Spatial variation in structural damage to a keystone plant species in the sub-Antarctic: interactions between *Azorella selago* and invasive house mice

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Abstract: On Southern Ocean islands the effects of the house mouse on plants are not well understood. In particular, its influence at the landscape scale has largely been overlooked. To address this issue, we systematically mapped the distribution of a keystone, cushion plant species, *Azorella selago*, and mouse damage to it across Marion Island. Mouse damage was observed in a third of the sampled sites from sea level to 548 m a.s.l. Damage to individual cushions ranged from single burrows to the disintegration of entire cushions. Mouse damage was high in sites with low *A. selago* density, suggesting that in areas of low cushion density the impact of mice may be substantial. Moreover, it is not simply direct impacts on the *A. selago* population that are ecologically significant. *Azorella selago* cushions serve as nurse plants for many epiphyte species, so increasing the altitudinal range of a variety of them, and also house high densities of invertebrates especially in fellfield landscapes. In consequence, this study demonstrates that mice are having a significant, negative impact at the landscape scale on Marion Island, so adding to the growing list of species and ecosystem-level effects attributable to this invasive rodent.

Introduction

The house mouse, *Mus musculus* L., is one of the most successful mammal invaders on Southern Ocean islands, having established on at least eight of them (Frenot *et al.* 2005). On several of these islands the impacts of this rodent are now clear. Mice consume large numbers of indigenous invertebrates, including important keystone species such as flightless moth caterpillars on Marion Island (Chown & Smith 1993, Smith *et al.* 2002); earthworms, weevils and aphids on Guillou Island in the Iles Kerguelen (le Roux *et al.* 2002); and several invertebrate species on Macquarie Island (Copson 1986). The effects of mice also extend beyond direct influences on the populations of their prey species, and these include alterations of nutrient dynamics (Smith & Steenkamp 1990), changes in the distribution of prey given mouse habitat preferences (Jones *et al.* 2003), and indirect effects on indigenous predators as a consequence of competition for the same food resources (Huyser *et al.* 2000). More recently, mice have been found to feed on live albatross and petrel chicks, so posing a considerable threat to species that are in many cases already impacted by long-line fishing activities at sea (Wanless *et al.* 2007). In consequence, the significance of the introduced house mouse in the terrestrial ecosystems of Southern Ocean islands is now widely appreciated (Frenot *et al.* 2005).

However, one aspect of their activities has, to date, been under-investigated: the direct impact that the species might have on plants, and the secondary landscape level effects that might arise as a consequence. Whilst many studies have documented the presence of seeds and other plant remains in the stomach contents of mice, food items which may have both a high percentage occurrence ($> 75\%$) (e.g. le Roux *et al.* 2002) and percentage contribution (at times $> 50\%$) (Smith *et al.* 2002), few investigations have sought to determine the impact that this level of consumption might have on the plants. Only Chown & Smith (1993) have shown that by consuming seeds of the sedge *Uncinia compacta*, mice may be restricting its range expansion as a consequence of drying conditions on Marion Island. Nonetheless, high levels of mouse activity and consumption may well have broader effects, especially by transporting alien species (e.g. *Taraxacum* on Kerguelen - le Roux *et al.* 2002), or by changing the landscape through seed harvesting or burrowing (Avenant & Smith 2003).

The latter seems especially probable on Marion Island, where Avenant & Smith (2003) found that more than

50% of mouse burrow entrances occurred in *A. selago* cushions at sites where the species was not the dominant plant. Their findings suggest that *A. selago* might be the preferred species for burrow entrances in habitats where it is present. Given the significance of this plant as a keystone species, especially in fellfield areas (Barendse & Chown 2001, McGeoch *et al.* 2008), and its effects on landscape structure (Boelhouwers *et al.* 2000), mouse activity in *A. selago* could potentially have considerable, landscape level implications for ecosystem functioning on the island. In this study we examine the extent and spatial distribution of disturbance to *A. selago* cushions by mice using systematic and *ad hoc* sampling of cushions at an island-wide scale. We do so especially to determine the extent to which the house mouse may be having impacts on the landscape: a scale of impact previously not investigated for this species on the islands to which it has been introduced.

Materials and methods

Study site and species

Marion Island (46°54'00"S, 37°45'00"E), is situated just to the north of the Antarctic Polar Frontal Zone, and together with neighbouring Prince Edward Island, makes up the Prince Edward Island (PEI) group. The island has an area of 290 km^2 and rises to 1230 m with a 72 km coastline (Verwoerd 1971). It has undergone rapid climate change over the last five decades, with mean annual temperature increasing by nearly 1.5°C (le Roux & McGeoch 2008, see also Chown & Froneman 2008 for further information on the island's ecosystems). Because of its low temperature and geographic isolation it has relatively low

species richness (Chown *et al.* 1998, Chown & Froneman 2008). The island's vegetation has been classified into seven vegetation complexes containing twenty-three habitats (Chown & Froneman 2008).

