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Do feral house mice have an impact on invertebrate communities on sub-Antarctic Marion Island?

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Abstract House mice (*Mus domesticus* L.) have been present on sub-Antarctic Marion Island since the early 1800s. Several authors have suggested that an increase in mice density as a result of a general warming trend in the sub-Antarctic climate from the 1960s has led to a decline in invertebrate biomass and abundance. These suggestions have been supported by the observation that the invertebrates of nearby mouse-free Prince Edward Island are apparently larger and more numerous than on Marion. Our experiment was designed to determine whether mice have a direct effect on invertebrate abundance, biomass and community structure, or an effect on the vegetation community and thus potentially an indirect effect on invertebrates. We constructed five wire-mesh mouse-free exclosures in one habitat type on Marion Island and recorded both the soil macro-invertebrate community and the vegetation inside and outside each of the exclosures before the start of the experiment in 1996 and twice thereafter (1998 and 2000). Mice had no significant effect on any of the eight prey groups' abundance or biomass, or on community structure (diversity and composition). Four of the prey groups changed significantly over time in either biomass or abundance, independent of the presence of mice. Our results, which may have been affected by generally low statistical power, suggest that factors other than mice had a larger impact on invertebrates than mice alone.

Key words: climate change, invasive species, *Mus domesticus*, predation.

INTRODUCTION

Sub-Antarctic islands are devoid of indigenous terrestrial mammals. Those occurring there have been introduced by humans, either accidentally or deliberately. The impacts of invasive mammal species such as cattle, sheep, reindeer, rats, mice and cats on island biota range from moderate to severe (Atkinson 1989) and may have affected ecosystem structure and function on most of the islands within the sub-Antarctic region. Such effects of invasive species on indigenous ecosystems have become serious global conservation issues. This is particularly important on the isolated Marion Island (46°54′S, 37°45′E), which, together with Prince Edward Island, forms the specially protected Prince Edward Island group (Anon. 1996). On Marion Island, the now exterminated domestic cat (*Felis catus*) and the domestic mouse (*Mus domesticus*) may have given rise to substantial changes in the biota (Gleeson & van Rensburg 1982; van Aarde 1983; Chown *et al.* 1998). (The high incidence of Robertsonian translocations noted for this mouse population suggests the species living on Marion Island is *Mus domesticus* (Nachman & Searle 1995)). The cats, introduced to control mice at the base station, never had a substantial effect on mouse numbers (van Aarde 1980), so that their eradication by 1991 (Bester *et al.* 2000) did more to save island-breeding birds from extermination than to change mouse population dynamics.

The present paper investigates the likely impacts of mice, present since the early 1800s (Berry *et al.* 1978), on terrestrial ecosystems at Marion Island. Based on previously published studies (Burger 1978; Gleeson & van Rensburg 1982; Rowe-Rowe *et al.* 1989; van Aarde *et al.* 1996) on mouse diet, energetic requirements, density estimates and prey availability, Rowe-Rowe *et al.* (1989), Crafford (1990) and van Aarde *et al.* (1996) estimated that between 0.7 and 2.9% of the standing crop of invertebrates were taken daily by mice.

In contrast, three studies (Crafford & Scholtz 1987; Crafford 1990; Chown & Smith 1993) comparing invertebrates of Marion Island with those of the neighbouring mouse-free Prince Edward Island (22 km north-east of Marion), suggested that body size on Marion declined for some invertebrates, that invertebrate community composition was altered and that some mating strategies of weevils were altered in the presence of mice. Chown and Smith (1993) also showed that diet selection of mice could alter vegetation composition. In addition, Smith and Steenkamp (1990) argued that as a consequence of a warming trend on Marion Island from the late 1970s to the late

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1980s (Smith 1992), mouse numbers would have increased. Through increased predation of invertebrate detritivores, mice would therefore impact on both decomposition and mineral cycling.

The studies comparing the invertebrates of these neighbouring islands (Crafford & Scholtz 1987; Crafford 1990; Chown & Smith 1993) assumed that their ecosystem features were similar prior to the arrival of mice. Others used an indirect modelling approach (Burger 1978; Gleeson & van Rensburg 1982; Rowe-Rowe *et al.* 1989; van Aarde *et al.* 1996). Although these studies were handicapped by a lack of information on recent mouse population trends and did not contain a control element to verify the apparent impact of mice on their prey, they were useful and appropriate at the time. Together, these studies suggested that, following a period of climate change, increased mouse densities might have significant impacts on terrestrial ecosystems on Marion Island. The exclusion of mice would therefore release invertebrate communities from their impact, resulting in increased invertebrate numbers (and biomass) relative to areas where mice were present.

In the present study, we investigated whether variation in invertebrate community properties (composition, richness and evenness) and population variables (abundance, size-class distributions and biomass) were associated with the presence of mice. Mice can have an indirect effect on invertebrates through their primary effect on vegetation. We therefore investigated whether variation in vegetation community composition was associated with the intensity of mouse impact and, related to this, whether vegetation composition explained variation in invertebrate communities.

