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RESEARCH

Do mice matter? Impacts of house mice alone on invertebrates, seedlings and fungi at Sanctuary Mountain Maungatautari

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Abstract: The advent of mammal-resistant fences has allowed multi-species eradications of mammals from ecosanctuaries on the New Zealand mainland. However, maintaining eradication of house mice (*Mus musculus*) has proven difficult, and at some fenced reserves they are the only exotic mammal present and reach a high population density. Over 5 years we examined the impacts of mice alone on biodiversity at Sanctuary Mountain Maungatautari by comparing forest blocks with relatively high and low numbers of mice. We managed two independently fenced sites within the sanctuary to achieve high mouse numbers (up to 46 per hectare) at one site and undetectable mouse numbers at the second site. We then reversed these treatments by eradicating mice from the first site and allowing their numbers to increase at the second. We found strong evidence that mice reduced the abundance of ground-dwelling invertebrates, in particular caterpillars, spiders, wētā, and beetles, and reduced the mean body size of some taxa. In addition, earthworm abundance, biomass and species richness increased with a decreasing mouse population in one study block. No significant impact of mice on land snails, seedlings or fungi was detected at Maungatautari. Overall, there is substantial biodiversity gain from eradicating the full suite of pest mammals other than mice. However, mice may be catastrophic in ecosanctuaries that focus on the recovery of invertebrates or lizards. We expect that mouse control tools will steadily improve so that in the future mice can be eradicated and excluded from forest reserves such as Maungatautari.

Keywords: earthworms, ecosanctuary, invertebrates, *Mus musculus*, New Zealand, seedlings, wētā

Introduction

Worldwide, the impacts of invasive species on native ecosystems have become a significant conservation issue. Extinctions, species declines, and ecosystem changes have been well documented on southern hemisphere islands, with introduced mammals, particularly rodents (*Rattus* spp. and house mice *Mus musculus*), causing the majority of these impacts (Towns & Broome 2003; Howald et al. 2007; Angel et al. 2009). House mice are one of the most widespread invasive mammals on the planet due to their rapid population growth rate, varied flexible diet, and close association with humans (Murphy & Nathan 2021). Mice are the smallest (mean weight range 17–26 g) of the four rodent species introduced to New Zealand, arriving after Norway rats (*R. norvegicus*) and before ship rats (*R. rattus*) as stowaways on ships in the early 1820s. House mice quickly spread, and by the early 1900s occupied most suitable environments throughout the North and South Islands (Murphy & Nathan 2021). New Zealand has no extant native terrestrial mammals except for bats.

New Zealand studies have shown that mice eat a range of small invertebrates (3–12 mm long) and plant material. Caterpillars are often the most common invertebrate group eaten by mice in forests, followed by spiders, beetles, and wētā (Jones & Toft 2006; Murphy & Nathan 2021). For example, invertebrates accounted for 94% of the stomach contents of mice from a podocarp–broadleaved forest in the Ōrongorongo River valley, southern North Island (Fitzgerald et al. 1996); these included caterpillars (found in 51% of stomachs), spiders (45%), beetles (27%), and wētā (17%). On Rangitoto Island, Miller and Miller (1995) also found that invertebrates were the major component of mouse diet, with Auckland tree wētā (*Hemideina thoracica*) being a dominant prey item. In alpine habitat in Fiordland, South Island, the diet of mice was dominated by wētā, spiders, and grasshoppers (Wilson & Lee 2010).

A few studies have shown that earthworms play a major role in the diet of mice, particularly during the winter (Le Roux et al. 2002; Jones et al. 2003). In contrast, two studies on sub-Aantarctic islands, such as Marion and Macquarie, concluded that earthworms are of negligible importance as a food item for mice (Gleeson & Van Rensburg 1982; Copson 1986). It is

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important to note that of the above studies, only Le Roux et al. (2002) and Jones et al. (2003) included earthworm chaetae in their analysis. Until recently, without chaetae, the importance of earthworms in animal diets could not be accurately determined, and the importance of soft-bodied prey, such as larvae and earthworms, is likely to have been underestimated in many studies (Jones & Toft 2006). However, novel eDNA techniques have the potential to identify invertebrate prey, including soft-bodied organisms, from mammalian stomach contents or faecal material (Clare et al. 2009). For example, Watts et al. (2020a) used DNA barcoding to identify a prey fragment extracted from a rat stomach as cave wētā (*Talitropsis sedilloti*; 99% sequence identity).