The house mouse was introduced to Marion Island over 200 years ago (Watkins & Cooper 1986), probably from Scandinavia (van Vuuren & Chown 2007). Following the successful eradication of feral cats (Bester *et al.* 2000), it is now the only naturalized terrestrial alien invasive mammal on Marion Island. Its population is thought to have increased over the last thirty years as a consequence of climatic amelioration. Nonetheless, the temporal demographic picture is complex with both temperature and population density acting in concert to affect population levels (Smith & Steenkamp 1990, Ferreira *et al.* 2006, van Aarde & Jackson 2007). Although the eradication of cats might have affected mouse densities, mice were never an important prey item for cats and cat predation probably did not limit the mouse population (Ferreira *et al.* 2006). At present, lowland mouse densities are in the region of 100–260 mice.ha^{-1}, depending on vegetation type, with peak densities occurring in April/May, and the lowest densities in October–December (Ferreira *et al.* 2006). The species has also increased its altitudinal range on the island. Anderson & Condy (1974) estimated that high mouse densities were found only below 300 m a.s.l. Later, Gleeson (1981) estimated that at 450 m a.s.l. mice were surviving close to their physiological limits on the island. Mice are now active, but not abundant, close to 800 m a.s.l. (in the Katedraalkrans field hut; personal observation) and sightings of dead mice have been reported from close to 1200 m a.s.l. (Avenant & Smith 2003).

Azorella selago Hook. f. (Apiaceae) is a cushion-forming plant and is an important constituent of sub-Antarctic plant
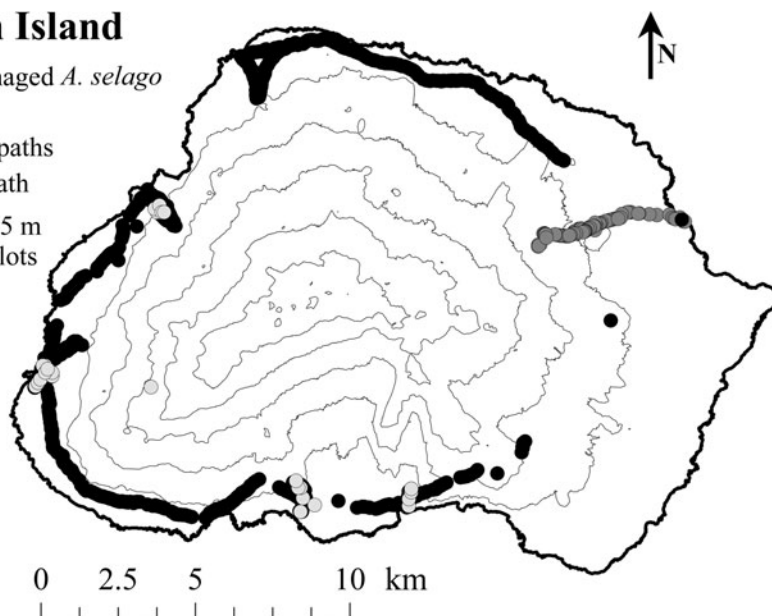

Fig. 1. *Ad hoc* observations of mouse activity (damage) in *Azorella selago* cushions along coastal and inland paths on Marion Island, as well as for the twenty-six *ad hoc* 10 m × 15 m plots.

Table I. Summary statistics for the number of *Azorella selago* cushions and the numbers of mouse burrows per plot and per cushion in the 26, 150 m² plots.

	n	Mean ± SE	Min.	Max.
No. *A. selago* cushions per plot	26	18.00 ± 1.46	5.00	34.00
Cushion density (m⁻²)	26	0.12 ± 0.01	0.033	0.227
No. mouse burrows per plot	26	19.65 ± 2.96	3.00	53.00
No. burrows overall found in *A. selago* cushions	26	11.38 ± 1.55	3.00	32.00
No. *A. selago* cushions containing burrows	26	6.12 ± 0.74	1.00	18.00
No. burrows per cushion	26	2 ± 0.2	1	4

communities (Huntley 1972). On Marion Island it is one of the five vascular plant species dominating the aerial standing crop (Smith 1978), and it is the only vascular plant that occurs in all vegetation complexes on the island (Smith *et al.* 2001), ranging from sea level to approximately 840 m a.s.l., so also setting the altitudinal limits for vascular plants on the island (Hedding 2006).

The leaves and stems of individual *Azorella selago* plants grow tightly together to form hard, compact surfaces of various shapes and sizes, resulting in two distinct growth forms - discrete cushions, and large, continuous mats (Frenot *et al.* 1993). The discrete cushions are spatially isolated individuals that are often surrounded by bare soil and rock, while the mat growth form is characterized by flat, continuous expanses of multiple plants (Mortimer *et al.* 2008), often associated with seepages (Huntley 1972, Gremmen 1981). Continuous mats of *A. selago* may extend over areas as large as 1200 m². The species is a slow growing perennial (le Roux & McGeoch 2004), with cushion age estimated to be between 30 and 80 years for cushions of 40 cm diameter (le Roux & McGeoch 2004).