METHODS

Study site and experimental design

Sub-Antarctic Marion Island (270 km^2) is one of two islands in the Prince Edward Island group. The geography and climate of Marion Island is described by Van Zinderen Bakker *et al.* (1971) and the vegetation by Gremmen (1981).

To investigate the effects of mice on the invertebrate and plant assemblages of the island, we established five treatment (exclosure) and five control plots during April 1996 in the animal and salt-spray-influenced vegetation types as defined by Gremmen (1981). These biotically influenced vegetation types are restricted to coastal areas, where salt spray and animal excreta provide a high influx of nutrients and a consequent productive vegetation community (Gremmen 1981). We restricted ourselves to biotically influenced areas in the first instance because the highest densities of invertebrates (Burger 1978; Gleeson & van Rensburg 1982; Crafford 1990) and mice (Matthewson *et al.* 1994; van Aarde *et al.* 1996) have been recorded there. In addition, the invertebrate communities associated with the different vegetation complexes in this habitat type tend to be similar (Hänel 1999). The experiment was conducted from April 1996 to April 2000 on Marion Island. We could not conduct a parallel experiment on the nearby pristine mouse-free Prince Edward Island because of its special protection status (Anon. 1996).

Five sites were located in areas of sufficient size to accept both an exclosure and a control plot, and with easy access from the Meteorological Base. At each site, a treatment–control (T–C) group consisted of one circular plot (71.6 m^2) fenced off with a 1-m-high wire mesh of which approximately 25 cm was dug into the ground to exclude mice (exclosure/treatment) and one circular plot of the same size, but without the wire-mesh fence (control). During erection of the fence, nobody walked on the inside of the exclosure plot. The closest distance between any two plots in a T–C group was 10 m and between any two T–C groups was 200 m. The construction of procedural controls was logistically and practically impossible and we were forced to control for the cage effect by sampling only in a central core area inside each exclosure (see below).

All mice were caught in the fenced-off area from the first night after the establishment of each exclosure plot. To maintain low mouse densities in the exclosures, two wire-mass live traps and 10 Sherman live traps were placed inside the exclosures. An average of 0.9 mice were captured per exclosure per week over a year (density 0.01 m^{-2}), with numbers ranging from <0.5 (most months) to a maximum of 4.75 $week^{-1}$ at the peak of the mouse annual population cycle in March The average density of mice inside and outside each exclosure per week differed by a factor of 18 after erection of the exclosures in 1996 (inside = 0.01 m^{-2}, outside = 0.18 m^{-2}). Assuming constant inside and outside densities (we have data for 1996–1997 only) over the whole study period, control areas must have supported a cumulative total of 30 mice m^{-2}, whereas control plots had 2 mice m^{-2}. However, in 1998 the fences were upgraded and electrified, so that the inside density was probably lower from then on than it was in 1996. Furthermore, since there were never any signs of mice habitation inside exclosures (suggesting that mice were caught soon after entering the exclosure), the effective density was probably even lower.

Mouse numbers (minimum number alive (MNA)) in the area surrounding the T–C groups were estimated during April for all years from 1996 to 2000 using a capture–mark–recapture method. At each T–C group, a 60 m × 60 m trapping grid consisting of 49 trapping stations (7 × 7 configuration) was laid out around the exclosure and control plots. At each trapping station,

one Sherman live trap was set for five consecutive nights. Traps were baited with peanut butter and raisins, and checked approximately 8 h later. Captured individuals were marked (by toe clipping) and released at the point of capture.

We sampled the invertebrate assemblage in the T–C plots in 25 soil cores per plot on three occasions: April 1996 (3–5 days after the establishment of the exclosure plots); April 1998; and April 2000. Soil cores, taken using a 70-mm diameter O'Connor split-corer, were located randomly (randomized independently between occasions) within a circular area of approximately 25 m^2 in the middle of each plot. A 2-m strip from the fence was excluded to minimize the potential effects of the fence on vegetation and invertebrate fauna. All invertebrates in a core, both on the surface and in the soil itself, were classified into ecologically similar prey groups.

Soil cores effectively sample only a part of the potential prey for mice, as surface insects are mostly excluded. Pitfall traps are the only viable alternative to soil-core sampling in these habitat types. However, ambient conditions on the island (for instance rainfall of 2500 mm $year^{-1}$) and the difficulty of controlling for immigration of free-ranging prey into the relatively small area of the exclosures, precluded their use over a long period. Furthermore, most of the invertebrate biomass occurs in or immediately on top of the soil (Burger 1978), and the insect life stages on which mice will likely have their largest impact (such as *Pringleophaga marioni* larvae) are restricted to the soil (Rowe-Rowe *et al.* 1989).

