



# Surface destabilisation by the invasive burrowing engineer *Mus musculus* on a sub-Antarctic island



Bert Eriksson<sup>a</sup>, David J. Eldridge<sup>b,\*</sup>

<sup>a</sup> Department of Social and Economic Geography, Uppsala University, Uppsala, Sweden

<sup>b</sup> Centre for Ecosystem Science, School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, NSW 2052, Australia

## ARTICLE INFO

### Article history:

Received 7 March 2014

Received in revised form 25 June 2014

Accepted 26 June 2014

Available online 8 July 2014

### Keywords:

Burrowing

Zoogeomorphology

Bioturbation

Soil movement

Ecosystem engineering

Climate change

## ABSTRACT

Invasive species are known to have substantial trophic effects on ecosystems and ecosystem processes. The invasion of the house mouse (*Mus musculus*) onto sub-Antarctic islands has had a devastating effect on plants, invertebrates, and birds with substantial changes in ecosystem functions. Less well understood, however, are the nontrophic, geomorphic effects of mice resulting from their burrowing activities. We examined the extent of burrow construction by *M. musculus* across an area of about 20 ha on Marion Island and the effects of burrows on water flow and sediment movement. We recorded a density of  $0.59 \pm 0.48$  (mean  $\pm$  SD) burrows  $m^{-2}$ , with more burrows at lower altitudes and shallower slopes, and twice the density in the solifluction risers ( $0.86 \pm 0.54 m^{-2}$ ) than the intervening terraces or treads ( $0.40 \pm 0.51 m^{-2}$ ). Most burrows were dug horizontally into the slope and tended to extend about 20 cm deep before turning. A very conservative estimate of sediment removed from burrows from this depth is  $2.4 t ha^{-1}$ . However, taking into account more detailed data on burrow morphology based on excavations, actual amounts may be closer to  $8.4 t ha^{-1}$ . Average soil displacement rate for a single burrow, measured over 5 days, was  $0.18 kg burrow^{-1} day^{-1}$ . Burrows acted as conduits for water and warmer air. Stones at burrow entrances were moved eight times farther by water (10.4 cm) than those not associated with burrows. Similarly, temperatures adjacent to burrow entrances were  $4.1 ^\circ C$  higher than sites 10 cm away. Together our data indicate that mice are having substantial deleterious and geomorphic effects on sub-Antarctic ecosystems through their burrowing. With lower rates of mouse mortality resulting from warmer climates predicted under global climate models, we can expect an increase in damage resulting from mouse activity.

Crown Copyright © 2014 Published by Elsevier B.V. All rights reserved.

## 1. Introduction

Invasive species present a major threat to the composition, structure and function of ecosystems worldwide (Lambertini et al., 2011). Despite the substantial number of species invasions over the last century there are still substantial gaps in our understanding of the ecosystem effects of invasive species (Chapin et al., 2000). Two of the most prolific, highly successful and devastating invaders have been the black rat (*Rattus rattus*) and the house mouse (*Mus musculus*). The success of both of these rodents is largely because they act as generalist scavengers, exploit habitats modified by humans, and produce multiple litters in any one year. These rodents now have a pan-global distribution, occupy most natural and human-constructed ecosystems, and spread diseases and spoil crops and food supplies.

The introduction of rodents, including *M. musculus* onto offshore islands has had a devastating impact on plants, invertebrates, and terrestrial birds and seabirds and has led to substantial changes in ecosystem functions such as nutrient cycling and hydrology (Huyser et al., 2000; Smith et al., 2002; Wardle et al., 2009). *M. musculus* was introduced

onto sub-Antarctic islands by sealers and whalers during the nineteenth century (Angel et al., 2009). It is now the only naturalised invasive mammal on Marion Island, one of the sub-Antarctic islands (Phiri et al., 2009). Mice can act as predators and eat eggs and chicks of both terrestrial birds and seabirds (Chapuis et al., 1994; Wanless et al., 2007) and have been shown to have substantial effects on the community composition of invertebrates (Newman, 1994; Angel et al., 2009). Their densities in lowland areas are estimated to be  $100\text{--}260 \cdot mice \cdot ha^{-1}$  (Ferreira et al., 2006). An obvious and generally overlooked effect of these rodents, however, has been the nontrophic effects, such as soil erosion or loss of nutrients, that might result from their burrow construction (e.g., Grant-Hoffman et al., 2010). Soil disturbance by mice may lead to substantial ecosystem effects such as increased soil erosion and altering soil nutrient cycling (Smith and Steenkamp, 1990).

