with a number of cooler years recorded (Pendlebury and Barnes-Keoghan 2007). There has been a 35% increase in annual rainfall between the 1970s and 2010s, which includes a 55% increase in winter rainfall (Bergstrom et al. 2015). However, the higher number of annual sunshine hours implies that generally the rainfall is more episodic, with larger rainfall events interspersed by longer periods of dry conditions. Together 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* ranges in form from discrete cushions, extensive mats, and distinctive terraces (Selkirk 2012). *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) (Bergstrom et al. 2015; Taylor 1955). *A. macquariensis* is a foundation species (see Ellison 2019), defining the structure of fellfield on Macquarie Island (Selkirk 2012), local micro-arthropod diversity, and importantly stabilising ecosystem processes by concentrating soil organic carbon (Bergstrom et al. 2015) and reducing variability and extreme temperatures within its canopy (Taylor 1955). Comparable with other large cushion-forming *Azorella* species, *A. macquariensis* is also likely to stabilise moisture content, temperature, and facilitate vascular flora diversity and cover (see 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 plateau (Fig. 2). The survey coincided 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 that 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 15 m radius (~700 m²) site, six plots (2 m x 1 m) were positioned across representative cover and condition of *A. macquariensis*. Each plot consisted of two immediately adjacent 1 x 1 m quadrats, which were photographed from directly above for image analysis.

Microclimate and terrain variables

Macquarie Island only has one permanent weather station (1.5 m above the ground). The weather station is considered unrepresentative of the alpine plateau because it is located at sea level on the northern most part of the island (Tweedie and Bergstrom 2000). A fine-scale network of temperature data-loggers were deployed over a 12 month timeframe to capture the influence of terrain and habitat complexity on the free-air microclimate (see Körner and Hiltbrunner 2018; Lembrechts et al. 2019). 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 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*. Data loggers were located on bare ground near to cushion plants to ensure the microclimate measured was experienced by the cushion plants and not the microclimate created by it. Data loggers recorded temperature (°C) and relative humidity (RH%), every four hours (0300, 0700, 1100, 1500, 1900, 2100). This measured the free-air microclimate, not the cushion surface temperatures, which are acknowledged to reach much higher temperatures (see Bramley-Alves et al. 2014).

Microclimate variables chosen for analysis are those 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

This article is protected by copyright. All rights reserved

variable was calculated for the active summer growing season (October – March) of *A. macquariensis* (see Bergstrom et al. 2015; Taylor 1955).

Soil pits were dug to 250 mm (approximate *A. macquariensis* root zone) at each site to characterise soil texture and gravel proportions, as potential determinants of *A. macquariensis* cover and condition. A visual estimate of the proportion of fine gravel (6 – 2 mm) was taken (following methods in Sonter et al. 2000). Additional terrain variables that were likely to affect plant stress or growth were derived from the 5 × 5m Macquarie Island digital elevation model (DEM; Brolsma 2008), including northwest and southwest wind shelter (the inverse of wind exposure) (Table 1). Terrain variables were calculated using SAGA (Conrad et al. 2015) and the RSAGA package (Brenning et al. 2018). For dataset, see Dickson et al. (2020).

Condition classes

Four *A. macquariensis* condition classes and eight subclasses were distinguished and described to enable comparison of cushion condition across sites: (1) ‘healthy’ (subclasses: ‘smooth’, ‘uneven’, ‘*Agrostis*’); (2) ‘wind-scour’; (3) ‘dieback’ (subclasses: ‘brown’, ‘olive’, ‘black’, ‘ablated’, ‘dieback with *Agrostis*’); and (4) ‘recovery’ (Full description see Table S1.1., Appendix S1). The overall ‘healthy’ and ‘dieback’ classes were described as the sum of the three and five individual subclasses, respectively. Three dieback progression classes were described to capture the approximate time since pathogenic infection and subsequent senescence of the leaves and canopy. These were defined as: ‘active’ dieback (‘brown’, ≤ one year since infection), ‘thinning’ dieback (‘olive’ + ‘dieback with *Agrostis*’, approximately one to two years since infection) and ‘advanced’ dieback (‘black’ + ‘ablated’, ≥ two years since infection) (Table S1.1., Appendix S1).