Sampling

Since most studies have examined the ecology and the impacts of mice on invertebrates at low altitudes (e.g. Gleeson & van Rensburg 1982, Chown & Smith 1993,
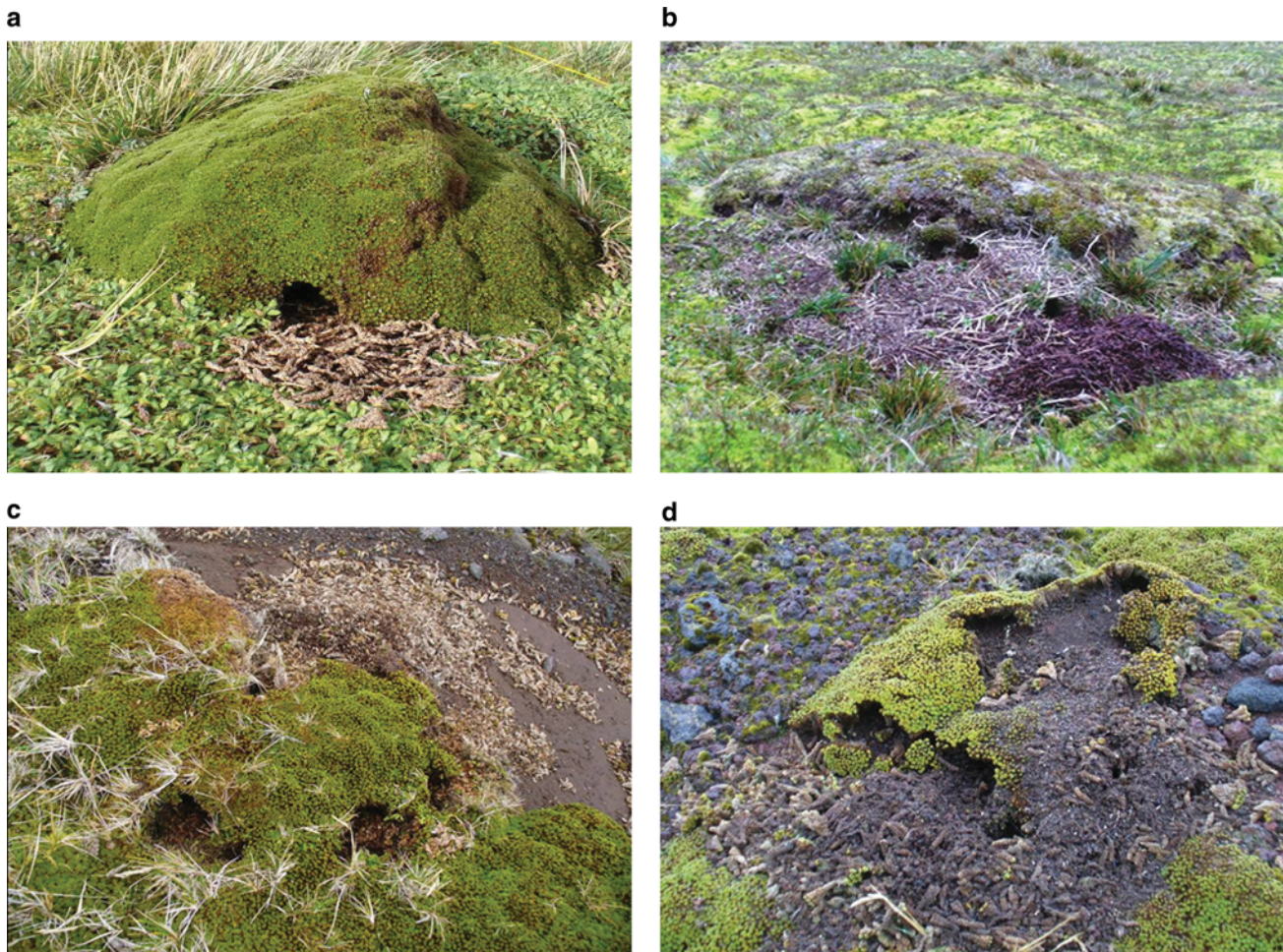

Fig. 2. The observed mouse damage to *Azorella selago* cushions along paths and across Marion Island (in systematic and *ad hoc* plots). *Azorella selago* with **a.** a single burrow entrance, **b.** multiple burrow entrances, **c.** multiple burrow entrances and partial disintegration, and **d.** a disintegrated cushion where mouse burrow entrances are barely visible.
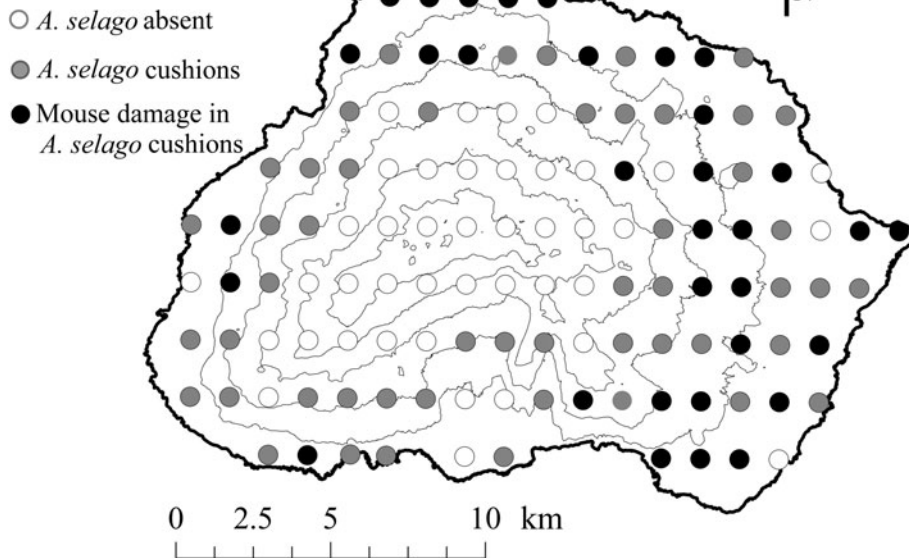
Fig. 3. The distribution of *Azorella selago* recorded on a minute-by-minute basis across Marion Island. The white circles indicate areas where *A. selago* is absent. The grey circles show areas where *A. selago* is present, but no mouse damage was found, while the black circles are indicative of *A. selago* cushions that had signs of mouse damage.