In this study we explore the biogeomorphic, or nontrophic effects, of burrowing by *M. musculus* on Marion Island, a sub-Antarctic island off the coast of South Africa. Though mice are small ( $<30 g$ ), they construct vast burrow systems, altering soil physical and hydrological properties (Avenant and Smith, 2003). Mice have a preference for burrowing into *Azorella* cushions (Avenant and Smith, 2003; Hugo et al., 2004; Phiri et al., 2009), their burrowing reduces cushion survival and is thought to destabilise *Azorella selago* supported terraces. They also produce an

\* Corresponding author. Tel.: +61 2 9385 2194; fax: +61 2 9385 1558.  
E-mail address: [d.eldridge@unsw.edu.au](mailto:d.eldridge@unsw.edu.au) (D.J. Eldridge).

apron of ejected soil that lies downslope of the burrow entrances. A large number of studies have demonstrated the impacts of semifossorial mammals on ecosystem function, soil genesis, and mass transport in periglacial and alpine environments globally (Thorn, 1978; Smith and Gardner, 1985; Hall et al., 1999; Smith and Foggin, 1999; Zhang and Liu, 2003). We are unaware, however, of any that have specifically examined the biogeomorphic impacts resulting from burrowing by *M. musculus*, apart from studies by Avenant and Smith (2003), which were more limited in scope and intensity of sampling. This is particularly surprising, however, given their widespread distribution, high population densities and activity, and thus their putative considerable negative effects on ecosystem processes.

Our objectives here are to quantify the nature and extent of burrowing by *M. musculus* and its effect on sediment displacement. Specifically, we examined (i) whether the density of mouse burrow entrances differed between the two main surface features; solifluction risers and treads; (ii) potential relationships amongst burrow density, altitude, aspect, and slope, (iii) the potential effects of burrows on water conductance and thus their tendency to move sediment; and (iv) the potential effects of burrows on frost and needle ice formation, as these processes are likely to have substantial effects on surface stability in sub-Antarctic systems.

## 2. Methods

### 2.1. The study area

Our study was conducted on Marion Island, which is situated between South Africa and the Antarctic continent about 1900 km southeast of Cape Agulhas (46°54' S, 37°45' E.). Marion Island is an isolated small volcanic island covering an area of 290 km<sup>2</sup> and is the peak of a shield volcano comprising grey basalts that were extensively glaciated during the late quaternary and early Holocene. The island is characterised by periglacial landforms, with large areas of glacial erosion and glacial till (Hall, 2002; Hall et al., 2010).

Marion Island has an oceanic climate with an annual precipitation of about 2000 mm and summer temperature of about 5.8 °C. It experiences gale force winds (>15 m s<sup>-1</sup>) on an average of 107 days year<sup>-1</sup> with wind predominantly from a northwesterly direction (Le Roux and McGeoch, 2008a). Diurnal frost occurs year round, and diurnal

frost-processes dominate the landscape, at lower altitudes through needle-ice formation, and at higher altitudes through frost heave and ice-lens formation (Boelhouwers et al., 2003). Needle ice loosens and sorts the upper layers of soil resulting in surface creep and, together with wind and water erosion, is a major component in turf exfoliation. Factors influencing these dynamic processes, such as the impacts of burrowing fauna, are therefore of particular geomorphic interest in this environment.

The landscape on Marion Island consists mainly of lava fellfields, which support a sequence of alternating solifluction terraces and risers. The terraces, created by frost processes and solifluction, have bare and sorted, clast-covered treads about 1–5 m wide, with a lateral extension from 2 to 20 m behind *A. selago* covered risers 0.2 to 0.7 m high (Fig. 1).

Fellfield areas are dominated by the keystone, pioneering vascular plant *A. selago* (*Apiaceae*), which in some areas, is the sole vascular plant (Mark et al., 2001). At lower altitudes, risers are still dominated by *Azorella*, but treads may also be covered by moss and grass. *Azorella* is typically rounded, elliptical or crescent-shaped, and has a dense cushion growth form (Boelhouwers et al., 2003; Phiri et al., 2009). Healthy cushions are up to 80 cm across by 10 to 40 cm high, and grow together to form long almost continuous structures up to 1200 m<sup>2</sup> (Phiri et al., 2009) at higher altitudes (Mortimer et al., 2008). Cushions are sturdy and long-lived (up to 100 years; Le Roux and McGeoch, 2004) and play an important geomorphological role in stabilising sub-Antarctic surfaces (Boelhouwers et al., 2000) and in plant facilitation processes (Phiri et al., 2009).

### 2.2. Field measurements

Field surveys were undertaken on Skua Ridge, in the northeastern section of Marion Island, during April and May 2009 to examine the extent and nature of surface destabilisation resulting from mouse burrowing. The site was characterised by *Azorella*-dominated grey lava fellfield with active solifluction terraces.

We measured the size distribution of mouse burrow entrances by counting all entrances within 27, 25 m<sup>2</sup> (5 × 5 m) quadrats located in fellfield areas with well-established *Azorella*-dominated terraces. The terraces were uniform in size and appearance and supported 30–50 cm high risers and associated treads located about 3 m apart. Within each quadrat we characterised the position of each burrow entrance in



Fig. 1. Typical view of the landscape on Marion Island showing solifluction terraces with bare, clast-covered treads and intervening *Azorella selago* covered risers.

relation to riser or tread and measured burrow entrance diameter and depth, aspect, and burrow angle (the angle of excavation of the tunnel). Size was assessed by measuring two diameters across the entrance and the depth until the burrow ended, turned or branched, and the angle of the burrow in relation to the horizontal plane. We also recorded altitude, slope, and aspect of each quadrat location.