The total *A. macquariensis* cover and the proportion of each subclass was delineated for each quadrat (1 m²) and subsequently measured in ImageJ 1.52i (Rueden et al. 2017). The proportion of each condition class per site (12 × 1 m² quadrats) was calculated as the total of the class in each plot divided by cover. The mean (± 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). For detailed methods see Appendix S1 and dataset availability see Dickson et al. (2020).

Regional condition and microclimate

The island was divided into three equal latitudinal regions, northern, central, and southern, in line with natural breaks in geology and elevation. To determine whether there was a relationship between the proportion of *A. macquariensis* within each cushion condition class and 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 post hoc 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 of the three dieback progression classes.

To determine if there was a significant relationship between summer growing season (Oct - Mar) 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 summer vapour pressure deficit (VPD, kPa) and summer freezing_{ext} (days with temperatures below 0 °C) were log-transformed, and summer 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.

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 microclimate temperature and the covariates latitude and elevation was modelled using a general linear model (similar to Córdova et al. (2016), i.e temperature = latitude + elevation). Models were run for the summer (Oct – Mar) and winter (Apr – Sep) seasons for each of the different temperature variables to capture aspects of daily variation (i.e. the daily mean, T_{mean} ; mean daily minimum, T_{min} ; and mean daily maximum, T_{max} for both seasons). 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.

245 The variables used to model the relationship between in situ summer microclimate variables
246 and the proportion of *A. macquariensis* cover affected by dieback across Macquarie Island
247 included, (i) variables previously suggested to stress the plants or promote pathogen virulence
248 and extent, and (ii) relevant terrain variables from Dickson et al. (2019) (wind shelter and soil
249 gravel content). *Azorella macquariensis* takes up most water through fine adventitious roots
250 within the canopy (Bergstrom et al. 2015), sourcing water from rainfall and low cloud that
251 condenses on the leaves. Therefore other potential proxies for atmospheric water, such as
252 cloud cover, cloud height and wind direction (moisture), were considered, however, they
253 would necessarily be topographically-derived and subject to the limitations identified in
254 Dickson et al. (2019). Soil moisture is an important determinant of plant water stress, which
255 we partially account for by incorporating gravel content in the models as a proxy for water
256 holding capacity. However, given the reliance of *A. macquariensis* on water sourced through
257 fine adventitious canopy roots (Bergstrom et al. 2015) and the lack of relationship between
258 cushion dieback and topographically-derived wetness index (Dickson et al. 2015), other soil
259 moisture variables were not included in the model. To reduce collinearity, microclimate
260 variable choice was informed by an exploratory principal component analysis (PCA, prcomp,
261 in 'stats' package). Summer (growing season) variables included in the models represented
262 the three main axes of the PCA (i) freezing_{ext}, representing cold_{ext}, (ii) humidity_{ext}
263 representing dry_{ext} (negative relationship), and (iii) VPD representing hot_{ext} and affecting
264 water availability.

265 The effect of microclimate on island-wide *A. macquariensis* dieback was modelled as the
266 proportion of Dieback class as a function of (i) summer microclimate conditions that may
267 affect pathogen activity, including freezing_{ext} and humidity_{ext} (%), (ii) variables that are likely
268 to influence plant available water, including summer VPD (Pa), Fine_Gravel (%) and
269 Wind_Shelter_{nw} (no units) and (iii) the covariate *A. macquariensis* cover (Cover,%). No
270 strong non-linear relationships between Dieback and predictor variables were identified in
271 preliminary analysis using Generalized Additive Models (GAM; family = beta, link = logit)
272 with smoothing applied to each of the predictor variables (mgcv; Wood 2017). Consequently,
273 no polynomial terms were included. Dieback (0 – 1) was modelled using a beta regression
274 model with a logit link function (betareg; Zeileis et al. 2016). The variance inflation factors
275 (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 zero to 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. The response curve was plotted for each predictor variable within the surveyed range, 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' (Peng 2019) in R.

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 model was described as $\text{humidity}_{\text{ext}}$ as a function of $\text{freezing}_{\text{ext}}$ with an interaction of the binary dieback class.

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 summer microclimate variables quantifying extremes (5th or 95th percentile) recorded during the growing season and selected for inclusion within models, $\text{freezing}_{\text{ext}}$ ($F_{2,59} = 17.13$, $p < 0.001$) and cold_{ext} ($F_{2,59} = 6.50$, $p < 0.01$) differed significantly between the three regions (Fig. 3). The number of summer southern $\text{freezing}_{\text{ext}}$ days was significantly higher than the number of northern ($p < 0.001$) and central ($p < 0.001$) freezing days (Fig. 3), however, there was no significant difference between the north and centre. Similarly, summer cold_{ext} ($r = -0.79$ with $\text{freezing}_{\text{ext}}$) was lower in the south than both the centre and north of the island ($p = 0.002$, $p = 0.03$, respectively; Fig. 3). Mean annual, summer growing season (Oct – Mar) and winter senescence season (Apr – Sep) microclimate statistics are presented in Table S2.1, Appendix S2.

