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

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SPATIAL VARIATION IN THE ONGOING AND WIDESPREAD DECLINE OF A KEYSTONE PLANT SPECIES

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

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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, terrain variables, dieback, sub-Antarctic

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 (Chen *et al.* 2011; Parmesan and Yohe 2003), and differing rates of species’ responses are resulting in the formation of novel communities (Chown *et al.* 2013; le Roux and McGeoch 2008). 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 (Allen *et al.* 2010; Breshears *et al.* 2005; Carnicer *et al.* 2011; Duke *et al.* 2017; Harris *et al.* 2018; Hoffmann *et al.* 2018). 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 1,000 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 1982-2003, which may be attributed to multiple factors including drought stress, insect damage, disease, wildfire and changes in resource allocation (Verbyla 2008). The first case of a landscape-scale plant mortality 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.* 2018).

Regardless of the proximate cause of mortality, climate change is implicated in the widespread dieback of *A. macquariensis* on the island (Bergstrom *et al.* 2015; Whinam *et al.* 2014). 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 (Bergstrom *et al.* 2015; Whinam *et al.* 2014). 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 – 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; Pendleybury and Barnes-Keoghan 2007; Tweedie and Bergstrom 2000), 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 (Bricher *et al.* 2013; Selkirk 2012). *Azorella macquariensis* is considered a keystone species on the fellfield ecosystem because it facilitates a larger more diverse microarthropod 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 and 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, is generally considered unrepresentative of conditions on the plateau (Fitzgerald and 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 less than 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 5m x5m resolution Macquarie Island Digital Elevation Model (DEM) (Brolsma 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 and statistical analyses is described in 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 (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 (m^2) 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 m^2 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 (Morrison 2016; Wintle *et al.* 2013). The area (m^2) of *A. macquariensis* was calculated per quadrant (cushion quadrant percent cover multiplied by quadrant area, 176.72 m^2) and summed to determine the total area (m^2) 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 (Cerfonteyn *et al.* 2011; Mortimer *et al.* 2008).

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 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 Generalized 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 (Table S2.1). We estimated effect sizes of predictors based on the model averaged regression coefficients using the 'MuMIn' package in R (Barton and Barton 2018), after standardizing estimates based on partial standard deviations (Cade 2015). This

standardization 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 standardized 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 (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 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 x 5m 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 2m x 2m 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 if 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 (m²), *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 and 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 $D^2 = (\text{null deviance} - \text{residual deviance})/\text{null deviance}$ (Guisan and 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 and 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.* 2018). 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 ($n = 8$) – 609.67 m² (Table 1, Figs. 3a and 4a). Where present, *A. macquariensis* cover was also highly variable within sites ($n = 82$), differing between quadrants by up to 114.9m² (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 standardized estimate (1.00) and approximately three times the effect size of the next most important coefficients, Elevation (0.34) and West_Dist² (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% ($\pm$ s.d. 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 Cover²) and the predictor latitude significantly explained dieback (Table 2). Dieback significantly increased with latitude, to the north of the 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 to 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 $32 \pm 29\%$ (s.d.) in 2008/2009 (Bergstrom *et al.* 2015) to $28.2 \pm 22.4\%$ (s.d.) 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 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 are 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 8-22 years across the island. Complete loss of cushion cover under the exponential model ranges from 8-10 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 is 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 monitoring sites are needed in each region to obtain a representative estimate of the conservation status of this species.

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, i.e. 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 to 16.6% of the relative effect size of latitude. Although small, these effects 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 macroscale 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, i.e. 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 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 (Bergstrom *et al.* 2015; Whinam *et al.* 2014), 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.* 2018).

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, i.e. 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 (Bergstrom *et al.* 1997; Taylor 1955), 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 and 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 are 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.

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SUPPORTING INFORMATION

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 dieback candidate models used in the multimodel inference approach to estimate effect sizes of predictor variables.

638 Abbreviated headings for SI tables and figures:

639 **Table S1.1** Topographic variables used the terrain class, *Azorella* cover and dieback models.

640 **Table S1.2.** Principle Component Analysis (PCA) results.

641 **Fig. S1.1.** Pair-wise correlations of terrain variables.

642 **Fig. S1.2.** Xie-Beni Index for cluster solutions.

643 **Fig. S1.3.** Average pairwise correlation for cluster solutions.

644 **Fig. S1.4.** The distribution of cluster solutions across Macquarie Island.

645 **Fig. S1.5.** Pair-wise parameter space of cluster solutions.

646 **Fig. S1.6.** Geographic blocking for stratified sampling.

647 **Fig. S1.7.** Site selection results.

648 **Fig. S1.8** Established sites.

649 **Table S2.1.** *Azorella macquariensis* cover candidate models.

650 **Table S2.2.** *Azorella macquariensis* dieback candidate models.

651

652 **Table 1.** *Azorella macquariensis* cover and dieback descriptive statistics at the 90 field sites
653 across Macquarie Island (total site area = 706.86 m²). Cover and dieback presented at an
654 island-wide and regional level, regions represent three equal latitudinal extents. Min†
655 excludes eight sites with no *A. macquariensis* cover ($n = 82$).

	N	Min. †	Max.	Mean (±s.d.)	c.v. (%)
Cover					
Total <i>Azorella</i> cover (m²)	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 (m²)	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

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). † measured as northing, i.e. the inverse of latitude.

Variable	Estimated coefficient (s.e.)	z	p
<i>(a) Azorella cover</i>			
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
<i>(b) Azorella dieback</i>			
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
Cover^2	-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

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
	Estimated coefficient	s.e.	z	p	Independent contribution (%)
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. 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.).

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.

Fig. 3. Total cover of *Azorella macquariensis* (m²) (a.) and *A. macquariensis* cover affected by dieback (%) (b.) at each 706.86 m² site 2017.

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

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

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 one year.

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Author/s:

Dickson, CR;Baker, DJ;Bergstrom, DM;Bricher, PK;Brookes, RH;Raymond, B;Selkirk, PM;Shaw, JD;Terauds, A;Whinam, J;McGeoch, MA

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