We recorded eight prey groups (Table 1), seven of which are known to be food sources for mice: *Pringleophaga* larvae, *Pringleophaga* adults, weevil larvae, weevil adults, spiders, earthworms and slugs (Gleeson & van Rensburg 1982; Rowe-Rowe *et al.* 1989; Chown & Smith 1993). Of these, *Pringleophaga* and weevils are the most important in terms of percentage occurrence in the mice diet (Gleeson & van Rensburg 1982; Rowe-Rowe *et al.* 1989). We distinguished between adults and larvae of both weevils and *Pringleophaga* on the assumption that these two life stages differ in their ecological roles. Invertebrates were weighed on a Mettler electronic balance (MicroSep, Johannesburg) before and after 48-h oven-drying. For each core, the dominant surface vegetation classes were recorded (Table 2). Abundance for each vegetation class was calculated as the proportion of cores per class recorded for each plot.

Statistical analysis

We calculated the abundance (number of individuals) and biomass (g dry weight) per invertebrate prey group for each exclosure or control plot as the sum over all cores in a plot. Missing dry-weight values were estimated by multiplying the wet weight and the average dry : wet weight ratio for the particular prey group. The two surface active prey groups, *Pringleophaga* adults and snails, occurred at very low abundances (5 and 13 individuals in total, respectively) throughout the study period, precluding the use of statistical tests. Their mean abundance and biomass values are therefore reported but not analysed.

Size classes were analysed for *Pringleophaga* larvae only, as these were the focus of Crafford's (1990) analysis. We calculated size-class frequency distribution using 10 weight classes with intervals of 0.005 g, from 0.000 to 0.050 g, and one class with all specimens over 0.050 g. We used *G*-tests (Sokal & Rohlf 1995) to compare size-class distributions of control and exclosure plots for each sample year, as well as over all years. We assessed diversity by calculating the number of prey groups (richness) and evenness. Evenness was calculated using the E_{var} measure of Smith and Wilson (1996), which is independent of richness.

We tested for homogeneity of variance in abundance and biomass values using an F_{max} variance test and for normality using a Kolmogorov–Smirnov test on pooled, standardized values (Sokal & Rohlf 1995).

Table 1. Taxonomy of invertebrate prey groups recorded in the course of the study in soil cores; the groups *Pringleophaga* and weevil were each divided into adult and larvae classes

Order	Family	Species	Prey group
Lepidoptera	Tineidae	*Pringleophaga marioni* Viette	*Pringleophaga*
Coleoptera	Curculionidae	*Ectemnorhinus marioni* Jeannel	Weevil
		Ectemnorhinus similis Waterhouse	Weevil
Stylommatophora	Endodontidae	*Notodiscus hookeri* Reeve	Snail
	Limacidae	*Deroceras caruanae* Pollonera	Slug
Haplotaxida	Acanthodrilidae	*Microscolex kerguelarum* (Grube, 1879)	Earthworm
		Microscolex kerguelenensis (Lankester, 1877)	Earthworm
	Lumbricidae	*Dendrodrilus rubidus* (Savigny, 1826)	Earthworm
Araneae	Agelinidae	*Myro paucispinosus* Berland, 1947	Spider
		Myro kerguelensis O. P. Cambridge, 1876	Spider
	Linyphiidae	*Erigone* sp.	Spider

Evenness and richness data were both normally distributed and homogenous. Variances for *Pringleophaga* larvae (biomass), weevil adults (biomass), weevil larvae (biomass and abundance) and earthworms (biomass) were heterogeneous. Only earthworm biomass data were non-normally distributed. To normalize data, all abundance data were transformed to $\log_{10}$ (x + 1) and biomass to square root. We then tested for mice-exclusion effect on community diversity (E_{var} and richness), and prey-group abundance and biomass using a general linear model for repeated measures in SPSS (SPSS for Windows, Release 11, 2001).

Vegetation and invertebrate community composition were investigated by calculating Bray-Curtis similarity (on fourth-root transformed abundance data) between treatment classes and between sample years. We used non-metric multiple dimensional scaling (Ludwig & Reynolds 1988) for ordination and tested for differences in prey-group community composition between sample year and treatment class with analysis of similarity (ANOSIM, Clarke 1993). A Mantel test (Sokal & Rohlf 1995) was used to test for association between the invertebrate assemblage and vegetation composition. Variances in density for mice (i.e. the treatment density) over the whole study period were normally distributed but not homogenous ($F_{\max 5,4} = 29.05$, $P < 0.05$), even after $\log_{10}$-transformation. A Friedman's test (Sokal & Rohlf 1995) was therefore used to test for differences among sites and over years in treatment density. This was done in order to assess

Table 2. Taxonomy of the 13 vegetation classes recorded in soil cores in the treatment–control groups; for each soil core, the dominant vegetation class on the surface was recorded and abundance was then calculated as the number of soil cores per vegetation class

Family	Species (vegetation class)
Rosaceae	*Acaena magellanica* (Lam.) Vahl.
Gramineae	*Agrostis magellanica* Lam.
	Poa cookii Hook. f.
	Agrostis stolonifera L.
Apiaceae	*Azorella selago* Hook. f.
Blechnaceae	*Blechnum penna-marina* (Poir.) Kuhn
Asteraceae	*Cotula plumosa* Hook. f.
–	Dead moss (species unknown)
Marchantiaceae	*Marchantia berteroana* Lehm. & Lindenb.
–	Moss (species unknown)
Ranunculaceae	*Ranunculus* sp.
Caryophyllaceae	*Sagina apetala* Ard.
Lycopodiaceae	*Lycopodium* sp.