There was a significant temperature lapse and latitudinal gradient for T_{mean} , T_{min} , and T_{max} for all three time periods (annual, summer growing season and winter senescence season). All

three temperature variables were significantly lower at high elevation sites for all three time periods and significantly colder towards the south for all variables but annual and summer $T_{\max}$ (Table S2.2, Appendix S2). 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 ± 0.19 °C 100 m⁻¹) and lowest for $T_{\min}$ (-0.58 ± 0.06 °C 100 m⁻¹) over the summer growing season (Table S2.2; Appendix S2). The latitudinal temperature gradient down the full extent of the island was highest during the summer growing season (change in T_{mean} north to south = -0.49 ± 0.15 °C) and lowest during winter (change in $T_{\min}$ north to south = -0.12 ± 0.06 °C) (Table S2.1, Appendix S2).

Cushion condition

Approximately two-thirds (67.8%, ± 3.19 s.e.) of the island-wide cushion cover was Healthy, with the highest proportion occurring in the south (Table S1.2., Appendix S1). Wind-scour and Recovery classes were very minor components of cushion cover ($< 2\%$); details are presented in detail in Appendix S1.

Across the island almost one third (29.66%, ± 3.08 s.e.) of cushion cover was affected by Dieback (Table 2). It differed significantly between the regions ($X^2 = 6.67$, $\text{df} = 2$, $p = 0.04$), 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. S1.1. Appendix S1). Dieback was 32% higher in the north ($47.3\% \pm 5.84$) than in the south ($15.2\% \pm 4.62$; Table S1.2., Appendix S1).

Azorella macquariensis affected by Dieback (%) was predicted by the summer microclimate variables, $\text{humidity}_{\text{ext}}$ and $\text{freezing}_{\text{ext}}$ ($\text{Pseudo-R}^2 = 0.27$, Fig. 4a, Table S2.3a, Appendix S2). Dieback was higher in sites with fewer $\text{freezing}_{\text{ext}}$ days and higher $\text{humidity}_{\text{ext}}$ (Fig. 4a. and Fig. S2.1. Appendix S2). Variables related to water-stress (NW wind shelter, fine gravel content, summer VPD) and the co-variate *A. macquariensis* cover were not significant in the dieback model (Fig. 4a, Table S2.3a, Appendix S2). The interaction between summer $\text{freezing}_{\text{ext}}$ and the presence of the healthy cushions ($< 5\%$ dieback) was significant (Table S2.3b., Appendix S2, $p = 0.002$), revealing a comparatively narrow band of conditions between summer $\text{humidity}_{\text{ext}}$ and summer $\text{freezing}_{\text{ext}}$ where healthy cushions ($< 5\%$ dieback) were present on the island (Fig. 4b). Healthy cushions were present at sites with low $\text{freezing}_{\text{ext}}$ days if $\text{humidity}_{\text{ext}}$ was also comparatively low, or alternatively could tolerate high $\text{humidity}_{\text{ext}}$ if $\text{freezing}_{\text{ext}}$ days were also high during the summer season (Fig. 4b).

Advanced dieback affected the most cushion cover of the three progression classes ($13.72\% \pm 2.50$ s.e., Fig. 2, Table S1.2. Appendix S1), differing between all 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. 2, Table S1.2. Appendix S1). Advanced dieback was considerably higher in the north, increasing from $2.5\% (\pm 0.84$ s.e.) cover in the south to $34.4\% (\pm 6.82$ s.e.) in the north (Fig. 2, Table S1.2. Appendix S1). Island-wide Thinning affected $12.96\% (\pm 1.83$ s.e.) of cushion cover. The least common progression class, Active dieback, affected $< 3.0\% (\pm 0.77$ s.e.) of cushion cover island-wide, highest in the centre ($5.3\% \pm 1.5$ s.e.) and lowest in the south ($0.9\% \pm 0.47$ s.e.) (Table S1.2. Appendix S1, Fig. 2). Neither Active nor Thinning dieback varied significantly between regions ($X^2 = 4.40$, $df = 2$, $p = 0.11$; $X^2 = 1.71$, $p = 0.43$, $df = 2$ respectively; Fig. 2).