To investigate whether mouse burrowing into *Azorella* cushions differed between windward (NW) and leeward (SE) aspects, we surveyed 15 pairs of 25 m<sup>2</sup> quadrats on the windward and leeward sides of Skua Ridge. All quadrats were placed between 90 and 105 m asl, with slopes of 4–8°, and supported *Azorella* as the only vegetation. We counted the total number of cushions per quadrat, the number supporting mouse burrows, and the number of cushions that were more than 33% eroded, which we used as our measure of erosion. Although somewhat arbitrary, 33% was chosen because it represents a significant proportion of the area that has been eroded. To test the potential effect of burrows as water conduits and thus their potential to move sediment, we placed four rows of painted stones on the downslope edge of terraces with and without mouse burrows. The stones averaged 16 × 10 × 6 mm and were placed about 50 mm apart in a straight line parallel to, and 200 mm downslope of, the riser. A total of 113 stones were used, 55 on the downslope side of entrances and 58 not associated with entrances. Stone movement was measured daily for 12 days, relative to a fixed reference line, and any visible signs of water erosion downslope of the burrow entrances were recorded.

### 2.3. Burrowing effects on surface temperatures, frost and needle ice formation

Bare soil below risers in low-lying (<90 m asl) areas is likely to form needle ice (Boelhouwers et al., 2003). We compared the occurrence of needle ice on risers with (i) intact *Azorella* vegetation, (ii) dead *Azorella*, and (iii) mouse burrow entrances to test the likely effect of bare soil on frost processes. The presence of needle ice formation was recorded after sunrise on mornings with clear and cold nights over five nights. We also measured surface temperatures around the burrow entrances at six locations: adjacent to the entrance, 10 and 20 cm below the entrance, and 10 cm above, left, and right of the entrance. These measurements were made in seven different 1-m<sup>2</sup> plots during periods when air temperatures were between freezing and 2 °C with temperature loggers (Thermochron i-Buttons DS 1922 L, accuracy 0.0625 °C, Maxim Semiconductors, USA).

Temperature sensors were used to assess differences in temperature between intact risers and those destroyed by mouse burrowing. We installed 25 temperature loggers (Thermochron i-Buttons DS 1922 L, accuracy 0.0625 °C, Maxim Semiconductors, USA) and moisture sensors (Decagon ECH<sub>2</sub>O, USA) at 3-cm depths in seven plots in different aspects across five of the 27 quadrats used to assess burrow densities. Loggers measured instantaneous temperature and soil moisture at 20-min intervals over periods ranging from 63 to 102 days at the top of solifluction terrace risers that were 40–50 cm high with intact or mouse-destroyed *Azorella*.

### 2.4. Statistical analyses

We used Student *t*-tests to examine potential differences in burrow densities between risers and treads and linear regression to explore potential relationships amongst burrow density, altitude, slope and cushion damage, and temperature in relation to distance from burrow entrances. Fisher's Exact Test was used to examine differences in burrow density between treads and risers in relation to different aspects. Finally, using mean diameter and depths of our burrow systems, we used algorithms in Avenant and Smith (2003) to derive a conservative estimate of sediment displacement.

## 3. Results

### 3.1. Distribution of mouse burrows

We recorded a total of 400 *M. musculus* burrow entrances across the 27 quadrats, with an average density of 0.59 ± 0.48 (mean ± SD) burrows m<sup>-2</sup> (Table 1). Mice exhibited a clear preference for burrowing into *Azorella* risers, which accounted for 24% of the grids but contained 62% of the burrows. When we accounted for the relative cover of treads and risers in the quadrats, risers supported twice the density of burrows (0.86 ± 0.54 m<sup>-2</sup>) as the treads (0.40 ± 0.51 m<sup>-2</sup>; Student *t* = 3.20, *df* = 51, *P* = 0.002). We found that mouse damage to *Azorella* cushions (at 33% damage) increased as the number of cushions increased, though the strength of this relationship was relatively weak (*F*<sub>1,28</sub> = 4.67, *R*<sup>2</sup> = 0.11, *P* = 0.039). More importantly, mouse damage to cushions increased with increases in burrow density (*F*<sub>1,28</sub> = 10.84, *R*<sup>2</sup> = 0.25, *P* = 0.003).

In general, burrow densities tended to decline with increasing altitude (*F*<sub>1,25</sub> = 11.18, *P* = 0.003, *R*<sup>2</sup> = 0.31) particularly for locations >110 m asl (Fig. 2) and with increasing slope (*F*<sub>1,25</sub> = 5.50, *P* = 0.027, *R*<sup>2</sup> = 0.15). We found only two burrows at sites with an easterly aspect, and in general, more burrows occurred at sites with a northerly (i.e. away from the wind direction) than a southerly aspect. Further, density did not vary between treads and risers for sites with a northerly aspect, and burrows were found on treads in a southerly direction (Fisher's Exact Test, *z* = -5.35, *P* < 0.001).