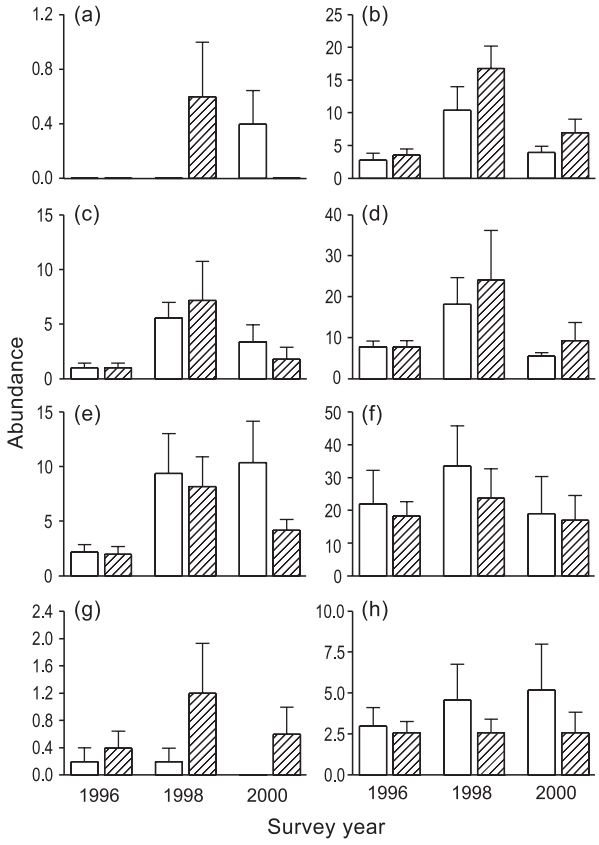

Fig. 1. The abundance (mean ± SE individuals per treatment class) of invertebrate prey groups on control and exclosure plots ($n = 5$) during 1996, 1998 and 2000 at Marion Island. Abundance was calculated as the total number of all individuals of a particular prey group in 25 randomly located soil cores in the central 25 m^2 of each plot. Only time had a significant effect and only for *Pringleophaga marioni* larvae, weevil adults and spiders (see also Table 4). (a) *P. marioni* adults; (b) *P. marioni* larvae; (c) weevil adults; (d) weevil larvae; (e) spiders; (f) earthworms; (g) snails; (h) slugs. (□), Control; (▨), exclosure.

Table 3. Density (minimum number alive ha^{-1}) of mice, *Mus domesticus*, on grids surrounding each treatment–control group from 1996 to 2000

Grid no.	1996	1997	1998	1999	2000
1	258	139	208	200	181
2	344	189	225	169	217
3	361	197	206	156	181
4	158	72	197	231	219
5	133	78	172	133	144
Mean (SD)	250.8 (104.1)	135.0 (59.1)	201.6 (19.4)	177.8 (38.3)	188.4 (30.9)

whether the magnitude of the treatment effect remained the same over time and space, a prerequisite for the experimental method.

RESULTS

The density of mice (MNA ha^{-1}) on the areas surrounding the exclosures ranged from 72 to 361 over the study period (Table 3), but mean density was not significantly different among sites or over time (Friedman test: $\chi^2_4 = 8.12$, $P = 0.09$). We therefore assumed that the treatment effect was consistent for the duration of the study.

There were indications of consistent treatment effects (consistent direction of difference between exclosure and control) on invertebrate abundance in *Pringleophaga* larvae, weevil larvae, spiders, snails and slugs, whereas results for *Pringleophaga* adults, weevil adults and earthworms were more ambiguous (Fig. 1). Only time had a statistically significant effect on abundance and only for *Pringleophaga* larvae, weevil adults and spiders (Table 4).

Table 4. Results of a general linear model for repeated measures test, using the Huynh & Feldt correction, on the abundances of six prey groups over three surveys in control and exclosure plots ($n = 5$) at Marion Island†

