

Spatial and temporal variation in damage and dieback in a threatened subantarctic cushion species

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Abstract. A decline was observed in the subantarctic Macquarie Island endemic cushion, *Azorella macquariensis*, during the summer of 2008–2009, resulting in the listing of the species as critically endangered in 2010. Photographs of *A. macquariensis* in the period 2009–2013 were used to (1) identify types of damage, (2) determine the likely causes of three distinct types of damage, (3) establish whether dieback was spreading from affected to unaffected sites and (4) find out whether dieback was associated with the expansion of *Agrostis magellanica*. Grey damage occurred on the most wind-exposed parts of cushions and on the most wind-exposed sites. Speck damage occurred in the opposite situations and was consistent in its location, attributes and timing with rabbit grazing. Yellow dieback was sporadic in its occurrence. Its symptoms were consistent with those of a pathogen. Yellow damage expanded between spring 2009 and autumn 2010, with neither grey nor speck damage increasing. Yellow damage was associated with a marked decline in live cushion cover in plots between 2010 and 2013. The cushion was not eliminated from any plots, despite increased cover of *A. magellanica* in plots with dead cushions. Only one site not affected by yellow damage in 2010 had become affected by 2013. Given these results, and given that yellow damage has been observed in the past, 2008–2010 may have been an infrequent extreme outbreak of a pathogen and/or a response of a pathogen to ongoing climatic change.

Additional keywords: cushion plant, pathogen, wind damage.

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Introduction

In an era of global climatic change and accelerated mixing of species from different biotic realms (Lebouvier *et al.* 2011), biologists have grown to expect the occasional rapid decline of a native species. In the first decade of the 21st century, there were several rapid declines of native species on subantarctic Macquarie Island associated with fluctuations in rabbit populations (Copson and Whinam 1998, 2001; Scott and Kirkpatrick 2008, 2013; Bergstrom *et al.* 2009; Shaw *et al.* 2011). During the 2008–2009 austral summer, a dieback in the Macquarie Island endemic cushion plant, *Azorella macquariensis* Orchard (henceforth *Azorella*), was reported (Threatened Species Section 2009; Threatened Species Scientific Committee 2010). Necrosis was observed across the entire range of the species, severely affecting up to 90% of cushions in some areas (Threatened Species Section 2009). By the winter of 2009, cushions on the northern plateau appeared to be worst-affected and only patches of cushions on isolated rock stacks and in wet valley bottoms were found to be unaffected (Threatened Species Section 2009). The species was listed as endangered under the

Threatened Species Protection Act (Tas.) 1995 in late 2009, and as critically endangered under the *Environmental Protection and Biodiversity Conservation Act (Cth) 1999* in August 2010 (Threatened Species Section 2009; Threatened Species Scientific Committee 2010).

Damage in cushions has been associated with climatic extremes, particularly strong winds (Taylor 1955a, 1955b; Kirkpatrick and Harwood 1980; Kirkpatrick *et al.* 2002), shading by other plants (Hauri and Schröter 1914; le Roux *et al.* 2005), mechanical damage from burrowing species (Selkirk *et al.* 1990; Phiri *et al.* 2009), herbivory (Chapuis *et al.* 1994; Rundel and Palma 2000), human trampling (Scott and Kirkpatrick 1994; Whinam and Chilcott 1999, 2003) and human exploitation for fuel and medicine (Núñez and Grosjean 2003; Kleier and Rundel 2004). There is no published work that shows that disease is a cause of the rapid spread of necrosis in and between individuals (TSS 2009), although diseases do damage cushion plants (e.g. Marr 1997). We make a distinction between dieback, as an observed process of expansion of morbidity or mortality, and damage, which is necrosis or foliage removal

observed at a particular time, which may, or may not, be a symptom of a process of dieback at the time of observation, as damage might be evident where a process of dieback has ceased or where recolonisation is taking place.

Azorella cushions on Macquarie Island have been suggested to be damaged by wind, rabbits, mice, birds and pathogens. Partial mortality of cushions has been posited to be a result of exposure to wind, with total death being suggested to occur when wind is extremely strong (Taylor 1955a, 1955b; Ashton and Gill 1965). Rabbits have been observed to scratch and dig into cushions (Taylor 1955b). Cushions die within the nesting areas of giant petrels (Taylor 1955b; Selkirk *et al.* 1990). Ashton and Gill (1965) observed that 11.4% of the area of *Azorella* cushions on the plateau was dead, hypothesising that necrosis radiated from the windward peak of the cushions, leaving a ring of live foliage. Selkirk (2012), presenting data from 1980, recorded a very low cover of dead cushions. *Azorella* exhibits seasonal leaf browning (winter senescence), which occurs between late autumn and mid-spring (Taylor 1955b).

During the austral summers of 1986–1987 and 1989–1990, several cushions on Macquarie Island were observed to have a form of damage that was brown, with a ring-shaped zone of yellow leaves on its margin, and that appeared as if it radiated within and among individual cushions, suggesting a fungus or another pathogen (P. Selkirk, pers. comm. 2010). The same yellow margin was thought to be associated with the patchy onset of winter browning by Taylor (1955b), and was widely observed where the cushions appeared to be dying in 2008–2009.

In response to the rapid cushion decline in 2008–2009, a need for spatial and temporal mapping of the cushion dieback to help determine possible causes, and the degree of threat to the species, was apparent (Kirkpatrick 2009). Our mapping occurred as part of a larger research program to identify the causes and consequences of the phenomenon (D. Bergstrom, pers. comm. 2009).

Our aim was to use temporal and spatial observations to suggest possible causes of damage and the implications of any dieback for the future of the species. In the first stage of our investigation, we determined whether there was variation in the symptoms of damage on the cushions. In the second stage, we determined whether spatial variation in each of three types of damage was consistent with patterns that could be expected from possible causes of damage. In the third stage, we determined whether any of the three types of damage was associated with dieback between spring 2009 and autumn 2010. Finally, we determined whether dieback was occurring between 2010 and 2013, whether it locally eliminated *Azorella*, and whether it promoted the expansion of *Agrostis magellanica* Lam. (henceforth *Agrostis*) into places previously occupied by *Azorella*.