Discussion

Azorella macquariensis dieback remains active across Macquarie Island, with dieback condition classes affecting almost one third of the critically endangered cushion cover island-wide. A north-south gradient in cushion condition is present, where advanced dieback was highest in the north, active dieback in the centre, and the extensive southern populations were healthiest. *Azorella macquariensis* dieback extent was best 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 few 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 the extensive southern populations on the island. 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, while the summer growing season drought-like conditions (Bergstrom et al. 2015) may have triggered the initial outbreak of dieback across the island, it now appears the effects of wetter (most pronounced in winter), warmer seasons favours pathogen infection and associated dieback. This, in combined with a warmer, more variable summer growing season is most likely to be driving the ongoing *A. macquariensis* dieback across Macquarie Island.

The development of clearly discernible and repeatable fine-scale *A. macquariensis* condition classes has provided a more nuanced understanding of the drivers of dieback, required to determine temporal trends and estimate the rate of cushion cover loss across the island. The

recent decline in cushion condition was represented by three dieback progression classes, 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 same dieback stage documented in 2010, then referred to as ‘yellow’ damage describing the leaf chlorosis (loss of green colouration) following senescence, natural or pathogenic (Whinam et al. 2014). Very low-levels of cushion recovery were recorded across the island, with the highest in the north of the island in areas of advanced dieback (Appendix S1). However, the repeated ‘waves’ of dieback at previously infected areas (see Dickson et al. 2019), strongly suggest that there may not be the capacity for the species to regain its previous cover, warning of an impending structural change in this landscape.

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 (Appendix S1). 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 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 rather than spreading from a northern infection point, dieback progression or pathogen virulence is higher in the north under more suitable conditions.

The decadal reduction in summer plant available water was previously considered the likely main driver of *A. macquariensis* decline, with weakened cushions more susceptible to secondary pathogenic infection (Bergstrom et al. 2015). However, here cushion dieback was related to microclimate extremes, with more dieback at sites experiencing higher humidity_{ext} and fewer freezing_{ext} days. This pattern supports the hypothesis that dieback extent is now better explained by pathogen ecology. Variables likely to affect plant water stress (VPD – highly correlated with hot_{ext}, wind exposure – inverse of wind shelter 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 solely by water stress.

High humidity is known to promote plant pathogens, while freezing days suppress them, with responses varying amongst taxonomic groups (Chakraborty 2013; Garrett et al. 2016; Harvell et al. 2002). For example, water moulds (Oomycetes) and fungal pathogens are both generally promoted under warmer, wetter climates (Homet et al. 2019; Welsh et al. 2014), making them likely candidates for the pathogens affecting cushion dieback, potentially acting individually or in consortium with multiple taxa. 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 S2.1, Appendix S2), 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. Cumulatively over time, this variation in extreme humidity may well represent a biologically significant shift in humidity. Given the importance of extreme humidity in the model, empirical soil moisture data and soil moisture modelling are worth future investment to better understand the relationship between soil moisture and atmospheric humidity, and its relationships with plant health and pathogen distribution on the island.

Disease is unlikely to be responding in isolation or as a straightforward linear relationship with one or several different drivers, rather as a response to highly complex interactions between climate, environment and pathogen variables (Chakraborty et al. 2000; Rohr et al. 2011). The ability of plants to resist and recover from novel pathogens can be further compromised when faced with a combination of novel extreme events such as drought, flooding, and frost (Stenlid and Oliva 2016). Despite plants no-longer appearing drought-stressed (DMB pers. obs.), it is likely the significantly higher maximum and extreme maximum temperatures during the growing season (Table S3.1., Appendix S3) are contributing to background stress. It therefore seems increasingly likely 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.

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 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 the southern region is significantly colder with more freezing days and there is a significant negative temperature gradient down the island in addition to the expected reduced temperatures at higher elevation. However, the availability of atmospheric water (represented here by relative humidity) was comparatively stable down the island. This suggests the latitudinal gradients of cushion condition shown here, may be driven by the prevalence of freezing days rather than available atmospheric water. It appears therefore, the extreme cold temperatures in the south have provided some refuge from the rapidly progressing and extensive dieback (see Burgess et al. 2017; Harvell et al. 2002; Marçais et al. 1996). 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 S3.1., Appendix S3). 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.