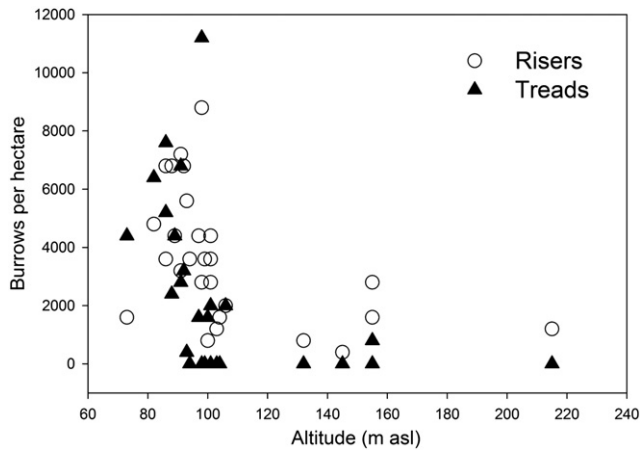
#### 3.1.1. Size and shape of mouse burrows

Burrow angles were highly variable, ranging from 10° upward to 90° downward (vertically down), with mean (±SE) angles of 10.4 ± 1.28 downward. Most burrows were dug horizontally into the slopes, and 80% of all burrows had angles within the range from -10° to +10° from the horizontal (Fig. 3A). Burrow diameters averaged 4.12 ± 0.18 cm, and depths before branching or turning, 20.7 ± 1.47 cm, with a maximum length of 50 cm (Fig. 3B). Burrow density tended to

**Table 1**

The distribution of mouse burrows in *Azorella* terraces across the 27, 25-m<sup>2</sup> quadrats.

Grid	Altitude (m)	Aspect (°)	Slope (°)	Number of burrows		Burrow density (m <sup>-2</sup> )
				Riser	Tread	
1	89	315	3	11	11	0.88
2	88	360	2	17	6	0.92
3	82	270	5	12	16	1.12
4	73	45	5	4	11	0.60
5	86	135	5	9	13	0.88
6	106	20	6	5	5	0.40
7	100	157	9	2	4	0.24
8	98	157	4	22	28	2.00
9	155	45	8	4	2	0.26
10	97	315	5	11	4	0.60
11	86	360	3	17	19	1.44
12	98	315	4	7	0	0.28
13	91	157	9	8	7	0.60
14	92	270	3	17	8	1.00
15	101	292	11	11	5	0.64
16	94	180	8	9	0	0.36
17	101	225	7	7	0	0.28
18	103	315	5	3	0	0.12
19	104	360	5	4	0	0.16
20	91	360	3	18	17	1.40
21	215	360	8	3	0	0.12
22	155	157	5	7	0	0.28
23	145	292	6	1	0	0.04
24	132	90	4	2	0	0.08
25	99	315	4	9	0	0.36
26	93	135	6	14	1	0.60
27	101	135	5	9	0	0.36
Av.	106.5		5.5	9.0	5.8	0.59



**Fig. 2.** Burrow entrance density (burrows  $\text{ha}^{-1}$ ) on risers and treads in relation to altitude (m asl).

increase with increasing slope angle ( $P = 0.22$ ). Given the size and density of *M. musculus* burrows, a conservative estimate of sediment displacement in burrows across the 27 grids, prior to branching or turning, is  $0.11 \text{ m}^3$ . This equates with an average of  $1.63 \text{ m}^3 \text{ ha}^{-1}$ , or  $2.4 \text{ t ha}^{-1}$ , assuming an average soil bulk density of  $1.5 \text{ mg m}^{-3}$ , which we derived from unpublished work carried out on Marion Island.

### 3.2. Influence of burrows on soil moisture and temperature, and disturbance by frost and ice

Soil moisture was greater, though equally variable, in intact (27.0%) compared with damaged (23.4%) surfaces ( $F_{1,76} = 46.7$ ,  $P < 0.001$ ), irrespective of riser or tread. Soil moisture was also greater in the treads (28 cf. 22%,  $F_{1,76} = 126.4$ ,  $P < 0.001$ ), but five times more variable ( $SD = 2.62\%$ ) than in the risers ( $SD = 0.59\%$ ;  $F_{1,76} = 28.1$ ,  $P < 0.001$ ). We reported evidence of water flowing out of the burrow entrances, often associated with the movement of freshly excavated soils. This greater water flow resulted in movement of all of the stones (Fig. 4). Stones in front of the burrow entrances moved significantly farther ( $10.4 \pm 2.31 \text{ cm}$ ; mean  $\pm$  SE;  $n = 55$ ) than those not in front of burrow entrances ( $1.25 \pm 0.20 \text{ cm}$ ;  $n = 58$ ; Student  $t = -0.70$ ,  $P < 0.001$ ).