Effect	d.f.	F	P	η_p^2
Pringleophaga larvae				
Time	2.00	8.650	0.003	0.5200
Exclosure	1.00	2.650	0.140	0.2500
Time × treatment	2.00	0.400	0.680	0.0500
Weevil larvae				
Time	2.00	2.640	0.100	0.2500
Exclosure	1.00	0.001	0.970	0.0002
Time × treatment	2.00	0.020	0.980	0.0030
Earthworms				
Time	2.00	1.110	0.350	0.1200
Exclosure	1.00	0.040	0.840	0.0100
Time × treatment	2.00	0.980	0.400	0.1100
Weevil adults				
Time	1.43	7.250	0.010	0.4800
Exclosure	1.00	0.260	0.620	0.0300
Time × treatment	1.43	0.330	0.660	0.0400
Spiders				
Time	2.00	9.300	0.002	0.5400
Exclosure	1.00	0.840	0.390	0.1000
Time × treatment	2.00	0.690	0.520	0.0800
Slugs				
Time	2.00	0.004	0.990	0.0004
Exclosure	1.00	0.230	0.650	0.0300
Time × treatment	2.00	0.250	0.780	0.0300

†Prey groups were sampled using soil cores; because of low abundances for *Pringleophaga* adults and snails, these were not tested. d.f., degrees of freedom; η^{p2}, partial eta squared, which gives an indication of the amount of variation explained by a particular effect.

Biomass was apparently consistently affected by exclosure only for weevil adults (Fig. 2). Again, differences between years were mostly larger than differences between the exclosure and control plots, with biomass peaks in 1998 for *Pringleophaga* larvae, weevil adults, weevil larvae, earthworms and snails (Fig. 2). These temporal biomass changes were significant for *Pringleophaga* larvae, weevil adults, weevil larvae and spiders (Table 5). Although treatment effect was marginally non-significant for *Pringleophaga* larvae abundance ($P = 0.07$), there were no statistically significant treatment effects or time–treatment interactions for either biomass or abundance for any of the prey groups (Tables 4,5).

Evenness apparently increased over time in the control (this was not significant, see Table 6), but was relatively stable in the exclosure plots, whereas richness remained stable in both control and exclosure

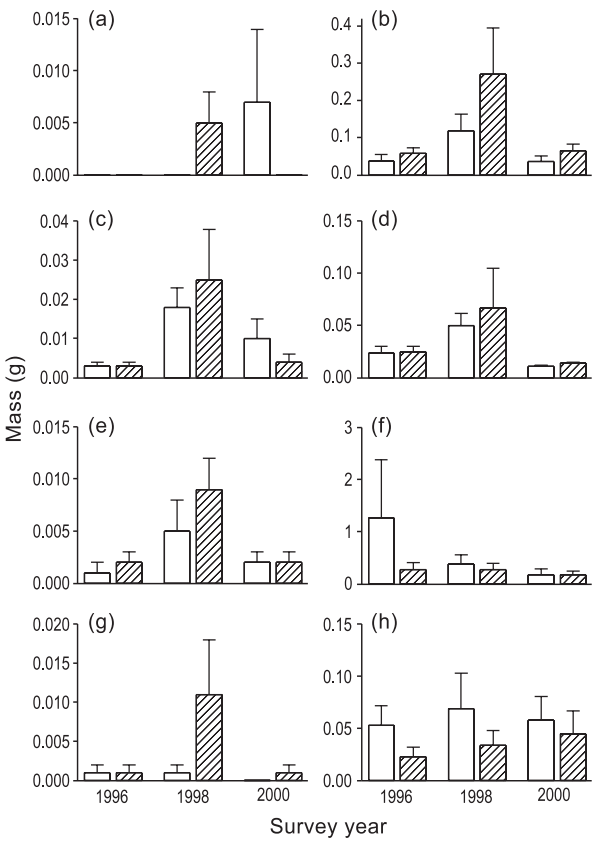

Fig. 2. The biomass (mean ± SE g per treatment class) of invertebrate prey groups on control and exclosure plots ($n = 5$) during 1996, 1998 and 2000 at Marion Island. Prey group biomass was calculated as the total mass of all individuals in 25 randomly located soil cores in the central 25 m^2 of each plot. Only time had a significant effect and only for *Pringleophaga marioni* larvae, weevil adults, weevil larvae and spiders (see also Table 5). (a) *P. marioni* adults; (b) *P. marioni* larvae; (c) weevil adults; (d) weevil larvae; (e) spiders; (f) earthworms; (g) snails; (h) slugs. (□), Control; (▨), exclosure.

(Table 7). The structure of the invertebrate community did not change significantly, either over time or across treatment (Fig. 3; stress = 0.17; ANOSIM: δ= 0.06, $P = 0.16$).

The size-class frequency distribution of *Pringleophaga* larvae was not affected by the presence of mice. The differences between control and exclosure plots before the onset of the experiment in 1996 ($G_{(adj),1} = 9.92$, $P = 0.44$), in 1998 ($G_{(adj),1} = 12.19$, $P = 0.27$) and in 2000 ($G_{(adj),1} = 10.08$, $P = 0.43$) were not significant. However, more heavy individuals were recorded during 1998 than during 1996 and 2000 ($G_{(adj),1} = 31.70$, $P < 0.01$; Table 8).

Vegetation composition (based on soil core surface vegetation classes) in the plots varied during the study period (ANOSIM: δ= 0.15, $P = 0.05$), but there was no significant treatment effect (δ = –0.30, $P = 0.99$) (Fig. 4; stress = 0.20). Variation in invertebrate communities was significantly associated with variation in vegetation communities (Mantel test: $Z = 173.21$, $P = 0.03$).