Materials and methods

Site selection

We collected three datasets with the purposes of spatial comparison, observation of short-term change and observation of medium-term change. The spatial-comparison dataset tested whether there was variation between sites in damage in the

2009–2010 summer. The sites were measured only once. Ten sites on the northern half of the plateau with *Azorella* (Fig. 1) were preselected from the stratified random study sites of Bricher *et al.* (2013).

For the set of observations of short-term change (spring 2009–autumn 2010), 31 *Azorella* sites on the northern half of the island, within 10–50 m of walking tracks, were randomly selected for monitoring using ESRI ArcMap (ESRI, Redlands, CA, USA) (Fig. 1). The sites were selected close to tracks to allow easy access for repeat visits, and far enough away from tracks to avoid disturbance by human traffic. Sites were rejected if they lacked cushion plants. The nearest cushion plant was placed in the centre of a repeat photograph quadrat, of which there was one per site.

For the set of observations of medium-term change (summer 2010–summer 2013), 30 sites with *Azorella* were subjectively selected in the northern third of the island (Fig. 1). Sixteen sites, on a range of aspects, elevations and soil types, had yellow discoloration of cushions. Fourteen sites, selected to be in the same range of environments, had no yellowing of any cushions. The change observations were repeated for the same plots so as to detect dieback.

Our spatial-comparison and medium term-change observations took place in mid-summer when winter browning of cushions was not evident anywhere on the island. Our short term-change observations picked up some winter browning in the earliest and latest observations. This was distinguished from yellow damage in spring by the greening of the foliage in later observations and in autumn by the lack of a yellow line.

Data collection for spatial comparison

At each of the 10 sites used for spatial comparison, one 30–80-cm maximum-diameter cushion in each of good health, medium health and poor health was selected. Cushions with green leaves forming the majority of the surface cover and with nil to minor damage were classed as in good health. Cushions with a surface cover comprising a mixture of green and yellow and/or brown leaves, and with minor to moderate damage were classed as in medium health. Cushions with brown and/or dead leaves forming the majority of the surface cover were classed as in poor health.

The nearest cushion in the direct line of every cardinal and intermediate directions from the three selected cushions was selected. Each of the 27 cushions per site was photographed vertically with its surrounds. A compass was located within the frame of each photograph. The elevation and geographic position of each of the 27 cushions at each site was mapped using a tape, compass and clinometer.

Data collection for short-term change

The 31 1 × 1-m quadrats were repeat photographed at intervals of ~3 weeks between 30 October 2009 and 24 March 2010. A tripod was used to position the camera ~2 m above the ground.

Data collection for medium-term change

The sites consisted of a marked 2 × 2-m space. This space was photographed in 1 × 1-m quadrat segments in January–February

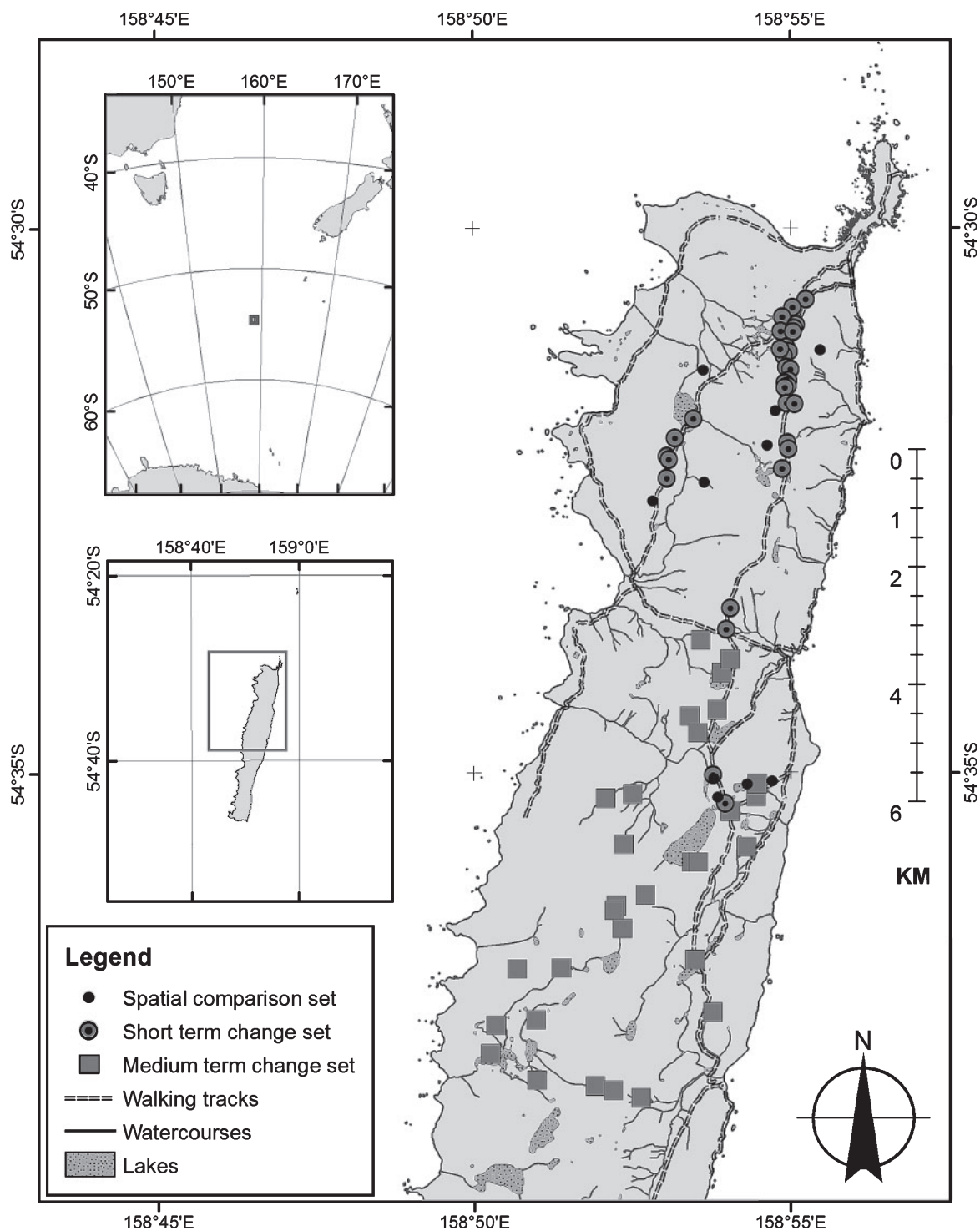


Fig. 1. Study site on Macquarie Islands in the Southern Ocean, indicating locations of spatial-comparison, short term-change and medium term-change sites. Spatial data courtesy of the Australian Antarctic Division and Tasmanian Parks and Wildlife Service 2012.