We recorded significantly more extensively damaged *Azorella* cushions on wind-exposed, northwesterly aspects ( $54.0 \pm 4.80\%$ ) than on leeward, southeasterly-facing slopes ( $41.6 \pm 3.09\%$ ;  $F_{1,28} = 4.72$ ,  $P = 0.038$ ). The lowest minimum temperatures were recorded in damaged/eroded *Azorella* cushions, but the absolute highest maximum and the lowest minimum were recorded in dead but intact cushions. Contrary to expectation, mean temperature between intact



**Fig. 4.** Study testing the potential effect of burrows on the movement of painted stones on the downslope edge of terraces. Note the mouse burrow entrance between the two clumps of *Azorella*. The small ruler is 15 cm.

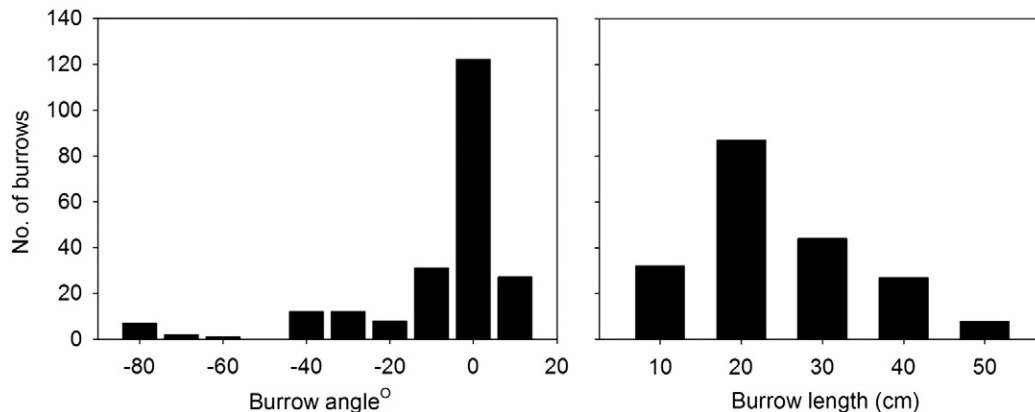
cushions and those destroyed by mice did not differ ( $5.2$  and  $5.0 \text{ }^\circ\text{C}$ , respectively,  $P = 0.46$ ), and this effect was consistent between risers and treads. Similarly, the range ( $2.7$ – $7.9 \text{ }^\circ\text{C}$ ) and standard deviation ( $1.6$ – $1.8 \text{ }^\circ\text{C}$ ) in temperature were similar across disturbed and intact surfaces ( $P > 0.05$ ).

Temperatures declined markedly away from the burrow entrances ( $F_{2,36} = 18.61$ ,  $P < 0.001$ ,  $R^2 = 0.48$ ) and were, on average,  $4.1 \text{ }^\circ\text{C}$  lower within 10 cm of the entrances (Fig. 5). Needle ice was observed during the early mornings on three separate days. No needle ice was observed within a 5-cm radius around mouse burrow entrances. This suggests that burrows serve as air conduits from the inner, warmer part of the terrace, preventing the formation of needle ice.

## 4. Discussion

A number of studies have demonstrated the considerable impact of *M. musculus* on the Southern Ocean and sub-Antarctic ecosystems, either directly through predation on invertebrates and sea bird chicks, dispersal and/or consumption of seeds and plants, or indirectly through nutrient cycling (Avenant and Smith, 2003; Phiri et al., 2009). In our study mice constructed an average of about  $6000 \text{ burrows ha}^{-1}$ . This substantial, nontrophic effect of soil removal resulted in vegetation disturbance and death, water runoff, movement of surface gravels, and alteration to surface temperatures, which was associated with needle ice formation.

Extrapolating from our measurements, we recorded considerable soil displacement from mouse burrows ( $1.63 \text{ m}^3 \text{ ha}^{-1}$  or  $2.4 \text{ t ha}^{-1}$ ). This soil displacement is of a similar order of magnitude to that of other semifossorial animals such as pocket gophers (*Thomomys* spp.),



**Fig. 3.** Frequency distribution of (A) burrow entrance angles ( $^\circ$ ) and (B) burrow length (cm).

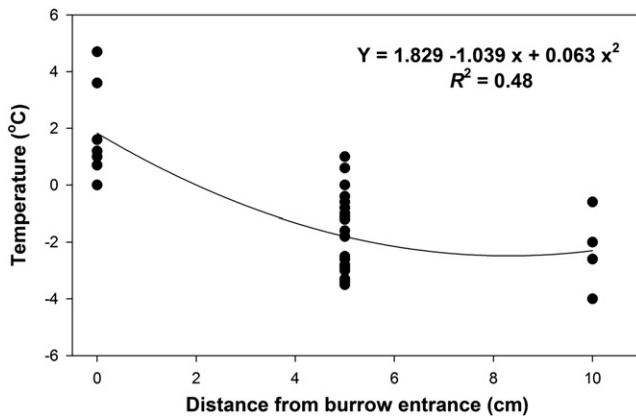


Fig. 5. Changes in ambient temperature (°C) in relation to distance from mouse burrow entrances (cm).