Table 5. Results of a general linear model for repeated measures test, using the Huynh & Feldt correction, on the biomass of six prey groups over three surveys in control and exclosure plots ($n = 5$) at Marion Island†

Effect	d.f.	*F*	*P*	η_p^2
Pringleophaga larvae				
Time	2.00	5.2400	0.020	0.4000
Exclosure	1.00	4.3400	0.070	0.3500
Time × treatment	2.00	0.4500	0.650	0.0500
Weevil larvae				
Time	1.71	5.6300	0.020	0.4100
Exclosure	1.00	0.0400	0.850	0.0050
Time × treatment	1.71	0.0009	0.990	0.0001
Earthworms				
Time	1.59	1.6780	0.230	0.1700
Exclosure	1.00	0.2400	0.640	0.0300
Time × treatment	1.59	0.5600	0.550	0.0700
Weevil adults				
Time	1.63	8.3500	0.006	0.5100
Exclosure	1.00	0.3500	0.570	0.0400
Time × treatment	1.63	0.5600	0.550	0.0700
Spiders				
Time	2.00	5.8300	0.010	0.4200
Exclosure	1.00	3.1200	0.110	0.2800
Time × treatment	2.00	0.1900	0.830	0.0200
Slugs				
Time	2.00	0.0400	0.960	0.0050
Exclosure	1.00	0.8100	0.390	0.0900
Time × treatment	2.00	0.0200	0.980	0.0030

†Prey groups were sampled using soil cores; because of low numbers for *Pringleophaga* adults and snails, these were not tested. d.f., degrees of freedom; η^{p2}, partial eta squared, which gives an indication of the amount of variation explained by a particular effect.

DISCUSSION

Earlier studies on Marion Island (Smith & Steenkamp 1990; Chown & Smith 1993; Matthewson *et al.* 1994; Hänel 1999; Huyser *et al.* 2000) have all in some way suggested that increased mouse predation as a result of climate change was responsible for the recorded decrease in invertebrate numbers (Crafford 1990;

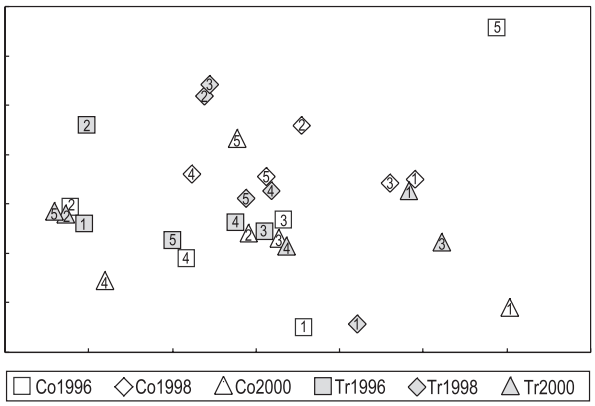

Fig. 3. Non-metric multiple dimensional scaling (on Bray-Curtis similarity, fourth-root transformed) of invertebrate prey group communities inside (exclosure (Tr)) and outside (control (Co)) mice, *Mus domesticus,* exclosures on Marion Island during 1996, 1998 and 2000 ($n = 5$ for all 3 three years; stress = 0.17). Symbols of similar shape refer to exclosure (shaded) and control plots in a particular sample year. Symbols with the same numbers refer to plots grouped together in the randomized block experimental design.

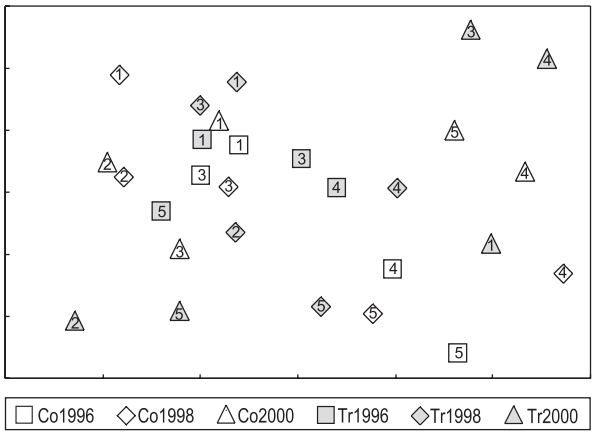

Fig. 4. Non-metric multiple dimensional scaling (on Bray-Curtis similarity, fourth-root transformed) of vegetation class assemblages inside (exclosure (Tr)) and outside (control (Co)) mouse, *Mus domesticus,* exclosures on Marion Island during 1996, 1998 and 2000 (stress = 0.20). For 1996 information is available for only four plots for both treatment classes. Symbols of similar shape refer to exclosure (shaded) and control plots in a particular sample year. Symbols with the same numbers refer to plots grouped together in the randomized block experimental design.