Avenant & Smith 2003, Ferreira *et al.* 2006) and to avoid bias towards paths, the abundance and distribution of *A. selago*, and damage to it by mice across its entire, island-wide range was quantified. That is, the extent of the sampling covered the entire island. Owing to the island's considerable size, the resolution of the sampling was chosen as 1 × 1 minute. These one minute latitude/ longitude gridline intersection points resulted in a total of 124 points sampled across the island. They were located in the field using a handheld GPS receiver unit, and at each sampling point a 64 m^2 grid was placed and the total number of *A. selago* cushions (cushion density) and number of mouse burrows and/or excavated *A. selago* cushions (burrow density) were counted in each plot. Thus, the extent of the sampling was 290 km^2, the resolution was 1 × 1 minute, and the sample unit size was 64 m^2 (see McGeoch & Gaston (2002) for additional discussion of this terminology). The sampling protocol was adopted after careful consideration of the total island area to be covered relative to the spatial variation in cushion densities that had been recorded previously (where present, *c.* 0.14 to 1.55 cushions.m^{-2}, McGeoch *et al.* 2008).

In addition to the systematic sampling, twenty-six, 150 m^2 plots (randomly located at low altitudes, below 300 m a.s.l.) at several locations around the island (see Fig. 1) were also surveyed. In these plots *A. selago* density, the number of mouse burrows (occurring in both *A. selago* and the surrounding vegetation), the number of *A. selago* cushions which had been burrowed into, and the number of mouse burrows occurring in each *A. selago* cushion were recorded.

Data analyses

Global positioning system point localities were converted to shapefiles and the distribution of *A. selago* cushions, including those that had signs of mouse damage, was mapped (ArcGIS^{TM} 9.1 ArcMap), for both the systematic and *ad hoc* sampling. Universal kriging (ArcGIS^{TM} 9.1 Geostatistical Analyst), a method used for producing interpolated maps by determining the level of spatial autocorrelation of the variable being analysed and for the prediction of abundances at unsampled sites (Zimmerman & Zimmerman 1991), was used to interpolate the distribution of *A. selago* density, recorded in the 124, 64 m^2 plots, across Marion Island. The proportion of mouse-damaged *A. selago* cushions per 64 m^2 plot (only plots with cushions that were burrowed into) was also interpolated by means of kriging. For both sampling approaches we also re-expressed the data on the basis of the number of burrows per cushion surface area using median cushion diameter estimates (given a right-skew in the frequency distribution) obtained from three different areas of the island (0.475 m, see le Roux & McGeoch 2004), and the assumption of an approximately spherical cushion shape.

Results

Opportunistic field observations showed that mouse damage to *Azorella selago* was almost continuous along coastal and inland paths on Marion Island (Fig. 1). In the twenty-six, 150 m^2 *ad hoc* plots, the number of burrow entrances in cushions ranged from one to four (Table I), and in some cases entire cushions were excavated by burrowing, causing the disintegration of the plant (Fig. 2). In the *ad hoc* plots, a mean of 18 *A. selago* cushions was found per plot (a mean density of 0.12 cushions.m^{-2}) (Table I). Of a total of 19.7 mouse burrows per plot, approximately
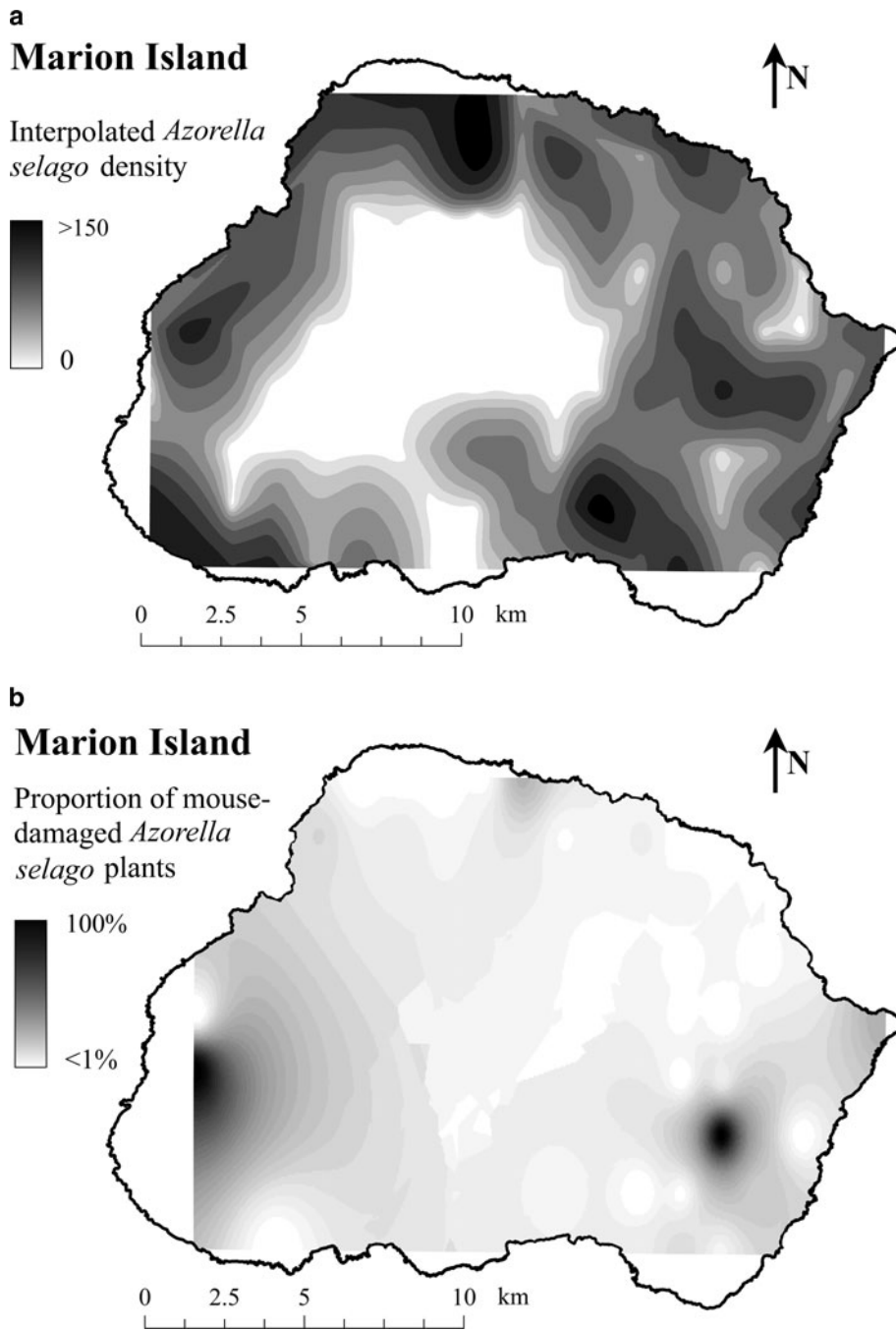
a