which have substantial effects on soil and plants through their surface disturbance and burrowing (Thorn, 1978). Previous studies have reported densities between 346 and 1000 burrow systems  $\text{ha}^{-1}$  for lowland areas close to the coast (Avenant and Smith, 2003) and values of 1310 burrows  $\text{ha}^{-1}$  for a landscape-level study of Marion Island that included areas of high as well as low mouse densities (Phiri et al., 2009). Our values were considerably higher (5930 burrows  $\text{ha}^{-1}$ ), and the differences reflect differences in the areas that we surveyed and the fact that these densities tend to be greater at lower (<100 m asl) elevations (Phiri et al., 2009). Nevertheless, available data indicate considerable mouse activity on Marion Island. Avenant and Smith (2003) recorded an average of 1.8 entrances per burrow system and an average volume per burrow system of 1705  $\text{cm}^3$  (Avenant and Smith, 2003). These systems can range from one single mouse tunnel to a more complex arrangement of interconnected tunnels up to 4  $\text{m}^2$  with up to four chambers (Avenant and Smith, 2003). When we combine the results of excavations by Avenant and Smith (2003) with those of the current study, a more accurate estimation of burrow volumes emerges. Combining our values of 14.8 burrows per 25  $\text{m}^2$  (0.59 burrows  $\text{m}^{-2}$  or 5930  $\text{ha}^{-1}$ ) with 1.8 entrances per burrow system (Avenant and Smith, 2003) results in 3289 systems  $\text{ha}^{-1}$ . At an average volume per system of 0.001705  $\text{m}^3$ , this equates to 5.61  $\text{m}^3 \text{ha}^{-1}$  or 8.4  $\text{t ha}^{-1}$ , a figure more likely to reflect the true volumes of mouse burrowing. Notwithstanding these results, mouse tunnels are exceptionally complex and branched (Avenant and Smith, 2003); thus we consider our values to be conservative because we could only measure tunnel depths to a point at which the tunnels turned. Our study was conducted across an area of about 20 ha in an environment with its own inherent variability. In deriving our estimates and scaling up to the landscape level, we necessarily assume that our sampling location was representative of the wider Marion Island landscape. In the absence of detailed information on the spatial variability in the distribution of terraces, risers, and vegetative features across the island, our figures should be viewed as best estimates only.

We also tracked the excavation of one mouse burrow system over a 5-day period on Marion Island by measuring the volume of the excavated tunnel over the entire period. This displacement averaged 113 ( $\pm 43$ )  $\text{cm}^3 \text{d}^{-1}$ . Even at an average density of 50 mice  $\text{ha}^{-1}$ , which is extremely conservative and half the density reported in other studies (e.g., van Aarde et al., 1996; Ferreira et al., 2006) and assuming daily digging, this suggests a sediment displacement potential of 20.6  $\text{m}^3 \text{ha}^{-1} \text{year}^{-1}$  or 30.9  $\text{t ha}^{-1} \text{year}^{-1}$ , which greatly exceeds estimates of rodent digging displacement in the literature (Smith and Gardner, 1985; Hall et al., 1999). We realise that this is only a single event and that excavation rates will likely vary because of many factors related to mouse population condition and environmental conditions.

Therefore, this excavation event could be considered anomalous. However, it does indicate the upper end of the scale of intensive digging carried out by *M. musculus* in a sub-Antarctic environment.

Mice in this study showed a preference for burrowing close to the horizontal plane. This preference could be explained by a number of mechanisms. First, digging is energetically expensive (Vleck, 1981; Seabloom et al., 2000), but digging horizontally into a vertical riser is more energetically efficient than digging vertically down in a tread because less energy is expended in removing sediment horizontally than lifting it up vertically. Second, vertically oriented mouse burrows within the treads will rapidly fill with water during rain events, which occur frequently on Marion Island under an annual rainfall regime of about 2000 mm (Le Roux and McGeoch, 2008a). Third, the risers are generally *Azorella*-covered, while the treads are mostly barren and clast-covered. *Azorella* cushions provide greater protection for mouse burrow entrances than unvegetated surfaces (Price, 1971; Phiri et al., 2009). Finally, the horizontal burrows provide a more favourable environment for mice by 'trapping' warmer air within the interior of the terrace. Indeed, our study of temperatures around the burrow indicated that burrows acted as conduits, conducting warm air from the inner section of the terrace to the outside. Unlike horizontal burrows, vertical burrows would act as points of much greater heat loss as a result of convection. We found that the risers on north-facing terraces acted as solar collectors and had significantly higher mean temperatures ( $\sim 5.9$  °C) than the south-facing slopes ( $\sim 4.8$  °C). This enhanced thermal environment may be one factor that could contribute to mouse preference for digging in these risers, although no clear preference was recorded. The fact that the strongest winds and rain storms also come from the northeast or north may counteract the effect of higher temperatures for mice to select northerly locations for burrowing.