Worldwide, as well as in New Zealand, mice in unmanaged urban, rural, and wild ecosystems are typically uncommon and inconspicuous when food is scarce and other competing and predatory mammal species are present. In New Zealand, larger introduced predatory mammals such as ship rats and Norway rats, mustelids (stoat *Mustela erminea*, feral ferret *M. putorius*, and weasel *M. nivalis*) and feral cats (*Felis catus*) limit mouse abundance or activity and obscure their impacts (Innes et al. 1995; King et al. 1996; Harper & Cabrera 2010; Bridgman et al. 2013; Murphy & Nathan 2021). In contrast, overseas examples show that mice alone on islands or in agricultural crops with abundant food and few or no predators can become abundant and cause substantial damage to biodiversity and crop yields (Pech et al. 1999; Jones et al. 2003; Angel & Cooper 2006). The discovery that mice on Gough Island ate the undefended chicks of large seabirds, including albatrosses (Cuthbert & Hilton 2004), greatly extended understanding of their potential impacts. This led, for example, to Angel et al. (2009) questioning whether the impacts of mice alone on islands should be regarded as equivalent to those of rats.

Mouse populations also increase when they are the only remaining terrestrial mammals on New Zealand islands (Newman 1994; Russell 2012), or when food supplies become plentiful, such as during mast seeding of beech trees (King 1983; Fitzgerald et al. 1996), podocarp trees (Ruscoe et al. 2004), and tussock grasses (Wilson & Lee 2010). Recently, mice have frequently been the only mammal species surviving in fenced wildlife sanctuaries on the mainland (Burns et al. 2012), either because they survive eradication attempts or because they subsequently reinvade through fences that exclude larger mammals. In this situation, as on oceanic islands, mice can become abundant and may prevent the achievement of predator-removal objectives and biodiversity restoration goals (Goldwater et al. 2012).

Conservation managers, ecosanctuaries, and community groups in New Zealand that are engaging in mammal eradication or control where mice are now the only exotic mammal present have raised concerns regarding the impacts of mice alone on native biodiversity. In response to this concern, we conducted a 5-year study examining the impacts of mice on native biodiversity in a mammal-resistant fenced sanctuary, Sanctuary Mountain Maungatautari (referred to hereafter as Maungatautari), Waikato, New Zealand. We managed two independently fenced sites within the sanctuary to achieve high mouse numbers (up to 46 per hectare) at one site and undetectable mouse numbers at the second site (Wilson et al. 2018). We then reversed these treatments by eradicating mice from the first site and allowing their numbers to increase at the second (Wilson et al. 2018). Here we focus on the impact of mice alone on invertebrates, particularly their common dietary taxa, including caterpillars, spiders, wētā, and beetles (referred to hereafter as the preferred diet taxa). In addition, we investigated the earthworm and land snail communities to detect any responses by these little-studied groups. As seeds are often an important component of mouse diets (Murphy & Nathan 2021), we also studied seedling responses to mice alone.

We expected that the presence of numerous mice as predators would reduce the abundance, species richness, and mean body size of invertebrates, and the density and species richness of seedlings. Previous studies have established that various fungi (e.g. *Rhizopogon*; *Elaphomyces*) are components of mouse diets (Maser & Maser 1987; Frank et al. 2009); however, these studies were primarily focused on hypogeous fungi (fungi with underground fruiting bodies e.g. truffles) not known to be present at Maungatautari. We anticipated that mice would eat the mushroom species found at Maungatautari.

Methods

Study area

Maungatautari (3239 ha) is a highly eroded andesitic cone (797 m asl) surrounded by farmland, but with a diverse range of native forest types remaining above 240 m asl. Rimu (*Dacrydium cupressinum*)–tawa (*Beilschmiedia tawa*) is the dominant forest type of the sites used in this study (Clarkson et al. 2002).

A mammal-resistant fence (Day & MacGibbon 2007) enclosing Maungatautari was completed in 2006, and a sustained operation to eradicate mammals from inside the fence followed (Speedy et al. 2007). Mice became scarce, but it is likely that they were never eradicated completely (Wilson et al. 2018). Further mouse control ceased in February 2012 and mice have since become abundant (for a detailed timeline, see Table 1 in Wilson et al. 2018).

Starting in April 2011 we used two independently mammal-fenced sites with contrasting mouse densities at Maungatautari (see Fig. 1 in Wilson et al. 2018). Our 'M block' is a small (24 ha) part of the fenced 3400 ha Maungatautari reserve that received ongoing mouse control, and mice were undetectable there when this study started. After aerial poison drops in 2004, 2006, and 2008, c. 3200 inked cards in footprint tracking tunnels baited with peanut butter were placed across Maungatautari (c. 1 hectare^{-1}). Tunnels were initially checked monthly, then cards were replaced monthly but checked after one week. Each time a mouse was detected, alternating mouse traps in tracking tunnels and brodifacoum bait in bait stations were placed in a 25 × 50 m grid covering a 200 × 200 m area around the location of the detection. In September 2011, eradication efforts across Maungatautari were suspended until cost-effective mouse control methods might become available, because monitoring and removal were too expensive to sustain. However, mouse control continued in M block due to our study design requirements.