The confirmation of southern refugia reinforces the value of maintaining the three existing Azorella special management areas (SMAs) in the south of the island, which still contain some the most extensive and healthiest cushion ‘mats’ on the island. The SMAs reduce expeditioner entry into the area and require soil hygiene procedures, both well accepted management actions for landscape disease containment (Monks et al. 2019). Unfortunately cushion dieback is present in the SMAs at low levels, however, while the pathogens and control measures remain unknown, the SMAs remain the best available option for reducing any additional movement of the pathogens or disturbance in the area (see Bergstrom et al. 2015). Bolder management actions are required to stop the ongoing decline of this endemic foundation species, commencing with the identification of the pathogens, potential disease containment or control options, and propagation techniques.

Conclusions

Changes in the regional climate towards a system that is warmer and more variable in the summer, and wetter and warmer in winter appear 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). Under current climate conditions, where Macquarie Island is more variable, warmer and wetter than historically experienced, dieback is likely to persist. The monitoring of microclimate and use of refined cushion condition classes to assess trends in plant condition are considered a priority to be able to identify the rate of regime change and to appropriately direct management effort. The distributional extent of this iconic foundation species, and its role in the diversity and functioning of the broader fellfield ecosystem are central to the natural value of Macquarie Island. The decline in this species in response to a changed regional climate emphasises the need to track and better manage shifting baselines, including within well conserved Natural World Heritage Sites. The extent of cushion dieback and resultant loss of cover signals a potential regime shift on the Island's fellfield plateau, and possibly 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.

Species Nomenclature

Azorella macquariensis Orchard, Apiaceae, Macquarie cushions

Acknowledgements

We thank Dr Patricia Selkirk and Dr Grant Duffy for constructive discussions about the manuscript, and John Burgess and Rowena Hannaford for assistance with field work. We thank the handling editor and reviewers for their comments on the manuscript. This study was funded by an Australian Government, Australian Antarctic Science Program Grant (#4312) and an Australian Government Research Training Program (RTP) Scholarship, the Holsworth Wildlife Research Endowment and The Ecological Society of Australia, and the Denis and Maisie Carr Award.

494

495 **References**

- 496 Adams N. (2009) Climate trends at Macquarie Island and expectations of future climate
497 change in the sub-Antarctic. *Pap. Proc. R. Soc. Tasman.* **143**, 1-8.
- 498 Allan J. R., Venter O., Maxwell S., et al. (2017) Recent increases in human pressure and
499 forest loss threaten many Natural World Heritage Sites. *Biological Conservation* **206**, 47-55.
- 500 Allen R. G., Pereira L. S., Raes D. & Smith M. (1998) Crop evapotranspiration-Guidelines
501 for computing crop water requirements-FAO Irrigation and drainage paper 56. Fao, Rome
502 **300**, D05109.
- 503 Anderson P. K., Cunningham A. A., Patel N. G., et al. (2004) Emerging infectious diseases
504 of plants: pathogen pollution, climate change and agrotechnology drivers. *Trends in Ecology*
505 *& Evolution* **19**, 535-44.
- 506 Badano E. I., Jones C. G., Cavieres L. A. & Wright J. P. (2006) Assessing impacts of
507 ecosystem engineers on community organization: a general approach illustrated by effects of
508 a high-Andean cushion plant. *Oikos* **115**, 369-85.
- 509 Barton K. & Barton M. K. (2018) Package 'MuMIn': Multi-Model Inference. Version: 1.40.4.
510 CRAN, <https://CRAN.R-project.org/package=MuMIn>.
- 511 Bebbler D. P., Ramotowski M. A. T. & Gurr S. J. (2013) Crop pests and pathogens move
512 polewards in a warming world. *Nat. Clim. Change* **3**, 985.
- 513 Bergstrom D. M., Bricher P. K., Raymond B., et al. (2015) Rapid collapse of a sub-Antarctic
514 alpine ecosystem: the role of climate and pathogens. *J. Appl. Ecol.* **52**, 774-83.
- 515 Bivand R., Altman M., Anselin L., et al. (2017) Package 'spdep': Spatial Dependence:
516 Weighting Schemes, Statistics and Models. Version 0.7-4. . CRAN, [https://CRAN.R-](https://CRAN.R-project.org/package=spdep)
517 [project.org/package=spdep](https://CRAN.R-project.org/package=spdep).
- 518 Bland L. M., Rowland J. A., Regan T. J., et al. (2018) Developing a standardized definition
519 of ecosystem collapse for risk assessment. *Front. Ecol. Environ.* **16**, 29-36.
- 520 Boyd I. L., Freer-Smith P. H., Gilligan C. A. & Godfray H. C. J. (2013) The Consequence of
521 Tree Pests and Diseases for Ecosystem Services. *Science* **342**, 1235773.
- 522 Bramley-Alves J., King D. H., Robinson S. A. & Miller R. E. (2014) Dominating the
523 Antarctic Environment: Bryophytes in a Time of Change. In: *Photosynthesis in Bryophytes*
524 *and Early Land Plants* (eds D. T. Hanson and S. K. Rice) pp. 309-24. Springer Netherlands,
525 Dordrecht.