Crafford & Scholtz 1987; Chown & Smith 1993; Hänel 1999). Invertebrate numbers (and biomass) should therefore increase if mice are excluded and the trajectories of areas where mice are excluded should diverge over time from areas where they have free access. Our analyses do not support such divergence in either community-structure or prey-group variables (abundance, size-class distributions and biomass), except on a qualitative level for some prey groups. The data in Figures 1 and 2 show that temporal variation, which was mostly similar for control and exclosure plots, dwarfed treatment differences. Treatment effects on *Pringleophaga* and weevil larvae, preferred food resources for mice (Rowe-Rowe *et al.* 1989; Crafford 1990), were consistent (exclosure > control; Fig. 4) and marginally non-significant for *Pringleophaga* larvae, but were still less than temporal effects. The 43% difference in biomass of *Pringleophaga* larvae between exclosure and control plots by the third survey was also less than what would have been expected on the basis of previous estimates of mice predation. Even the lowest previous predation estimate of 0.7% of daily standing crop (Crafford 1990) implies an annual removal of more than twice the total standing crop, which would translate to larger differences between exclosure and control plots than those we found. Furthermore, mice had no significant effect on prey-group community composition, whereas the prey-group community associated closely with the plant community (which also varied significantly over time, but was not influenced by the mice). In short, the results of the present study suggest that variation in invertebrate communities on Marion Island is not strongly affected by mouse presence.

Previous studies have ascribed an apparent increase in peak mouse densities during late summer (Chown & Smith 1993; Matthewson *et al.* 1994) to increased temperatures and decreased rainfall on Marion during the 1970s and 1980s (Smith 1992; Chown & Smith 1993). Several more studies have found indirect support for an impact of this reported mouse population increase on the island's invertebrates (Chown & Smith 1993; Bergstrom & Chown 1999; Huyser et al. 2000). The present study, in contrast, points in the opposite direction. Why this apparent discrepancy?

The results of the present study are bedevilled by low statistical power for all univariate tests, because of the high variability characteristic of low-diversity systems (Cottingham *et al.* 2001). Furthermore, all factors explained relatively small amounts of variability. This

Table 6. Results of a general linear model for repeated measures test, using the Huynh & Feldt correction, on the prey-group diversity over three surveys in control and exclosure plots (n = 5) at Marion Island†

Effect	d.f.	F	P	η_p^2
Richness				
Time	2	0.03	0.97	0.004
Exclosure	1	2.89	0.13	0.270
Time × treatment	2	0.10	0.90	0.010
Evenness				
Time	2	0.40	0.68	0.048
Exclosure	1	1.16	0.31	0.130
Time × treatment	2	0.17	0.85	0.020

†Prey groups were sampled using soil cores. d.f., degrees of freedom; η^{p2}, partial eta squared, which gives an indication of the amount of variation explained by a particular effect.

Table 7. Mean (±SE) richness (no. prey groups per plot) and evenness (E_{var}; Smith & Wilson 1996) of the prey-group community on Marion Island, in two treatment levels during 1996, 1998 and 2000 (n = 5)

	1996		1998		2000	
Weight class	Control	Exclosure	Control	Exclosure	Control	Exclosure
Richness	4.40 ± 0.68	5.20 ± 0.20	4.40 ± 0.40	5.20 ± 0.38	4.60 ± 0.40	5.00 ± 0.45
Evenness	0.56 ± 0.11	0.55 ± 0.07	0.59 ± 0.11	0.47 ± 0.06	0.67 ± 0.11	0.56 ± 0.09

Table 8. Number of *Pringleophaga marioni* larvae in soil core samples (n = 125) in six weight classes (g) during 1996, 1998 and 2000†

	1996		1998		2000	
Weight class	Control	Exclosure	Control	Exclosure	Control	Exclosure
0.00–0.01	7	5	29	49	9	20
0.01–0.02	3	8	15	15	5	12
0.02–0.03	2	3	3	11	3	2
0.03–0.04	2	1	4	4	0	2
0.04–0.05	0	1	1	1	0	0
>0.05	0	0	0	4	0	0

†Size classes are lumped together in intervals of 0.01 g; *G*-tests were carried out on 11 classes of 0.005-g intervals.

was particularly true for the most important factor, the interaction between time and treatment, where all η_p^2 (effect size) values were consistently below 0.11 and observed power below 0.2. This is generally regarded as too low to detect significant differences and suggests that more replication is necessary (Ortiz 2002). Future exclosure studies on sub-Antarctic islands thus need to take the variability in invertebrate distribution into account. In addition, the surface-active *Pringleophaga* adults and snails were found in particularly low numbers in all surveys, making it impossible to test and difficult to interpret differences. The lack of significant impact by mice on prey-group abundance and biomass could therefore be the direct result of high spatial variability in prey-group variables and low sampling abundances.