2010, 2011, 2012 and 2013, although some sites were not relocated in 2011 and 2013. Elevation (m), slope ($0-2^\circ$, $>2^\circ$), aspect (south-westerly, north-easterly) and vegetation type (fjaeldmark or herbfield) were noted.

Observations on root systems

Twelve plants of *Azorella* with yellow damage were excavated in 2009 and observations made of the state of their root systems. In 2013, 10 plants that had previously had yellow damage and had

surviving green shoots were excavated and observations made on the origin and characteristics of the live shoots. Several apparently healthy seedlings in adjacent rocky areas were excavated and examined at the same time.

Laboratory analysis in spatial-comparison study

The photographs were examined to determine whether there were different types of damage on the cushions. The percentage of each of the cushions that consisted of each of three types of damage (Fig. 2) was estimated to the nearest per cent by using a grid overlay as a guide. Cushion size was classed into large (>70-cm maximum diameter), medium (31–70-cm maximum diameter) and small (<30-cm maximum diameter).

Dominant wind direction (north, north-east, east, south-east, south, south-west, west, north-west) was recorded from the photographs on the basis of the orientations of distortions to vegetation surrounding the target cushion, following Noguchi (1979), Robertson (1987) and Wooldridge *et al.* (1996). We assumed that asymmetry in mosses, herbs and grasses was equivalent to asymmetry in tree crowns. The direction, or lack thereof, of concentration of each type of damage on each cushion was recorded. The sector with the highest proportion of damaged cushion surface of the particular type was selected. Thus, if the slope of the cushion facing south-west had the most grey damage, south-west was recorded.

By using the photographs, cushions were subjectively classed by one observer (JAR) as sheltered from the direct force of the wind, partially protected or exposed (>50% of windward side unprotected from the direct force of the wind). Protection from

wind was deduced by identifying obstacles that could reduce the impact of the wind against the cushion surface, such as rocks, tall vegetation to the windward or plants growing epiphytically on the windward part of the cushions.

The photographs were used to determine ground cover, which was the nature of the surrounding surface material. Cushions growing on an approximately equal combination of moss-bed, organic material and particles <2 mm in diameter were classed as having a substrate of moss-bed and soil. Cushions observed to be growing mainly on particles <2 mm in diameter were classed as having a substrate of soil. Cushions observed to be growing on an approximately equal combination of particles <2 mm and >2 mm in diameter were classed as having a substrate of soil and gravel. Cushions observed to be growing only on particles >2 mm were classed as having a substrate of gravel.

Areas in the photographs in the immediate vicinity of each cushion with vegetation dominated by bryophytes, cushions and lichens and with a ground cover consisting mainly of exposed gravel and aeolian sediments were classified as fjaeldmark. Areas with vegetation dominated by herbs, cushions and sedges and with a ground cover consisting mainly of vegetation were classified as herbfield.

Laboratory analysis of data from short and medium term-change sites

Areas of cushion damage were marked in layers overlaid onto the images from each visit to the 31 1 × 1 short term-change sites, identifying the three damage types. The covers of live and dead *Azorella* and live *Agrostis* were measured on the 2 × 2 m medium

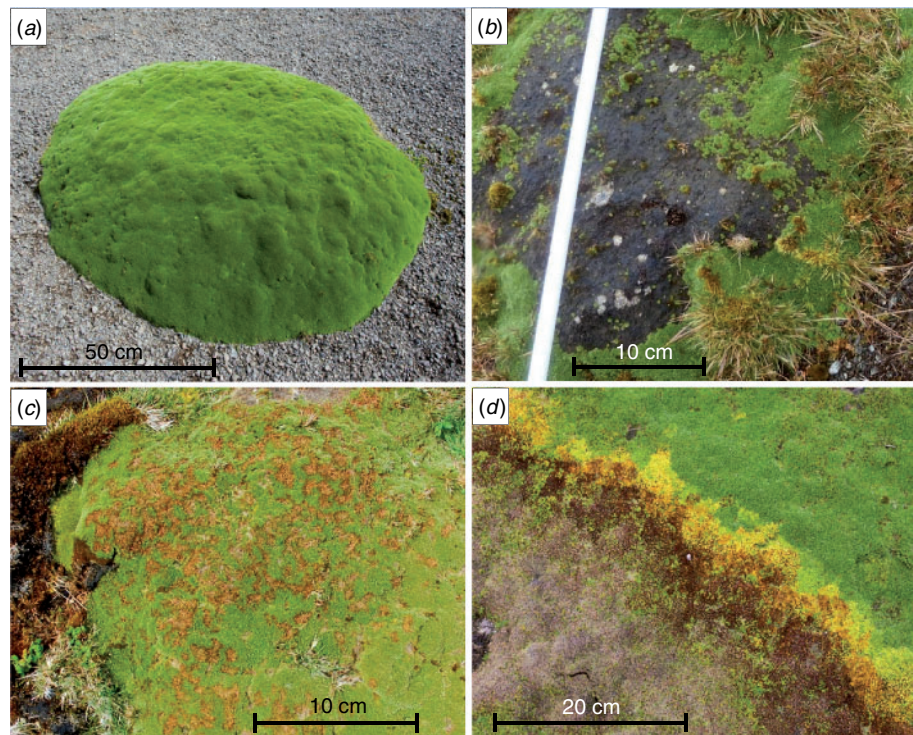


Fig. 2. The three damage types observed in *Azorella*. (a) Healthy *Azorella*, showing no signs of damage. (b) Grey damage, characterised by the surface of the cushion being smooth and grey to black. (c) Speck damage, characterised by small reddish-brown patches or streaks of leaves, with their tips removed and their stems exposed. (d) Yellow damage where intact leaves had yellow discoloration adjacent to leaves with brown discoloration.

term-change plot photographs, and the presence of yellow damage was noted. A wind-exposure variable was calculated from the aspect readings (south-west=1, south and west=2, north-west and south-east=3, north and east=4, north-east=5). The strongest winds on the island are south-westerly.