526 Brenning A., Bangs D., Becker M., Schratz P. & Polakowski F. (2018) Package 'RSAGA',
 527 Version 1.3.0. <https://github.com/r-spatial/RSAGA>.
 528 Brolsma H. (2008) Macquarie Island AIRSAR DEM (Digital Elevation Model).
 529 <http://data.aad.gov.au/aadc/metadata/>.
 530 Burgess T. I., Scott J. K., McDougall K. L., et al. (2017) Current and projected global
 531 distribution of *Phytophthora cinnamomi*, one of the world's worst plant pathogens. *Global*
 532 *Change Biol.* **23**, 1661-74.
 533 Cahill A. E., Aiello-Lammens M. E., Fisher-Reid M. C., et al. (2013) How does climate
 534 change cause extinction? *Proc. R. Soc. B.* **280**, 20121890.
 535 Cerfonteyn M. E., Le Roux P. C., Van Vuuren B. J. & Born C. (2011) Cryptic spatial
 536 aggregation of the cushion plant *Azorella selago* (Apiaceae) revealed by a multilocus
 537 molecular approach suggests frequent intraspecific facilitation under sub-Antarctic conditions.
 538 *American Journal of Botany* **98**, 909-14.
 539 Chakraborty S. (2013) Migrate or evolve: options for plant pathogens under climate change.
 540 *Global Change Biol.* **19**, 1985-2000.
 541 Chakraborty S., Tiedemann A. V. & Teng P. S. (2000) Climate change: potential impact on
 542 plant diseases. *Environ. Pollut.* **108**, 317-26.
 543 Cohen J. M., Civitello D. J., Venesky M. D., McMahon T. A. & Rohr J. R. (2019) An
 544 interaction between climate change and infectious disease drove widespread amphibian
 545 declines. *Global Change Biol.* **25**, 927-37.
 546 Conrad O., Bechtel B., Bock M., et al. (2015) System for automated geoscientific analyses
 547 (SAGA) v. 2.1. 4. *Geoscientific Model Development* **8**, 1991-2007.
 548 Córdova M., Céleri R., Shellito C. J., et al. (2016) Near-Surface Air Temperature Lapse Rate
 549 Over Complex Terrain in the Southern Ecuadorian Andes: Implications for Temperature
 550 Mapping. *Arct. Antarct. Alp. Res.* **48**, 673-84.
 551 Dickson C. R., Baker D. J., Bergstrom D. M., et al. (2019) Spatial variation in the ongoing
 552 and widespread decline of keystone plant species. *Austral Ecol.* **44**, 891-905.
 553 Dickson C. R., McGeoch M. A., Bergstrom D. M., Whinam J. & Baker D. J. (2020) Fine-
 554 scale *Azorella macquariensis* condition and site microclimate extremes data from Macquarie
 555 Island, v1. (ed Australian Antarctic Data Centre -
 556 <http://dx.doi.org/doi:10.26179/5e71aba2c846a>).
 557 Dinno A. & Dinno M. A. (2017) Package 'dunn.test'. Version 1.3.5., [https://cran.r-](https://cran.r-project.org/web/packages/dunn.test/dunn.test.pdf)
 558 [project.org/web/packages/dunn.test/dunn.test.pdf](https://cran.r-project.org/web/packages/dunn.test/dunn.test.pdf).

Ellison A. M. (2019) Foundation Species, Non-trophic Interactions, and the Value of Being Common. *iScience* **13**, 254-68.