But it is also possible that the interaction between mouse population size and climate change is too complex to detect differences in invertebrate abundance and biomass as a result of mouse exclusion. Several indirectly related variables could limit both mice and invertebrates, whereas climate change itself might have either positive or negative effects for both. So far, support for a mouse effect has been only indirect, coming mainly from differences in invertebrate abundance/biomass between Marion and (mouse-free) Prince Edward Island and between prey and non-prey items (Bergstrom & Chown 1999). For example, Huyser *et al.* (2000) ascribed the comparatively low sheathbill (*Chionis minor*) numbers and breeding performance on Marion Island to increased competition with mice for food, as a result of the assumed climate-induced increase in mouse numbers and concurrent decline in invertebrate numbers. Similarly, Chown and Smith (1993) found that the body sizes of two weevil prey species, but not those of two non-prey species, decreased between 1986 and 1992, concurrent with an increase in temperature. Some other studies, such as a recent one by Smith *et al.* (2002), have calculated the potential impact of mice on invertebrates based on diet, consumption rates and available prey biomass.

However, climate change itself could increase invertebrate abundance as a result of ambient warming (Smith & Steenkamp 1990, 1993), or decrease it as a result of the characteristically low water-loss tolerances of sub-Antarctic invertebrates (Klok & Chown 1997, 2001) in a drying environment (Smith & Steenkamp 1990; Chown & Smith 1993). It has been shown before that invertebrates could undergo range expansions or population changes as a result of even small increments in temperature, or changes in precipitation (Masters *et al.* 1998; Bale *et al.* 2002; Beaumont & Hughes 2002). If invertebrates adapt more readily to climatic changes than to predation, which is likely because climate-adaptation is essentially a physiological response (Addo-Bediako *et al.* 2000), at the very least the short-term effect of a predator might be drowned out by climate effects (Bergstrom & Chown 1999).

A second possibly confounding factor is the relationship between invertebrates and vegetation. The present analysis found no evidence for a mice-related variation in crude vegetation composition, one of Chown and Smith's (1993) suppositions. However, we did find that variation in invertebrate communities was significantly associated with variation in vegetation composition on both exclosure and control plots. Current changes in vegetation composition on Marion Island (Gremmen 1997; Gremmen *et al.* 1998), unrelated to the presence of mice, could therefore lead to changes in the invertebrate component (Gremmen *et al.* 1998). Furthermore, feral cats, which were present on Marion from 1948 to 1991 (Bester *et al.* 2000), decimated the Island's main source of minerals and nutrients, the burrowing seabird populations (Williams 1978; Crafford & Scholtz 1987; Smith 1987). Such a disturbance would have created a lasting influence on the vegetation and the abundance and biomass of invertebrates on Marion to a greater extent than predation by mice alone could have done.

Clearly, we need to know more, both about mice and about invertebrates, before we can correctly apportion factors responsible for variation in invertebrate abundance. Future studies should be directed at determining long-term invertebrate population dynamics (Smith *et al.* 2002), autecology of the various prey items of mice and the proximate controlling factors for mice and invertebrate populations. For instance, there is some evidence that desiccation and, to a lesser extent, temperature may be population-limiting factors for some invertebrates (Klok & Chown 1997, 2001). Exactly how critical levels in these limiting factors translate to conditions on Marion Island is not known. Where and when do critical desiccation levels occur, and is there any evidence of behavioural adaptation by the invertebrates? The activities of the soil macro-fauna may be temperature dependent (Smith & Steenkamp 1990; Marshall & Chown 1995), but there are no data to demonstrate how this affects their numbers.

Similarly, several authors (Smith & Steenkamp 1990; Chown & Smith 1993; Huyser *et al.* 2000) have suggested that mice are strongly temperature-dependent. However, our previous analyses suggest no relation between minimum temperatures and mouse mortality rates (van Aarde *et al.* 1996). Moreover, trends in mouse numbers on Marion between 1991 and 2001 are habitat dependent, with numbers on biotically influenced areas being stable, but numbers on wetlands increasing by approximately 12% per year. Such trends suggest that mouse numbers are not limited by food availability and the impact that mice may have on invertebrates as suggested by Smith and Steenkamp

(1990), Chown and Smith (1993) and Huyser *et al.* (2000) would thus be difficult to account for.

Finally, the effects of mice on invertebrates cannot be judged without more information on the biology of the different invertebrate species. Information on life-history variables is lacking for all the invertebrates. The larval period of the moth *P. marioni* has been variously estimated as more than 3 years (Crafford & Scholtz 1987), 2–3 years (Crafford 1990) and up to 5 years (Klok & Chown 1997). This is an important factor to consider. A 5-year larval stage for an insect would preclude changes in abundance or biomass of adults over the 5-year period of the present study. The effect of mice on the insects might only become apparent after ≥10 years of exclusion if other species have similar duration of larval stages. Over a longer term, the effect of mice could potentially be much greater than was measured in the present experiment. Under ideal conditions, we would have liked this trial to continue for at least a decade, providing enough opportunity for invertebrate communities to respond to the release from mice predation.

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