Statistical methods for the spatial-comparison data

All analyses for all datasets were undertaken in Minitab16 (Minitab Inc. 2010) or R (version 2.15.1, R Core Team 2012). Chi-square was used to determine the significance of the co-occurrence of counts of each type of damage with classes of each of cushion size, exposure, ground cover and vegetation type. Chi-square was also used to determine whether the relationships between these predictor variables deviated from random.

Beta regression models (R betareg package, Cribari-Neto and Zeileis 2010) were used to determine the influence of ground cover, cushion size, vegetation type and exposure on percentage damage for each of the damage types. Both maximum likelihood and Akaike information criterion (AIC) were used to determine the combination of variables best related to percentage *Azorella* damage. The β regression model was selected for its appropriateness of use for proportion response variables that display both asymmetry and heteroscedasticity. The model was fitted via maximum likelihood using a parameterisation with a mean and precision parameter (ϕ) (Cribari-Neto and Zeileis, 2010). In instances of 0, the following conversion was applied: $y \times (n-1) + 0.5/n$, where n is the sample size (Smithson and Verkuilen 2006). The variables were assessed using partial Wald tests.

The size-class distributions of the three types of damage were graphed. The strong wind directions as indicated by vegetation distortion and the direction of concentration of each type of damage were graphed. The relationships between percentage damage of each type and elevation were analysed for each site by using Pearson's product moment correlation coefficient.

Statistical methods for the temporal-change data

One-way ANOVA was used to determine whether elevation varied between the medium term-change plots with yellow damage in 2010 and those without such damage. For each of slope, aspect and vegetation type, chi-square was used for the same purpose.

The changes in the live cover of each of *Azorella* and *Agrostis* between 2010–2011, 2011–2012 and 2012–2013 were calculated for the 2×2 m medium term-change plots and standard errors were calculated. Analysis of covariance with quasibinomial errors was applied in two generalised linear models, as follows: live *Azorella* cover in 2013 = live *Azorella* cover in 2010, yellowing in 2010, live *Azorella* cover in 2010 \times yellowing in 2010; *Agrostis* cover in 2013 = *Agrostis* cover in 2010, yellowing in 2010, *Agrostis* cover in 2010 \times yellowing in 2010. Pearson's product moment correlation coefficient was used to determine the relationship between the wind-exposure index and percentage damage to cushions for each of 2010, 2011, 2012 and 2013, and the relationship between change in live *Azorella* cover between

2010 and 2013 and the change in *Agrostis* cover between 2010 and 2013.

Results

Damage type

The three types of damage that were discerned were distinguished by colour, surface characteristics and size. In grey damage, the surface of the cushion was smooth and grey to black (Fig. 2b). In speck damage, there were small reddish-brown patches or streaks of leaves, with their tips removed and their stems exposed (Fig. 2c). In yellow damage, intact leaves had yellow discoloration, and were adjacent to leaves with brown discoloration (Fig. 2d).

Spatial variation in damage type

Grey damage was dominant at eight of the spatial-comparison sites, yellow damage was dominant at two and speck damage was dominant in none, while being absent from several (Fig. 3). Grey damage varied enormously in its cover (Fig. 4). Most cushions had no yellow damage, but those cushions that did have it varied widely in its percentage cover (Fig. 4). Speck damage was rare and usually did not cover much of the cushion (Fig. 4).

The four predictor variables were partly coincident in their variation, with $P < 0.001$ (χ^2) for all pairs. The frequency of yellow damage was low on the most sheltered cushions (Table 1). The other available predictor variables did not explain yellow-damage frequency (Table 1) and no model for yellow-damage cover could be derived (Table 2).

Ground cover, vegetation type and exposure were the variables retained in the final model for percentage grey damage (Table 2), which was high on gravelly soils, in fjaeldmark and on the most exposed cushions (Table 1). There was significant variation in the frequency of grey damage in relation to these variables and cushion size, grey damage being most frequent on larger cushions (Table 1).

Cushions size and ground cover were the components in the model for percentage speck damage, with values being highest on soil and larger cushions (Table 2). The same two predictors were significant for frequency, as was vegetation type, with speck damage being greater in herbfield than fjaeldmark (Table 1).

Grey damage was concentrated in the south-west of the cushions (Fig. 5), the direction from which the prevailing winds emanate (Fig. 5), whereas speck damage was concentrated to the north and east (Fig. 5) and yellow damage, although tending to the south-west, was variable in its direction of concentration (Fig. 5).

Grey damage increased with elevation at one site ($r_{25} = 0.575$, $P = 0.002$), while decreasing with elevation at others ($r_{25} = -0.565$, $P = 0.002$; $r_{25} = -0.669$, $P < 0.001$; $r_{25} = -0.678$, $P < 0.001$). Speck damage decreased with elevation at one site ($r_{25} = -0.397$, $P = 0.040$). Yellow damage increased with elevation at the same site ($r_{25} = 0.449$, $P = 0.019$), but decreased with elevation at another ($r_{25} = -0.419$, $P = 0.030$).

Short-term change

Grey damage was observed on 28 of the 31 cushions when first photographed. This type of damage exhibited minimal temporal variation, although, in some cases, being partially replaced by