Marion Island

Interpolated *Azorella selago* density

b

Marion Island

Proportion of mouse-damaged *Azorella selago* plants

Fig. 4. a. Interpolated *Azorella selago* cushion density in 64 m^2 plots on a minute-by-minute basis across Marion Island. White areas indicate sites where *A. selago* is absent and the black areas represent high *A. selago* densities (>150 cushions per plot).
b. Interpolated proportions of mouse-damaged *Azorella selago* cushions in 64 m^2 plots based on the thirty-two plots where *A. selago* was damaged or burrowed into by mice, with mouse damage ranging from <1% (white areas) to 100% (black areas).

11.4 burrows were found in *A. selago* cushions, the remainder being found in other vegetation (Table I). Based on a median cushion diameter of 0.475 m (le Roux & McGeoch 2004), and the assumption of a roughly spherical cushion (giving a median area of 0.746 m^2), the density of mouse burrows per cushion surface area was estimated as 0.85 burrows.m^{-2} on average, ranging from a minimum estimate of 0.44 burrows.m^{-2} of cushion area to a maximum estimate of 3.0 burrows.m^{-2} of cushion area.

In the systematic sampling (the 124, 64 m^2 plots), *A. selago* was recorded in 83 of the 124 plots, between 37 m and 667 m a.s.l. (Figs 3 & 4a). Cushion density ranged from 0.016 to 3.25 cushions.m^{-2} (mean $\pm$ SE: 0.81 $\pm$ 0.08 cushions.m^{-2}), excluding coalesced, mat-like cushions which were found in 14 of the 83 plots. Mouse burrows were found in 32 of the 83 plots (39%) and in cushions up to 548 m a.s.l. (Fig. 3). In these, mostly higher elevation plots, the number of burrows per *A. selago* cushion was low (mean $\pm$ SE: 0.13 $\pm$ 0.04), and 28 plots had < 15% of their *A. selago*

cushions affected by mice (Fig. 4b). Areas that had high *A. selago* densities tended to have a lower proportion of mouse-damaged cushions (compare Fig. 4a & b).

Discussion

To date, investigations of the impacts of house mice on Southern Ocean ecosystems have been concerned largely with their direct effects on invertebrates and seabirds, and indirect effects on nutrient cycling. By contrast, little attention has been given to their impacts on plant populations (beyond documenting the inclusion of plant material in the diet) and certainly not at a landscape scale. This study makes it clear that neglect of such landscape scale impacts will lead to an underestimate of the significance of introduced mice in Southern Ocean island ecosystems. Structural damage by mice to *A. selago* is widespread on Marion Island, being found across nearly the full range of the cushion plant and up to 548 m in elevation, close to the elevational limit of cushions (667 m a.s.l.) identified in the systematic sampling. In addition, *c.* 39% of plots sampled contained mouse damage, and within these plots damage was sometimes extensive, although more typically fewer than 15% of cushions were affected.

In lowland areas, the *ad hoc* sampling revealed a mean density of *c.* 0.85 burrows.m^{-2} of cushion surface area. Moreover, it can be assumed that *A. selago* cushions constitute *c.* 5% of overall surface area at these typically lower elevations, given that other plant species dominate the lowland vegetation (Chown & Froneman 2008). At higher elevations, the percentage surface area covered by cushions ranges from 7 to 33% with a mean of *c.* 20% (Nyakatya *et al.* unpublished data; see also Barendse & Chown (2001) who found a value of 8.7%). On this basis, an estimate of *c.* 425 mouse burrows per hectare can be made (0.85 burrows.m^{-2} × 500 m^2 of cushion.ha^{-1} = 425 burrows.ha^{-1}), which is in keeping with the 340 to 1000 burrow.ha^{-1} recorded by Avenant & Smith (2003) in other lowland vegetation types. At the mostly higher elevation, systematic sampling plots, mean cushion density was high, at 0.81 cushions.m^{-2}, and burrow density was low, typically 0.13 burrows per cushion or 0.16 burrows.m^{-2} of cushion surface area. Assuming a mean surface area covered by *A. selago* cushions of *c.* 20% of the total surface area available (see above), burrow density at these mostly higher elevations amounts to *c.* 320 ha^{-1}, a value also in keeping with the lower end of those found by Avenant & Smith (2003) for coastal areas. These estimates provide grounds for a whole-island first estimate of mouse impact on *A. selago*. If it is assumed that at low elevations (200–400 m) 0.85 burrows are found per m^2 of cushion surface, that 5% of surface area is covered by *A. selago* cushions, and that the total surface area of these elevations is 6705 ha (Meiklejohn & Smith 2008), *c.* 2.8 million burrows are likely. At the higher elevations (400 to 600 m,