#### 4.1. Mouse burrowing as a mechanism for surface destabilisation

*Azorella* cushions act as a bioprotective layer on the soil surface, mechanically stabilising the risers and buffering fluctuations in surface temperatures and moisture (Nyakataya and McGeoch, 2008) and therefore moderating frost processes. We found that burrows were most likely to be built directly into *Azorella* cushions (Phiri et al., 2009), and this is the primary process leading to mouse-initiated surface destabilisation. Three potential mechanisms could explain how this burrowing leads to cushion plant mortality and destruction. First, burrows dug through the central stems and roots of the *Azorella* cushion result in cushion death, but sometimes only part of the plant dies off. Dead cushions lose their structural stability and attachment to the soil once the roots die. This dead plant material is easily eroded, leaving only a ring of living *Azorella* surrounding a patch of bare soil. This bare soil is often exposed to needle ice formation, which loosens the surface soil structure and speeds up wind and/or water erosion until the cushion is completely destroyed and is further degraded by wind and rain. A similar mechanism occurs in turf exfoliation pans in the Lesotho highlands in southern Africa from the activity of ice rats (*Otomys sloggetti*; Grab, 2010). Once the cushion has been removed, the bare soil is exposed to needle ice creep.

Second, tunnelling by rodents through the solifluction terraces creates conduits for rainwater, which, combined with the high levels of precipitation on Marion Island (Le Roux and McGeoch, 2008b), substantially increases erosion and displacement of sediment. Although our study of the movement of stones adjacent to burrow entrances was carried out during an unusually dry period ( $\sim 13$  mm rainfall), stones placed adjacent to burrow entrances moved more than those away from burrows. This indicates that burrows are acting as conduits for water and that the erosive effect is likely to be markedly greater during periods of greater precipitation. Third, burrowing and grazing of moss cushions may alter local microclimates. This occurs when tunnels act as chimneys, inducing thermal leakage from the interior of the terraces, thereby promoting soil frost creep. Similarly, we observed that the

greatest soil surface temperature differences were recorded in risers where mouse burrows occurred close to destroyed *Azorella* cushions. The net effect of these processes is to create further destabilisation of subpolar surfaces.

#### 4.2. Concluding remarks

Our study demonstrates the substantial effects of mouse activity induced by burrowing, which leads directly to sediment accumulation, enhanced runoff, and the downslope movement of this sediment by wind and water. Our study also shows that burrowing influences terrace microclimates and probably frost and ice processes. Apart from two small islands in the Kerguelen group (Le Roux et al., 2002; Frenot et al., 2005), no concerted efforts have been made to eradicate mice from sub-Antarctic islands. Given the lower rates of mouse mortality resulting from milder winter temperatures predicted under global climate models (van Aarde et al., 2004), we can expect an increase in ecosystem damage resulting from mouse activity.

#### Acknowledgements

Jan Boelhouwers initiated this study, which formed part of the 'Geobiology of sub-Antarctic ecosystems, sensitivity and responses to climate change' project (2007–2010), funded by the Swedish National Development Corporation Agency/NRF research links programme between Sweden and South Africa. The senior author participated in the annual South African National Antarctic Program expedition to Marion Island in April–May 2009.