Garrett K. A., Nita M., De Wolf E. D., et al. (2016) Chapter 21 - Plant Pathogens as Indicators of Climate Change. In: *Climate Change (Second Edition)* (ed T. M. Letcher) pp. 325-38. Elsevier, Boston.

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.

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.

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.

Homet P., González M., Matías L., et al. (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. *Annu. Rev. Phytopathol.* **30**, 553-77.

Körner C. & Hiltbrunner E. (2018) The 90 ways to describe plant temperature. *Perspect. Plant Ecol. Evol. Syst.* **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**, 733-45.

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.

Lembrechts J. J., Lenoir J., Roth N., et al. (2019) Comparing temperature data sources for use in species distribution models: From in-situ logging to remote sensing. *Global Ecol. Biogeogr.* **28**, 1578-96.

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**, 369-82.

Monks L., Barrett S., Beecham B., et al. (2019) Recovery of threatened plant species and their habitats in the biodiversity hotspot of the Southwest Australian Floristic Region. *Plant Diversity* **41**, 59-74.

593 Ockendon N., Baker D. J., Carr J. A., et al. (2014) Mechanisms underpinning climatic
 594 impacts on natural populations: altered species interactions are more important than direct
 595 effects. *Global Change Biol.* **20**, 2221-29.

596 Pauchard A., Milbau A., Albiñ A., et al. (2016) Non-native and native organisms moving
 597 into high elevation and high latitude ecosystems in an era of climate change: new challenges
 598 for ecology and conservation. *Biological Invasions* **18**, 345-53.

599 Pendlebury S. F. & Barnes-Keoghan I. P. (2007) Climate and climate change in the sub-
 600 Antarctic. *Pap. Proc. R. Soc. Tasman.* **141**, 67-82.

601 Peng R. D. (2019) simpleboot: Simple Bootstrap Routines. CRAN, [https://CRAN.R-](https://CRAN.R-project.org/package=simpleboot)
 602 [project.org/package=simpleboot](https://CRAN.R-project.org/package=simpleboot).

603 Preisler H. K., Hicke J. A., Ager A. A. & Hayes J. L. (2012) Climate and weather influences
 604 on spatial temporal patterns of mountain pine beetle populations in Washington and Oregon.
 605 *Ecology* **93**, 2421-34.

606 R Core Team. (2019) R: A Language and Environment for Statistical Computing. R
 607 Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.

608 Rohr J. R., Dobson A. P., Johnson P. T. J., et al. (2011) Frontiers in climate change–disease
 609 research. *Trends in Ecology & Evolution* **26**, 270-77.

610 Rolland V., Bergstrom D. M., Lenne T., et al. (2015) Easy Come, Easy Go: Capillary Forces
 611 Enable Rapid Refilling of Embolized Primary Xylem Vessels. *Plant Physiol.* **168**, 1636-47.

612 Rueden C. T., Schindelin J., Hiner M. C., et al. (2017) ImageJ2: ImageJ for the next
 613 generation of scientific image data. *BMC Bioinformatics* **18**, 529.

614 Sato C. F. & Lindenmayer D. B. (2018) Meeting the Global Ecosystem Collapse Challenge.
 615 *Conservation Letters* **11**, e12348.

616 Selkirk P. M. (2012) Plateau Vegetation On Sub-Antarctic Macquarie Island. *Pap. Proc. R.*
 617 *Soc. Tasman.* **146**, 71-79.

618 Selkirk P. M., Seppelt R. D. & Selkirk D. R. (1990) Subantarctic Macquarie Island:
 619 environment and biology. Cambridge Press University Press, Cambridge.

620 Sicard A., Zeilinger A. R., Vanhove M., et al. (2018) *Xylella fastidiosa*: Insights into an
 621 Emerging Plant Pathogen. *Annu. Rev. Phytopathol.* **56**, 181-202.

622 Sonter R. O., Semple W. S. & Lawrie J. W. (2000) Soils, vegetation and land use. In: *Soils:*
 623 *their properties and management* (eds P. E. Charman and B. W. Murphy) pp. 271-86. Oxford
 624 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 and P. Broady) pp. 272-81. 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**, 212-19.

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.

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. <https://CRAN.R-project.org/package=betareg>

Supporting Information

Appendix S1: Extended methods and description of *Azorella macquariensis* condition classes with associated summary statistics. Additional analysis provided of the Healthy, Wind-scour and Recovery condition classes.