Our 'Q block', approximately 100 m south of M block, is a mammal-fenced 17 ha, private forest block covenanted by the Queen Elizabeth II National Trust (i.e. an agreement between QEII Trust and a landowner protects land in perpetuity) and separated from the main reserve only by a vehicle track. All mammals were removed from Q block by 2008, but mice were detected in August 2009 and then became abundant.

In August 2013, half-way through our study, we switched mouse management treatments (referred to hereafter as the treatment switch) between the two blocks, to experimentally test mouse impacts on indigenous biodiversity. Maungatautari

Ecological Island Trust (a private, non-profit-making registered charitable Trust established in 2001 to restore and sustain Maungatautari) eradicated mice from Q block while mouse control ceased in M block to allow the population to increase. As a result, mouse population density in Q block was high from April 2011 to August 2013, and low from November 2013 to February 2016. We refer to these block–treatment combinations as QH and QL, respectively (as in Wilson et al. 2018). In contrast, mouse density in M block was low and then higher (ML and MH) on average during the same periods.

Mouse population density and abundance indices (traps and tracking tunnels)

The population density of mice (mice hectare^{-1}) in each study block was estimated every 3 months using spatially explicit capture–recapture (Wilson et al. 2018). Relative indices of mouse abundance in each block were also estimated every 3 months (autumn: April/May; winter: August; spring: November; summer: February), between April 2011 and February 2016, using footprint tracking based on established protocols (Gillies & Williams 2013). We placed inked cards in tracking tunnels (24 in Q block and 36 in M block) set in lines 150 m apart, each with 5–12 tunnels 50 m apart (a different layout from the standard method because of our small block sizes; Wilson et al. 2018). Tunnels were baited with peanut butter and checked the next morning. Tracking rate (percentage of tunnels tracked by mice) was calculated for each occasion on each block.

Invertebrates

Invertebrate sampling protocols and timing are summarised in Table 1.

Sampling the invertebrate community using pitfall traps

The ground-dwelling invertebrate fauna was sampled using pitfall traps, each a 100 mm-deep plastic cup (105 mm diameter) containing 100 mL of 50% monopropylene glycol. Pitfall traps were placed at 5 m intervals along a 45 m transect located between two tracking tunnels. Two transects were located randomly within each study block, giving a total of 20 pitfall traps in each block. Traps were set for 1 month in April in 2011–2015, and for 3 months over summer (late November to late February, set and collected each month) from 2011/12 to 2015/16. Specimens were preserved in 70% ethanol.

Captured invertebrates (≥ 3 mm in length) were sorted and counted to order level using a binocular microscope. We focused on caterpillars, spiders, beetles, and wētā as these have been identified previously as dominant prey items in diets of mice (preferred diet taxa) in the presence of other mammals (see references in Murphy & Nathan 2021). Beetles were sorted on the basis of external morphology into recognised taxonomic units (RTUs; hereafter referred to as species, see Appendix

Table 1. Summary of methods used to sample invertebrates, seedlings and fungi in the study blocks M and Q at Sanctuary Mountain Maungatuatari between April 2011–February 2016.

Target Group	Sampling method	Number of traps/samples	Duration of sampling	Frequency of collection
Ground-dwelling invertebrate community	Pitfall trap	20 traps in each block (10 traps located 5 m apart along a 45 m transect × 2)	April 2011–2015 Summer 2011/12–2015/16	Annually (1 month in April; late Nov–late Feb, collected monthly)
Leaf-litter invertebrate community	Leaf-litter sample (33 cm diameter circular frame (0.086 m^2))	32 sampling points in each block	April 2011–2015	Annually
Land snails	Extracted via Tullgren funnel from leaf-litter samples	32 sampling points in each block	April 2011 and 2012	Twice
Wētā	Tracking tunnels	24 tracking tunnels in Q block; 36 tracking tunnels in M block	April 2011–February 2016	Every 3 months in Autumn (April/May), Winter (August), Spring (November) and Summer (February)
Earthworms	Searching leaf-litter and soil (depth of 10cm) from 50 × 50 cm quadrats (0.25 m^2)	20 sampling points in each block	November 2013 and 2015	Twice
Seedlings (cotyledonary, mixed-leaf and true-leaf seedlings)	Counted seedlings in circular 0.75 m^2 plots	36 sampling points in each block	April 2011, April 2013 and June 2016	Three times
Fungi	Offered mice six known edible and other mushrooms at cafeteria and filmed with cameras	One	48 hours in July 2011	Once
	Fungal DNA from mouse faecal pellets	54 faecal pellets examined	August 2011 and February 2012	Once

S1 in Supplementary Materials) and, where possible, given generic and species-level identifications by Stephen Thorpe (independent researcher, Auckland). Each beetle captured was measured, and then mean beetle body length (mm) per trap was calculated. Wētā size was calculated by measuring the width of the pronotum (mm), and then a mean per trap was calculated.