5206 ha), by similar calculation, *c.* 1.7 million burrows are present. In total, 4.5 million mouse burrows are likely to have been present at the time of sampling. These values appear extraordinarily high, but on closer assessment are not unrealistic. By using the digital elevation model surface area data provided by Meiklejohn & Smith (2008) and the lowest (0.12 cushions.m^{-2}) and highest (2.81 cushions.m^{-2}) cushion density estimates for all studies of this species (Hugo 2006, Nyakatya 2006, this study), the estimated total number of cushions on the island, between 200 and 600 m a.s.l., varies between 11.4 and 267 million cushions (acknowledging that much spatial variation is present (Fig. 4b), and in many areas cushions coalesce to form mats (Gremmen 1981, Mortimer *et al.* 2008)). These numbers provide an estimate of 0.02 to 0.4 mouse burrows per cushion, which encompasses the recorded value of 0.13 burrows per cushion in the systematic sampling plots.

Given that mice are clearly capable of causing total disintegration of cushions, that *A. selago* cushions are in the order of 30 to 80 years old on average (le Roux & McGeoch 2004), and that special, and currently unknown, conditions appear to be required for seedling establishment (McGeoch *et al.* 2008), this level of 'standing damage' is substantial and of considerable concern for a species of which the population dynamics and turnover are so poorly known. Certainly it appears that impacts in fellfield systems may be much more significant than previously thought (e.g. Gleeson & van Rensburg 1982). However, establishing the real significance of these impacts will require an estimate of annual mouse damage to cushions as well as recruitment to the *A. selago* population because it is the interaction of these two rates that will provide the most meaningful estimate of impact. Such estimates will require long-term studies of both mouse and *A. selago* populations in a spatially explicit fashion. The spatial detail will be especially necessary because mouse damage to cushions is not uniformly distributed across the island, as is clear from the landscape scale variation in the proportion of cushions affected by mouse burrowing (Fig. 4b) relative to cushion density (Fig. 4a). High cushion density areas are less affected by mice than low cushion density areas. It seems likely that, given temperature and density regulation of mouse abundances (Ferreira *et al.* 2006), this spatial asynchrony may well be a consequence of a surplus of cushion resources in high cushion density areas. However, only further, detailed demographic studies will reveal its cause. At present, explicit demographic work of this form is not being undertaken on the island, although several long-term plots to assess *A. selago* population dynamics have been established (McGeoch *et al.* 2008).

Of course, it is not simply direct impacts on the *A. selago* population that may be ecologically significant. *Azorella selago* serves as a nurse plant for many epiphyte species, so increasing the altitudinal range of a variety of them, and also houses high densities of invertebrates, acting as a

keystone species especially in fellfield landscapes (Barendse & Chown 2001, McGeoch *et al.* 2008). In this way it significantly influences the structure and dynamics of fellfield systems, also contributing substantially to successional patterns found on Marion Island (Yeloff *et al.* 2007). By damaging cushions, and in some cases by causing their disintegration, mice might, to an unknown and quite likely large extent, be affecting this keystone role of *A. selago*. Moreover, because warming and drying on the island (le Roux & McGeoch 2008) are predicted to have deleterious effects on cushions and their associated biota (McGeoch *et al.* 2006), and because further climate change is predicted to lead to greater impacts by mice (Smith & Steenkamp 1990), the landscape level impacts of mice on ecosystem functioning, as a consequence of their predilection for *A. selago* cushions, might be larger than presently estimated.

In addition to quantifying levels, distribution and rates of impact, understanding the reasons for the selection of cushions by mice is also important. It seems likely that a combination of thermally stable environments and significant food resources may prompt mice to select cushions for burrowing and for nest construction. Cushions act as a thermal buffer (Nyakatya & McGeoch 2008) and the difference in temperature between the plant surface and 10 cm below it may be as high as 2°C in summer. In winter, cushions are thermally stable. Overall, cushion interiors experience less extreme and less variable temperatures than the surface of the plants, irrespective of where they occur on the island (Nyakatya & McGeoch 2008). Cushions also house high densities of arthropods (Barendse & Chown 2001), including the species on which mice feed. For instance, weevils of the genus *Ectemnorhinus* are among the preferred prey of mice (Smith *et al.* 2002), and the biomass of weevil larvae in *A. selago* cushions is more than double that found in mire communities at similar elevations, and peaks during the winter months when resources may be most critical to survive harsh conditions (Chown & Scholtz 1989). Moreover, large weevil adults, preferred by mice (Chown & Smith 1993) are also abundant on *A. selago* cushions. Therefore, both milder temperatures and greater food availability in cushions may have provided mice with a means of colonizing high altitudes as climates have ameliorated in these areas (see le Roux & McGeoch 2008).

The present results have added to a growing list of the impacts that the house mouse has on Southern Ocean island species and ecosystems (Copson 1986, Smith & Steenkamp 1990, Huyser *et al.* 2000, Chown *et al.* 2002, le Roux *et al.* 2002, Jones *et al.* 2003, Wanless *et al.* 2007). Indeed, it is clear that this species constitutes a significant conservation challenge in the region, as do other rodent species, such as rats, that occur on several Southern Ocean islands (see e.g. Chapuis *et al.* 1994, Frenot *et al.* 2005). In a report concerning the possibility of eradicating

mice from Marion Island, Chown & Cooper (1995) stated that the eradication of mice from Marion Island is both "desirable and feasible". Rodents, including house mice, have been successfully eradicated from several New Zealand islands (reviewed by Towns & Broome 2003, see also Howald *et al.* 2007), but most of these islands are smaller in area (Towns & Broome 2003) than is the *c*. 290 km^2 Marion Island. Nonetheless, given their significant, and probably growing impacts, the eradication of mice from Marion Island is indeed desirable and should be made a priority during the implementation of the new Environmental Management Plan for the Prince Edward Islands (see Davies *et al.* 2007).