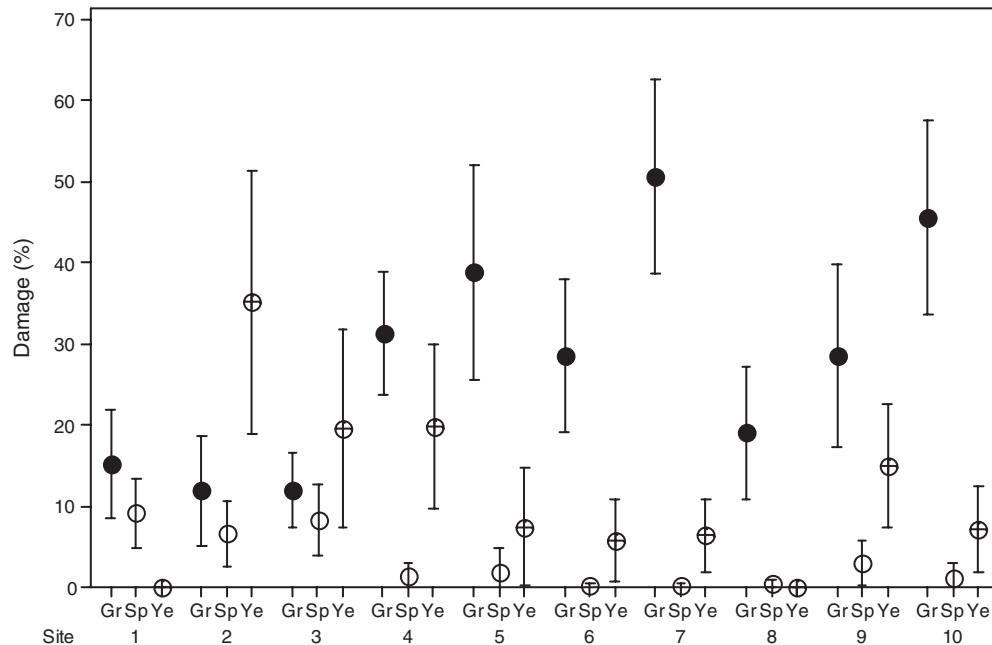


Fig. 3. Percentage mean cushion damage, with 95% confidence intervals by type and site for the 10 spatial-comparison sites. Gr, grey damage; SP, speck damage; Ye, yellow damage.

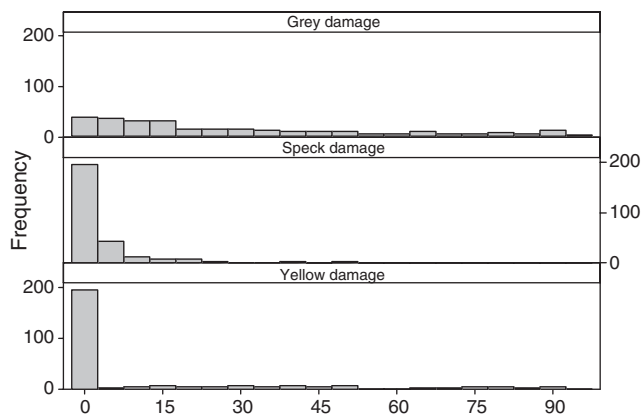


Fig. 4. Histograms for percentage damage to *Azorella macquariensis* cushions by type of damage from all the cushions in the spatial-comparison sites; $n = 270$.

green foliage between visits. Speck damage occurred in 26 of the 31 sites. Mild speck damage often disappeared between visits, whereas severe damage persisted. Overall, speck damage remained constant. Yellow damage occurred during observations in 5 of the 31 sites. At all of these sites, it expanded markedly in a clear dieback process, sometimes apparently spreading from one cushion to another (Fig. 6).

Medium-term change

Elevation did not differ between the plots with and without yellow damage in 2010 ($F_{1,28} = 0.59$, $P = 0.856$). There was also no significant difference for aspect ($\chi^2 = 0.11$, d.f. = 1,

Table 1. Percentage frequency of grey, speck and yellow damage on cushions against cushion size, exposure, surface condition and vegetation classes in the spatial-comparison study, showing results of chi-square analysis

Variable and class (n)	Grey (%)	Speck (%)	Yellow (%)
Cushion size			
Large (45)	95.6	55.6	28.9
Medium (104)	93.3	31.8	28.9
Small (121)	77.7	18.2	24.8
χ^2	15.4	22.33	0.6
d.f.	2	2	2
P	<0.001	<0.001	0.756
Exposure			
Exposed (47)	95.7	29.8	23.4
Intermediate (190)	95.3	28.9	31.6
Sheltered (33)	24.2	33.3	6.1
χ^2	126.8	0.3	9.7
d.f.	2	2	2
P	<0.001	0.878	0.008
Ground cover			
Gravel (114)	93.9	17.5	26.3
Soil and gravel (33)	93.9	39.4	27.2
Moss/soil (84)	78.6	26.2	22.6
Soil (39)	76.9	64.1	28.5
χ^2	14.6	32.2	3.4
d.f.	3	3	3
P	0.002	<0.001	0.328
Vegetation type			
Fjaeldmark (127)	94.5	20.5	27.6
Herbfield (143)	79.7	37.8	26.6
χ^2	12.7	9.6	0.1
d.f.	1	1	1
P	<0.001	0.002	0.856

Table 2. Beta regression coefficients with s.e. (mean model with logit link), Wald's z-value and modelled mean in percentage damage on individual cushions for each factor level for speck damage and grey damage in the spatial-comparison study
The yellow-damage model was not significant

Parameter	Coefficient (s.e.)	z	Mean (%)	P
Speck damage				
Intercept	−3.31 (0.22)	−15.32		<0.001
Ground cover				
Gravel			2.6	
Moss and soil	0.24 (0.16)	1.55	2.8	0.12
Soil	0.72 (0.19)	3.8	5.4	<0.001
Soil/gravel	0.29 (0.20)	1.45	3.4	0.15
Cushion size				
Large			4.6	
Medium	−0.36 (0.18)	−1.94	3.1	0.05
Small	−0.53 (0.19)	−2.78	2.6	0.005
Phi coefficient 3.9, log-likelihood 1957 on 7 d.f., pseudo- <i>R</i> ² 18.01%				
Grey damage				
Intercept	−0.76 (0.18)	−4.17		<0.001
Ground cover				
Gravel			33.7	
Moss and soil	0.24 (0.36)	0.68	19.4	0.5
Soil	−0.17 (0.36)	−0.47	14.4	0.64
Soil and gravel	0.69 (0.31)	2.27	35.7	0.02
Vegetation type				
Fjaeldmark			34.6	
Herbified	−0.89 (0.33)	−2.72	18.9	0.01
Exposure				
Exposed			30.9	
Intermediate	0.18 (0.19)	0.96	29	0.33
Sheltered	−1.96 (0.26)	−7.59	3.9	<0.001
Phi coefficient 1.7, log-likelihood 552 on 8 d.f., pseudo- <i>R</i> ² 45.63%				

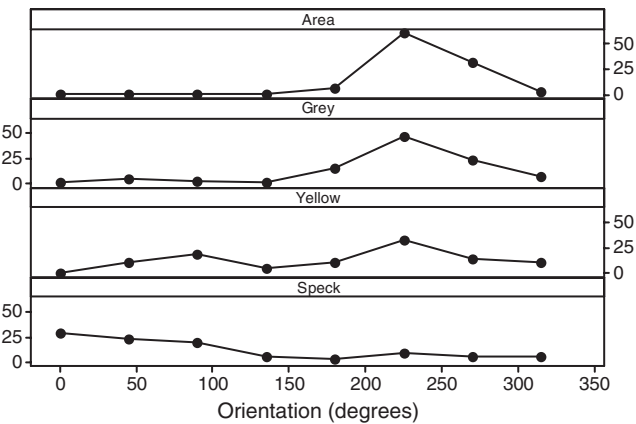


Fig. 5. Percentage frequency of wind direction in the proximity to cushion, as indicated by vegetation distortion (area, *n* = 270) and the orientation on the cushions of grey damage (*n* = 234), speck damage (*n* = 80) and yellow damage (*n* = 73). Data are from the spatial-comparison sites.