#### References

- Angel, A., Wanless, R.M., Cooper, J., 2009. Review of impacts of the introduced house mice in the Southern Ocean: are mice equivalent to rats? *Biol. Invasions* 11, 1743–1754.
- Avenant, N.L., Smith, V.R., 2003. The microenvironment of house mice on Marion Island (sub-Antarctic). *Polar Biol.* 26, 129–141.
- Boelhouwers, J., Holness, S., Sumner, P., 2000. Geomorphological characteristics of small debris flows on Junior's Kop, Marion Island, maritime sub-Antarctic. *Earth Surf. Process. Landf.* 25, 341–352.
- Boelhouwers, J., Holness, S., Sumner, P., 2003. The maritime subantarctic: a distinct periglacial environment. *Geomorphology* 52, 39–55.
- Chapin, F.S., Zavaleta, E.S., Eviner, V.T., Naylor, R.L., Vitousek, P.M., Reynolds, H.L., Hooper, D.U., Lavorel, S., Sala, O.E., Hobbie, S.E., Mack, M.C., Diaz, S., 2000. Consequences of changing biodiversity. *Nature* 405, 234–242.
- Chapuis, J.L., Bousset, P., Barnaud, G., 1994. Alien mammals, impact and management in the French sub-Antarctic islands. *Biol. Conserv.* 67, 97–104.
- 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 Biol.* 30, 83–94.
- 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. *Biol. Rev.* 80, 45–72.
- Grab, S.W., 2010. Alpine turf exfoliation pans in Lesotho, Southern Africa: climate-process-morphological linkages. *Geomorphology* 114, 261–275.
- Grant-Hoffman, M.N., Mulder, C.P.H., Bellingham, P.J., 2010. Effects of invasive rats and burrowing seabirds on seeds and seedlings on New Zealand islands. *Oecologia* 162, 1005–1016.
- Hall, K.J., 2002. Review of present and quaternary periglacial processes and landforms of the maritime and sub-Antarctic region. *S. Afr. J. Sci.* 98, 71–81.
- Hall, K., Boelhouwers, J., Driscoll, K., 1999. Animals as erosion agents in the alpine zone: some data and observations from Canada, Lesotho and Tibet. *Arct. Antarct. Alp. Res.* 31, 436–446.
- Hall, K., Meiklejohn, I., Bumby, A., 2010. Marion Island volcanism and glaciations. *Antarct. Sci.* 1–9.
- Hugo, E.A., McGeoch, M.A., Marshall, D.J., Chown, S.L., 2004. Fine scale variation in microarthropod communities inhabiting the keystone species *Azorella selago* on Marion Island. *Polar Biol.* 27, 466–473.
- Huysler, 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? *Biol. Conserv.* 92, 299–310.
- Lambertini, M., Leape, J., Marton-Lefèvre, J., Mittermeier, R.A., Rose, M., Robinson, G.J., Stuart, S.N., Waldman, B., Genovesi, P., 2011. Invasives: a major conservation threat. *Science* 333, 404–405.
- 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). *Arct. Antarct. Alp. Res.* 36, 509–517.
- Le Roux, P.C., McGeoch, M.A., 2008a. Changes in climate extremes, variability and signature on sub-Antarctic Marion Island. *Clim. Chang.* 86, 309–329.
- Le Roux, P.C., McGeoch, M.A., 2008b. Spatial variation in plant interactions across a severity gradient in the sub-Antarctic. *Oecologia* 155, 831–844.
- Le Roux, V., Chapuis, J.L., Frenot, Y., Vernon, P., 2002. Diet of the house mouse (*Mus musculus domesticus*) at Guillaou Island, Kerguelen archipelago, sub-Antarctic. *Polar Biol.* 25, 49–57.
- Mark, A.F., Dickinson, K.J.M., Allen, J., Smith, R., West, C.J., 2001. Vegetation patterns, plant distribution and life forms across the alpine zone in southern Tierra del Fuego, Argentina. *Aust. Ecol.* 26, 423–440.
- Mortimer, E., McGeoch, M.A., Daniels, S.R., Jansen van Vuuren, B., 2008. Growth form and population genetic structure of *Azorella selago* on sub-Antarctic Marion Island. *Antarct. Sci.* 20, 381–390.
- Newman, D.G., 1994. Effects of a mouse, *Mus musculus*, eradication programme and habitat change on a lizard population on Mana Island, New Zealand, with special reference to McGregor's skink, *Cyclodina macgregori*. *N. Z. J. Zool.* 21, 443–456.
- Nyakataya, M.J., McGeoch, M.A., 2008. Temperature variation across Marion Island associated with a keystone plant species (*Azorella selago* Hook. f., Apiaceae). *Polar Biol.* 31, 139–151.
- Phiri, E., McGeoch, M., Chown, S., 2009. Spatial variation in structural damage to a keystone plant species in the sub-Antarctic: interactions between *Azorella selago* and invasive house mice. *Antarct. Sci.* 21, 189–196.
- Price, L.W., 1971. Geomorphic effect of the arctic ground squirrel in an alpine environment. *Geogr. Ann.* 53A, 100–105.
- Seabloom, E.W., Reichman, O.J., Gabet, E.J., 2000. The effect of hillslope angle on pocket gopher (*Thomomys bottae*) burrow geometry. *Oecologia* 125, 26–34.
- Smith, A.T., Foggin, J.M., 1999. The plateau pika (*Ochotona curzoniae*) is a keystone species for biodiversity on the Tibetan plateau. *Anim. Conserv.* 2, 235–240.
- Smith, D.J., Gardner, J.S., 1985. Geomorphic effects of ground squirrels in the Mount Rae area. *Can. Rocky Mountains Arctic Alpine Res.* 17, 205–210.
- 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 Biol.* 25, 703–715.
- Thorn, C.E., 1978. A preliminary assessment of the geomorphic role of pocket gophers in the alpine zone of the Colorado Front Range. *Geogr. Ann.* 60A, 181–187.
- van Aarde, R.J., Ferreira, S.M., Wassenaar, T.D., Erasmus, D.G., 1996. With the cats away the mice may play. *S. Afr. J. Sci.* 92, 357–358.
- van Aarde, R.J., Ferreira, S.M., Wassenaar, T.D., 2004. Do feral house mice have an impact on invertebrate communities on sub-Antarctic Marion Island? *Austral Ecology* 29, 215–224.
- Vleck, D., 1981. Burrow structure and foraging costs in the fossorial rodent, *Thomomys bottae*. *Oecologia* 49, 391–396.
- Wanless, R.A., Angel, A., Cuthbert, R.J., Hilton, G.M., Ryan, P.G., 2007. Can predation by invasive mice drive seabirds extinctions? *Biol. Lett.* 3, 241–244.
- Wardle, D.A., Bellingham, P.J., Bonner, K.I., Mulder, C.P.H., 2009. Indirect effects of invasive predators on plant litter quality, decomposition and nutrient resorption on seabird-dominated islands. *Ecology* 90, 452–464.
- Zhang, Y., Liu, J., 2003. Effects of plateau zokors (*Myospalax fontanierii*) on plant community and soil in an alpine meadow. *J. Mammal.* 84, 644–651.