References

ANDERSON, G.D. & CONDY, P.R. 1974. A note on the feral house cat and house mouse on Marion Island. *South African Journal of Antarctic Research*, **4**, 58–61.

AVENANT, N.L. & SMITH, V.R. 2003. The microenvironment of house mice on Marion Island (sub-Antarctic). *Polar Biology*, **26**, 129–141.

BARENDSE, J. & CHOWN, S.L. 2001. Abundance and seasonality of mid-altitude fellfield arthropods from Marion Island. *Polar Biology*, **24**, 73–82.

BESTER, M.N., BLOOMER, J.P., BARTLETT, P.A., MULLER, D.D., VAN ROOYEN, M. & BUCHNER, H. 2000. Final eradication of feral cats from sub-Antarctic Marion Island, southern Indian Ocean. *South African Journal of Wildlife Research*, **30**, 53–57.

BOELHOUWERS, J., HOLNESS, S. & SUMNER, P. 2000. Geomorphological characteristics of small debris flows on Junior's Kop, Marion Island, maritime sub-Antarctic. *Earth Surface Processes and Landforms*, **25**, 341–352.

CHAPUIS, J.L., BOUSSÈS, P. & BARNAUD, G. 1994. Alien mammals, impact and management in the French Subantarctic islands. *Biological Conservation*, **67**, 97–104.

CHOWN, S.L. & COOPER, J. 1995. *The impact of feral house mice at Marion Island and the desirability of eradication: Report on a workshop held at the University of Pretoria*, 16–17 February 1995. Pretoria: Directorate Antarctica and Islands, Department of Environmental Affairs and Tourism.

CHOWN, S.L. & FRONEMAN, P.W., eds. 2008. *The Prince Edward Islands. Land-sea interactions in a changing ecosystem*. Stellenbosch: African SunMedia, 450 pp.

CHOWN, S.L. & SCHOLTZ, C.H. 1989. Biology and ecology of the *Dusmoecetes* Jeannel (Col. Curculionidae) species complex on Marion Island. *Oecologia*, **80**, 93–99.

CHOWN, S.L. & SMITH, V.R. 1993. Climate change and the short-term impact of feral house mice at the sub-Antarctic Prince Edward Islands. *Oecologia*, **96**, 508–516.

CHOWN, S.L., GREMMEN, N.J.M. & GASTON, K.J. 1998. Ecological biogeography of southern ocean islands: Species-area relationships, human impacts, and conservation. *American Naturalist*, **152**, 562–575.

CHOWN, S.L., MCGEOCH, M.A. & MARSHALL, D.J. 2002. Diversity and conservation of invertebrates on the sub-Antarctic Prince Edward Islands. *African Entomology*, **10**, 67–82.

COPSON, G.R. 1986. The diet of the introduced rodents *Mus musculus* L. and *Rattus rattus* L. on Subantarctic Macquarie Island. *Australian Wildlife Research*, **13**, 441–445.

DAVIES, S.J., CHOWN, S.L. & JOUBERT, L.S. 2007. Renewed management system and provisions for South Africa's sub-Antarctic islands. *Papers and Proceedings of the Royal Society of Tasmania*, **141**, 115–120.

FERREIRA, S.M., VAN AARDE, R.J. & WASSENAAR, T.D. 2006. Demographic responses of house mice to density and temperature on sub-Antarctic Marion Island. *Polar Biology*, **30**, 83–94.

FRENOT, Y., GLOAGUEN, J.C., PICOT, G., BOUGÉRE, J. & BENJAMIN, D. 1993. *Azorella selago* Hook. used to estimate glacier fluctuations and climatic history in the Kerguelen Islands over the last two centuries. *Oecologia*, **95**, 140–144.

FRENOT, Y., CHOWN, S.L., WHINAM, J., SELKIRK, P.M., CONVEY, P., SKOTNICKI, M. & BERGSTROM, D.M. 2005. Biological invasions in the Antarctic: extent, impacts and implications. *Biological Reviews*, **80**, 45–75.

GLEESON, J.P. 1981. *The ecology of the house mouse*, Mus musculus *Linnaeus, on Marion Island*. MSc thesis, University of Pretoria, Pretoria, 112 pp.

GLEESON, J.P. & VAN RENSBURG, P.J.J. 1982. Feeding ecology of the house mouse *Mus musculus* on Marion Island. *South African Journal of Antarctic Research*, **12**, 34–39.

GREMMEN, N.J.M. 1981. *The vegetation of the subantarctic islands Marion and Prince Edward*. Dr. W. JUNK, The Hague, 149 pp.

HEDDING, D.W. 2006. *Geomorphology and geomorphological responses to climate change in the interior of sub-Antarctic Marion Island*. MSc thesis, University of Pretoria, Pretoria, 99 pp.

HOWALD, G., DONLAN, C.J., TERSHY, B.R., CROLL, D.A., RUSSELL, J., SAUNDERS, A. & CLOUT, M. 2007. Invasive rodent eradications on islands. *Conservation Biology*, **21**, 1258–1268.

HUGO, E.A. 2006. *Spatial patterns in the microarthropod community associated with* Azorella selago (Apiaceae) *on the sub-Antarctic Prince Edward Island*. PhD thesis, Stellenbosch University, Stellenbosch, 162 pp.