P = 0.772), slope (χ^2 = 0.01, d.f. = 1, *P* = 0.919) or vegetation type (χ^2 = 0.15, d.f. = 1, *P* = 0.696).
By 2013, yellow-coloured cushion foliage had disappeared from all plots in which it occurred in 2010. In all cases, this disappearance was associated with a transition from chlorosis to

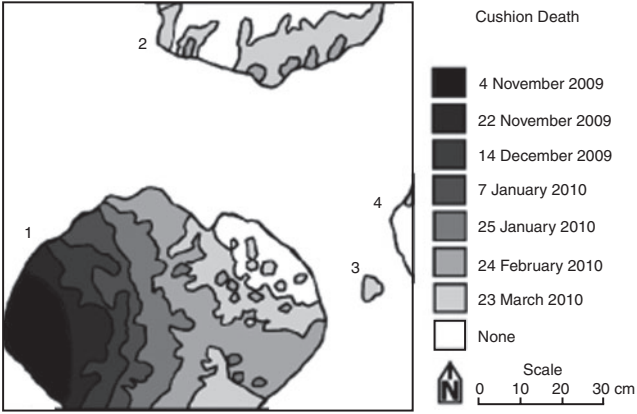


Fig. 6. The typical progression of dieback from yellow damage in a short term-change 1 × 1-m plot. Numbers are adjacent to individual cushions that are shown in outline.

Table 3. Generalised linear models for the percentage cover of live *Azorella* in 2013 and percentage cover of *Agrostis* in 2013 in the medium term-change study, showing estimated coefficients, the s.e. of the estimated coefficients, and *t* and *P*

Parameter	Coefficient	s.e.	<i>t</i>	<i>P</i>
Model for <i>Azorella</i> 2013				
Intercept	−2.329	0.315	−7.39	<0.001
Yellow 2010	0.709	0.477	1.49	0.151
<i>Azorella</i> 2010	4.109	0.633	6.49	<0.001
Interaction	−2.695	0.894	−3.02	0.006
Dispersion parameter for quasibinomial family taken to be 0.04546223				
Null deviance: 3.6477 on 26 d.f.				
Residual deviance: 1.0378 on 23 d.f.				
Model for <i>Agrostis</i> 2013				
Intercept	−2.837	0.322	−8.795	<0.001
Yellow 2010	1.038	0.368	2.821	0.01
<i>Agrostis</i> 2010	9.15	2.281	4.011	<0.001
Interaction	−4.451	2.37	−1.878	0.073
Dispersion parameter for quasibinomial family taken to be 0.02945486				
Null deviance: 3.94276 on 26 d.f.				
Residual deviance: 0.67353 on 23 d.f.				

extensive necrosis rather than recovery to healthy tissue. In 1 case of 14, yellow foliage became apparent in a plot in 2012 and 2013 that had green (healthy) cushions in 2010.
Yellow damage, *Azorella* live cover in 2010 and their interaction were all good predictors of *Azorella* live cover in 2013 in the generalised linear model (Table 3). *Azorella* live cover in 2013 less its live cover in 2010 was −4.65% for plots without yellow damage in 2010 and −21.73% for plots with some yellow damage at this time. *Azorella* had a live cover of >10% of cushion area in all plots in 2013. On the plots with the most dieback, *Azorella* was present as live branchlets in or between dead cushions. Heterogeneity in change in healthy cushion cover increased through time in the 2010 yellow-damage plots (Fig. 7).
Azorella live cover had an increasingly significant relationship with the wind-exposure variable as time elapsed (2010, *r*₂₈ = 0.334, *P* = 0.072; 2011, *r*₁₄ = 0.494, *P* = 0.052;

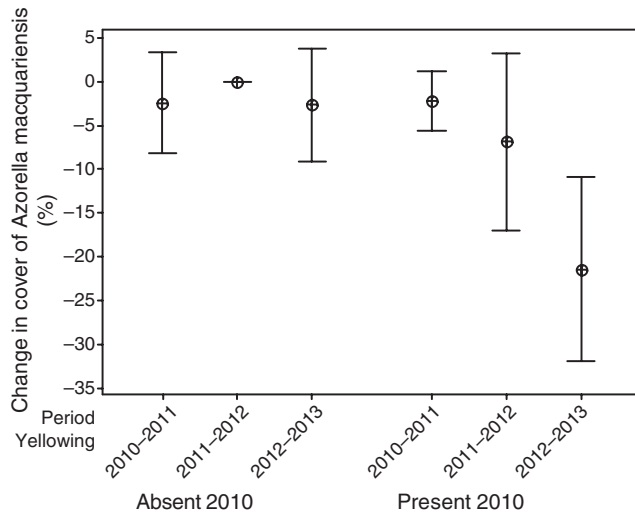


Fig. 7. Ninety-five per cent confidence limits for percentage cover change of healthy *Azorella macquariensis* in the $2 \times 2\text{-m}^2$ medium term-change plots ($n = 30$) for three periods. Plots with missing records were excluded.

2012, $r_{28} = 0.4$, $P = 0.028$; 2013, $r_{25} = 0.430$, $P = 0.025$). In all four years, the less exposed the site was, the greater the live cover. Grey damage began to appear on the windward surfaces of cushions two years after the passage of the chlorosis (Fig. 8d).

Change in live *Azorella* cover between 2010 and 2013 was negatively related to change in *Agrostis* cover ($r_{25} = -0.571$, $P = 0.002$). The generalised linear model for percentage *Agrostis* cover in 2013 had both yellow damage in 2010 and *Agrostis* cover in 2010 as significant components, but not the interaction (Table 3). Between 2010 and 2013, *Agrostis* cover increased by an average of 4% where there was no yellow damage in 2010, whereas where there was yellow damage in 2010, there was an increase of 12%. The response of *Agrostis* was highly heterogeneous (Fig. 9). Examination of the photographs suggested that *Agrostis* expansion, where it occurred, partly consisted of growth of established individuals and partly consisted of establishment of new individuals on cushion surfaces (e.g. Fig. 8).