Appendix S2: Supplementary abiotic and biotic data, and modelled response of *Azorella macquariensis* condition to microclimate and terrain variables.

Appendix S3: Analysis of long-term trends of temperature variables at Macquarie Island Bureau of Meteorology weather station between 1948 and 2018.

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

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 inverse of exposure). The northwest wind is the direction of the strongest gusts and predominant wind direction on the island (Adams 2009).
Fine gravel content	Fine_Gravel	Proportion of fine gravel (6 – 2 mm), as an indication of water holding capacity.

Table 2. 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 (± s.e.)
Healthy (%)	62	6.0	100.0	67.8 (± 3.19)
Wind-scour (%)	62	0	13.4	1.5 (± 0.30)
Dieback (%)	62	0	86.9	29.7 (± 3.08)
Active Dieback (%)	62	0	26.9	3.0 (± 0.77)
Thinning Dieback (%)	62	0	54.3	13.0 (± 1.83)
Advanced Dieback (%)	62	0	85.6	13.7 (± 2.50)

Recovery (%)	62	0	15.3	1.1 (± 0.38)
Island-wide <i>A. macquariensis</i> cover (%)	62	0.5	88.3	41.7 (± 2.73)

Fig. 1. A. Healthy *Azorella macquariensis* cushions with *Pleurophyllum hookeri* and graminoid epiphytes (central region of Macquarie Island, MI, south of Lake Prion). B. Active dieback (yellow to brown) spreading through a thin *A. macquariensis* mat, which is subsequently replaced with the dominant grass *Agrostis magellanica* (central region of MI) (see models in Hoffmann et al. 2019).

Fig. 2. Location of Macquarie Island (A) and survey sites on the island (B, black circles), with the island divided into three equal latitudinal regions. Proportion of *Azorella macquariensis* (% , with standard error bars) within each Dieback progression class (Active, Thinning and Advanced) in each region is presented individually. Dieback progression classes that are significantly different across regions (i.e. north, central and south) are indicated on the figure by a different letter, the same scale is used across classes and subclasses, hill shading is included across the island. For the distribution of healthy, wind-scour and recovery classes see Fig. S1.1. Appendix S1.

Fig. 3. Summer 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). (A.) Freezing_{ext} (number of days <0°C); (B.) VPD (vapour pressure deficit); (C.) Dry_{ext} (daily average 5th percentile of relative humidity,%); (D.) Humidity_{ext} (daily average 95th percentile of relative humidity,%); (E.) Cold_{ext} (daily average 5th percentile of temperature, °C); and, (F.) Hot_{ext} (daily average 95th percentile of temperature, °C).

Fig. 4. (A.) 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 (*, $p < 0.05$). Freezing_{ext} (number of days with temperatures $< 0^{\circ}\text{C}$), Humidity_{ext} (average daily 95th percentile of relative humidity,%), VPD (average daily vapour pressure deficit, kPa), NW Windshelter (no unit, inverse of wind exposure), Fine Gravel (%) and covariate, mean *A. macquariensis* Cover (%) at site. **(B.)** Relationship between significant variables Humidity_{ext} and Freezing_{ext} during the growing season (Oct – Mar) for sites with $< 5\%$ (black triangles) and $\geq 5\%$ (grey circles) *A. macquariensis* dieback. Generalised linear regression lines showing a significant interaction between Freezing_{ext} and sites with $< 5\%$ (black line) or $\geq 5\%$ dieback (grey line) ($p = 0.002$).

aec_12958_f1.jpg

aec_12958_f2.jpg

aec_12958_f3.jpg

aec_12958_f4.jpg

Minerva Access is the Institutional Repository of The University of Melbourne

Author/s:

Dickson, CR;Baker, DJ;Bergstrom, DM;Brookes, RH;Whinam, J;McGeoch, MA

Title:

Widespread dieback in a foundation species on a sub-Antarctic World Heritage Island: Fine-scale patterns and likely drivers

Date:

2021-02-01

Citation:

Dickson, C. R., Baker, D. J., Bergstrom, D. M., Brookes, R. H., Whinam, J. & McGeoch, M. A. (2021). Widespread dieback in a foundation species on a sub-Antarctic World Heritage Island: Fine-scale patterns and likely drivers. *Austral Ecology: a journal of ecology in the Southern Hemisphere*, 46 (1), pp.52-64. <https://doi.org/10.1111/aec.12958>.

Persistent Link:

<http://hdl.handle.net/11343/276439>