HUNTLEY, B.J. 1972. Notes on the ecology of *Azorella selago* Hook. f. *Journal of South African Botany*, **38**, 103–113.

HUYSER, O., RYAN, P.G. & COOPER, J. 2000. Changes in population size, habitat use and breeding biology of Lesser Sheathbills (*Chionis minor*) at Marion Island: impacts of cats, mice and climate change? *Biological Conservation*, **92**, 299–310.

JONES, A.G., CHOWN, S.L. & GASTON, K.J. 2003. Introduced house mice as a conservation concern on Gough Island. *Biodiversity and Conservation*, **12**, 2107–2119.

LE ROUX, P.C. & MCGEOCH, M.A. 2004. The use of size as an estimator of age in the subantarctic cushion plant, *Azorella selago* (Apiaceae). *Arctic, Antarctic and Alpine Research*, **36**, 509–517.

LE ROUX, P.C. & MCGEOCH, M.A. 2008. Changes in climate extremes, variability and signature on sub-Antarctic Marion Island. *Climatic Change*, **86**, 309–329.

LE ROUX, V., CHAPUIS, J.-L., FRENOT, Y. & VERNON, P. 2002. Diet of the house mouse (*Mus musculus*) on Guillou Island, Kerguelen archipelago, Subantarctic. *Polar Biology*, **25**, 49–57.

MCGEOCH, M.A. & GASTON, K.J. 2002. Occupancy frequency distributions: patterns, artefacts and mechanisms. *Biological Reviews*, **77**, 311–331.

MCGEOCH, M.A., LE ROUX, P.C., HUGO, E.A. & CHOWN, S.L. 2006. Species and community responses to short-term climate manipulation: microarthropods in the sub-Antarctic. *Austral Ecology*, **31**, 719–731.

MCGEOCH, M.A., LE ROUX, P.C., HUGO, E.A. & NYAKATYA, M.J. 2008. Spatial variation in the terrestrial biotic system. *In* CHOWN, S.L. & FRONEMAN, P.W., *eds. The Prince Edward Islands. Land-sea interactions in a changing ecosystem*. Stellenbosch: African Sun Media, 245–270.

MEIKLEJOHN, K.I. & SMITH, V.R. 2008. Surface areas of altitudinal zones on sub-Antarctic Marion Island. *Polar Biology*, **31**, 259–261.

MORTIMER, E., MCGEOCH, M.A., DANIELS, S.R. & VAN VUUREN, B.J. 2008. Growth form and population genetic structure of *Azorella selago* on sub-Antarctic Marion Island. *Antarctic Science*, **20**, 381–390.

NYAKATYA, M.J. 2006. *Patterns of variability in* Azorella selago Hook. f. (Apiaceae) *on sub-Antarctic Marion Island: climate change implications*. MSc thesis, Stellenbosch University, Stellenbosch, 127 pp.

NYAKATYA, M.J. & MCGEOCH, M.A. 2008. Temperature variation across Marion Island associated with a keystone plant species (*Azorella selago* Hook. f. (Apiaceae)). *Polar Biology*, **31**, 139–151.

SMITH, V.R. 1978. Plant ecology of Marion Island: a review. *South African Journal of Antarctic Research*, **8**, 21–30.

SMITH, V.R. & STEENKAMP, M. 1990. Climatic change and its ecological implications at a subantarctic island. *Oecologia*, **85**, 14–24.

SMITH, V.R., AVENANT, N.L. & CHOWN, S.L. 2002. The diet and impact of house mice on a sub-Antarctic island. *Polar Biology*, **25**, 703–715.

SMITH, V.R., STEENKAMP, M. & GREMMEN, N.J.M. 2001. Terrestrial habitats on sub-Antarctic Marion Island: their vegetation, edaphic attributes, distribution and response to climate change. *South African Journal of Botany*, **67**, 641–654.

TOWNS, D.R. & BROOME, K.G. 2003. From small Maria to massive Campbell: forty years of rat eradications from New Zealand islands. *New Zealand Journal of Zoology*, **30**, 377–398.

VAN AARDE, R.J. & JACKSON, T.P. 2007. Food, reproduction and survival in mice on sub-Antarctic Marion Island. *Polar Biology*, **30**, 503–511.

VAN VUUREN, B.J. & CHOWN, S.L. 2007. Genetic evidence confirms the origin of the house mouse on sub-Antarctic Marion Island. *Polar Biology*, **30**, 327–332.

VERWOERD, W.J. 1971. Geology. *In* VAN ZINDEREN BAKKER, E.M., WINTERBOTTOM, J.M. & DYER, R.A., *eds. Marion and Prince Edward Islands. Report on the South African biological and geological expedition 1965/1966*. Cape Town: A.A. Balkema, 40–62.

WANLESS, R.M., ANGEL, A., CUTHBERT, R.J., HILTON, G.M. & RYAN, P.G. 2007. Can predation by invasive mice drive seabird extinctions? *Biology Letters*, **3**, 241–244.

WATKINS, B.P. & COOPER, J. 1986. Introduction, present status and control of alien species at the Prince Edward Islands. *South African Journal of Antarctic Research*, **16**, 86–94.

YELOFF, D., MAUQUOY, D., BARBER, K., WAY, S., VAN GEEL, B. & TURNEY, C.S.M. 2007. Volcanic ash deposition and long-term vegetation change on Subantarctic Marion Island. *Arctic, Antarctic, and Alpine Research*, **39**, 500–511.

ZIMMERMAN, D.L. & ZIMMERMAN, M.B. 1991. A comparison of spatial semiviogram estimators and corresponding ordinary kriging predictors. *Technometrics*, **33**, 77–91.