Observations on the process of dieback

The general pattern of progression of dieback associated with yellow damage was that a small (2–10 cm), diffuse yellow stippling appeared in a zone up to 50 cm in front of a 5–10-cm wide line of yellow leaves (Fig. 2d). In the wake of the front, the majority of the cushion was brown, although individual branchlets and small patches of cushions were usually left in an apparently healthy green state (Fig. 8b–d). This process was observed both on individual cushions and on cushion-banked terraces.

Between February 2010 and January 2011, examples of the yellowing front were seen to progress between 30 and 100 cm, the progression being at a greater speed in lower-profile plants than in higher relief cushions. The disease front appeared to progress at similar speeds in the inter-cushion spaces. Rosettes of *Pleurophyllum hookeri* Buchan. greater than 10 cm in diameter

died with the passage of the yellow line, although smaller rosettes survived. Some areas of cushion did not come out of winter senescence, suggesting that dieback was active in dormant cushions. By February 2013, many cushions with yellow damage in 2010 and 2011 had some expansion of live foliage, although most of the previously live cushion foliage was dead and decaying.

The twelve plants with yellow lines or patches that were excavated in 2009 had rotted tap roots. Several instances of a lesion between healthy and dead tissue in the tap root were also observed (Fig. 8e). Live cushion shoots in dieback areas in March 2013 had imbricately packed dead leaves and leaf scars from previous seasonal cycles (Fig. 8f). These characteristics differed from those of young seedlings in rocky areas, which had short branches split off from a basal node, below which a well developed tap root was present (Fig. 8g).

Discussion

Types of damage and dieback

Two of the three distinct damage types evident in 2009–2010 were also evident in the 2013 photographs, speck damage having largely healed. The series of photographs between 2010 and 2013 (Fig. 8) showed that yellow damage could be a precursor to grey damage, especially on the parts of cushions exposed to strong winds, as further indicated by the increasing significance of the correlation between percentage live cushion and wind exposure between 2010 and 2013. We cannot determine whether all grey damage develops from yellow damage, but we can conclude that recovery from yellow damage disproportionately occurs on the sheltered parts of cushions, and that a lack of recovery is expressed in grey damage.

Although yellow damage had a low incidence (16%) in the randomly located $1 \times 1\text{-m}$ short term-change plots and averaged only 12% of the surface area of cushions at the 10 spatial-comparison sites (cf. 3% for speck damage and 28% for grey damage), it was present on all cushions that exhibited an increase in dieback between spring and autumn 2009–2010 and was associated with all of the high level of ongoing dieback between 2010 and 2013 in the medium term-change plots.

Possible causes of types of damage

Much of our data are consistent with exposure to strong winds as a major contributor to grey damage, including its preferential occurrence in fjeldmark, on gravelly surfaces and in areas with high levels of exposure (Tables 1, 2), and its concentration on the windward sections of the cushions (Fig. 6). An association between wind exposure and damage has been widely observed in cushion plants (Taylor 1955a; Ashton and Gill 1965; Molau 1996; le Roux and McGeoch 2008). In our study area, wind damage might have been at least partly facilitated by the dieback that followed the chlorosis of yellow damage. Additionally or alternatively, the apparent wind damage may have been caused by increased drought stress, as has been suggested as a possibility for other Macquarie Island species by Scott and Kirkpatrick (2013) and for another *Azorella* species by le Roux *et al.* (2005).

The localised clipping of leaves characteristic of speck damage strongly suggested that rabbit-grazing was its cause.

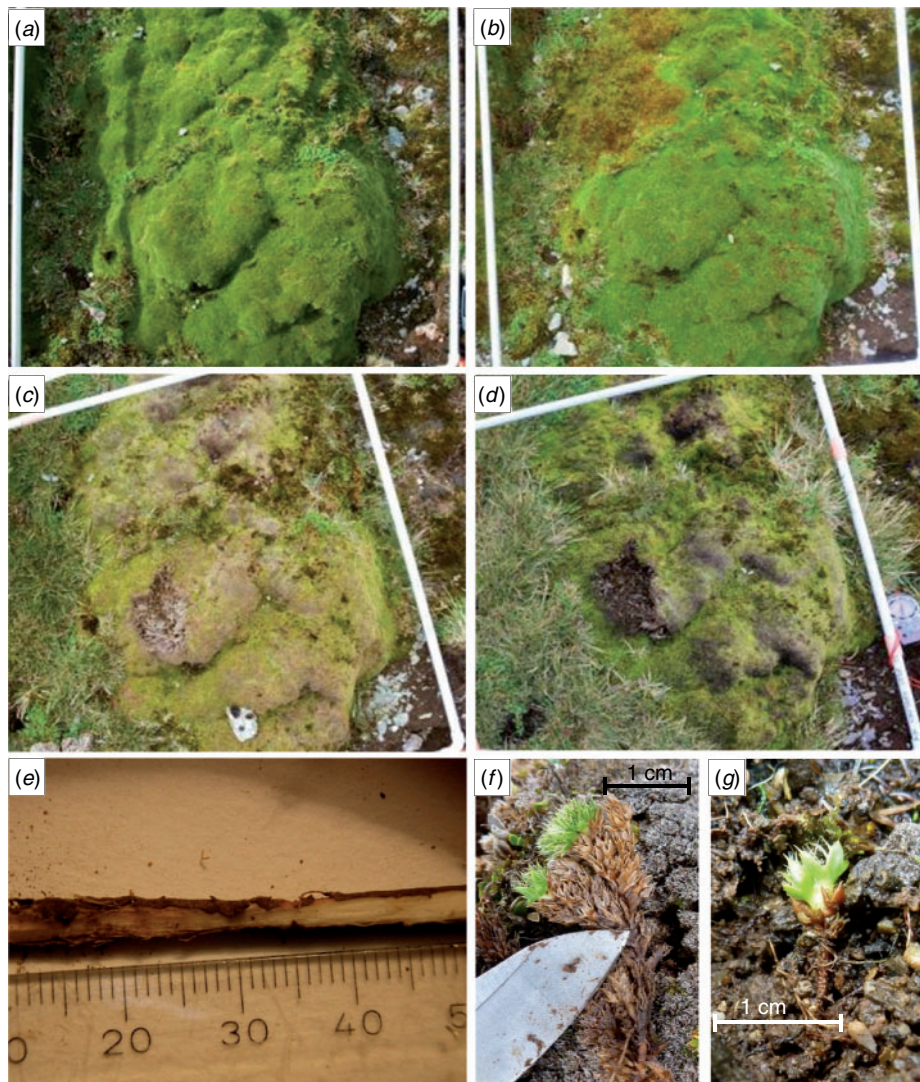


Fig. 8. (a–d) Progression of yellow dieback (the quadrat frame is 1×1 m). (a) February 2010, no apparent symptoms. (b) January 2011, yellow dieback progressing from top-left corner. (c) February 2012, dieback front has passed through cushion, majority of tissue appearing dead, *Agrostis magellanica* expanding. (d) February 2013, recovery of part of cushion and expansion of *A. magellanica*. (e) Lesion in excavated *Azorella* tap root on left, with healthy root on right. (f) Excavated surviving branchlet from died back cushion, compared with (g) structure of first- or second-year seedling. Quadrat frame is 1×1 m.

Consistent with our directional data (Fig. 6), rabbits are known to minimise their exposure to strong winds (Southern 1940, 1948; Rowley 1957; Wheeler *et al.* 1981; Fraser 1992; Ballinger and Morgan 2002). Speck damage was strongly associated with herbfield, rather than fjeldmark, reflecting the known relative abundance of rabbits (Copson *et al.* 1981). New speck damage was not noted after 2011, which coincides with the completion of aerial baiting for the Macquarie Island Pest Eradication Project, with no live rabbit observed on the island since November 2011 (Parks and Wildlife Service 2012).

Rabbits could not have been the primary cause of yellow damage (Figs 2d, 8a–d) because yellow damage persisted after rabbit extermination. Yellow damage was prominent on sheltered parts of the cushions as well as exposed parts, so wind was unlikely to have been its primary cause. Frost and drought are unlikely to be the causes of yellow damage because it had no

consistent association with topographic position or the tops of cushions, and no associated moss dieback was observed.

The patchy incidence in relation to environment of yellow damage is consistent with the presence of a soil-borne pathogen (Gilligan 1995). Such patchiness is largely a function of the variability in pathogen infectivity and host susceptibility in the primary and secondary infection phases (Burdon *et al.* 1989; Kleczkowski *et al.* 1997). The association of yellow damage with lesions and rotted tap roots further supports this hypothesis. A yellow discoloration of leaf tissue has been previously observed in pathogen-affected plants (Tamada and Baba 1973; Trapero-Casas and Jiménez-Díaz 1985). Brown discolorations have been observed in other cases (Scortichini and Lazzari 1996; Unger *et al.* 2005; Bobev *et al.* 2009), and a variety of discolorations ranging from yellow to brown in still others (Johnson and Littrell 1969; Fradin and Thomma 2006).

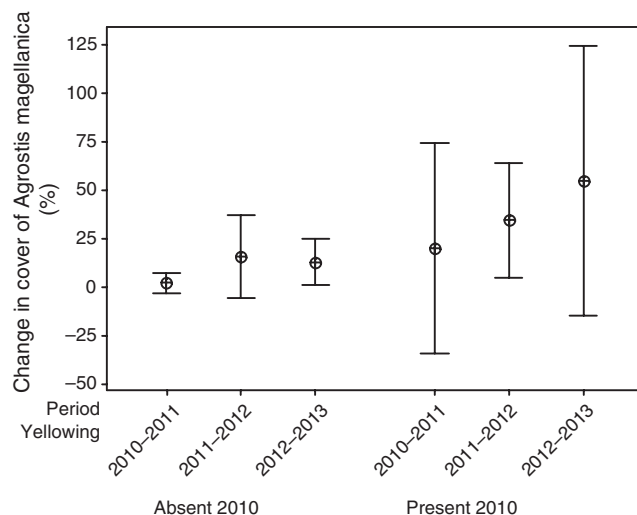


Fig. 9. Ninety-five per cent confidence limits for percentage cover change of *Agrostis magellanica* in the 2×2 -m² medium term-change plots ($n = 30$) for three periods. Plots with missing records were excluded.

Is Azorella on a path to extinction?

Our data did not indicate local extinction of *Azorella*, with the passage of the yellow front being followed by recovery (Fig. 8a–d). The individual shoots that survived dieback could be surviving branches of the parent plant, previously split off vegetative individuals or small genetically distinct individuals that have established within the parent cushion (Fig. 8f).

Given that there were no environmental or vegetation differences between the medium term-change plots with yellow damage in 2010 and those without damage at the time, the putative pathogen has not realised its potential range, at least based on the variables measured in the present study. Yet, it did not attack cushions in 13 of the 14 plots from which it was absent in 2010. These data, combined with the observations of yellow lines in cushions by scientists in the 1950s and the 1980s, could mean that the widely observed cushion death of 2008–2010 represented a peak in fluctuations of a pathogen that is widespread on the island. However, the climate of the island is changing (Adams 2009), possibly in a way that favours the organism that may cause the necrosis preceded by yellow damage, so a precautionary approach is required.

Is Agrostis replacing Azorella?

There was no indication in our data that *Agrostis* was displacing *Azorella* in plots where cushions were healthy throughout the period 2010–2013. However, *Agrostis* has proven effective in occupying the dead parts of cushions. Whether this strong shift in vegetation dominance is likely to persist is uncertain. Further long-term observation of our plots is desirable to determine whether the replacement of *Azorella* by *Agrostis* will be persistent. Persistence may vary in response to the severity of the environment and cushion size, as for the closely related species, *Azorella selago* Hook. (le Roux and McGeoch 2008; le Roux *et al.* 2013).

Conclusions

We conclude that there is strong circumstantial evidence that the fast-spreading dieback associated with yellow damage is caused by a pathogen, and that specks were mechanical damage caused by grazing by the recently eradicated rabbits. Grey damage is strongly associated with wind exposure, but wind may not always be its primary cause. The dieback associated with yellow damage does not appear to cause local extinction of *Azorella*, but is associated with a decline in cushion cover and an expansion of *Agrostis*.

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