Sampling the leaf-litter invertebrate community

Litter-dwelling invertebrates were collected from leaf-litter samples, each within a 33 cm diameter circular frame (0.086 m^2) at 32 sampling points in each block. Sampling points were chosen using a random compass bearing and distance (< 5 m) from each tracking tunnel. Eight extra litter samples (two from each line of tunnels) were collected from the Q block to achieve 32 samples from each block. Each April, from 2011 to 2015, eight litter samples were taken weekly from each block (32 samples per block). At collection, all leaf litter and friable humus were scraped rapidly from the frame, placed in individual bags and transported back to the laboratory. Invertebrates were extracted from the leaf litter over a 72 hr period using Tullgren funnels (Moeed & Meads 1986).

Preservation, sorting, counting and identification of invertebrates from the leaf litter followed the same protocols as used for the pitfall-trapped invertebrates. Litter weight was recorded per sample.

Sampling land snails

After the 72 hr Tullgren funnel extraction described above, land snails were extracted manually from the litter samples in April 2011 (QH; ML) and 2012 (QH; ML) from both blocks.

Sampling wētā with tracking tunnels

Tracking tunnels used to monitor mice (described above) were also used to record the footprints of invertebrates. Each tracking card was examined for the presence of wētā footprints, which are readily recognisable. Protarsal, mesotarsal, and metatarsal prints longer than 2.5, 3.5, and 4.4 mm, respectively, indicate the presence of adult Auckland tree wētā (*H. thoracica*; Watts et al. 2011). Smaller wētā, including subadult and juvenile Auckland tree wētā, all age classes of ground wētā (*Hemiandrus* species), and all age classes of cave wētā (Rhaphidophoridae species) were recorded as 'other wētā'.

Sampling earthworms

In November 2013 (QL; MH; 3 months after treatment switch) and 2015 (QL; MH) a headlamp was used to search leaf litter and then soil to a depth of 10 cm from within twenty 50 × 50 cm quadrats (0.25 m^2) in each of the Q and M blocks. To avoid potential trampling effects, each sampling point was located 10 m west of a randomly selected tracking tunnel in 2013, and 10 m east of a tunnel in 2015. Earthworms were immediately placed into labelled vials containing 70% ethanol; later they were dabbed dry and individuals weighed to the nearest milligram. Identification to RTU was completed using a binocular microscope and the keys of Lee (1959) and Sims & Gerard (1985).

Sampling seedlings

Seedling sampling protocols and timings are summarised in Table 1. We counted cotyledonary seedlings (i.e. with their first leaf), true-leaf seedlings (< 15 cm tall) and mixed-leaf (both cotyledons and true leaves combined) seedlings in 36 circular plots, each 0.75 m^2, placed systematically along transects in each of Q and M blocks in April 2011 (QH; ML), April 2013 (QH; ML), and June 2016 (QL; MH). Plots were placed 5 m from tracking tunnels, on alternating sides perpendicular to each line of tunnels. In Q block, 12 additional plots were placed opposite other plots to achieve 36 plots in each block. Total density of all seedlings (number $metre^{-2}$), total seedling species richness, and densities of cotyledonary, true-leaf and mixed-leaf seedlings were then calculated by species and size class.

Sampling fungi

Fungi sampling protocols are summarised in Table 1. Fruiting bodies of six known human-edible and other mushrooms were translocated from ML to QH and placed at a cafeteria site at ground level. Video cameras were set up for a period of approximately 48 hr in July 2011 to observe if mice, when presented with a choice of mushrooms, would consume certain species preferentially.

In a second approach, mouse faecal pellets were collected during trapping operations in August 2011 and in February 2012. The pellets from August were analysed using molecular methods, and the pellets from February were analysed using both microscopy and molecular methods. DNA was extracted from pellets surface-cleansed with 70% ethanol. The internal transcribed spacer region (ITS) was amplified using the fungal and Basidiomycota-specific primers ITS, 1F, and ITS 4B (Gardes & Bruns 1993), since the fungi most likely to be consumed by mice are larger Basidiomycota.

Seventeen faecal pellets were examined microscopically. Fungal tissues are mostly digested, leaving only spores in the faecal matter (Castellano et al. 1989).

Data analysis

Pitfall trap invertebrate community data

A linear mixed model (LMM) with smoothing splines over time, fitted using Residual Maximum Likelihood, was used to model the temporal trends in the pitfall trap invertebrate data for each study block (Q and M) and the covariance structure of the repeated measurements. The random and fixed effects of the LMM are described in Table 2. Mouse density was not used as a predictor in our statistical models because dates of mouse and invertebrate sampling sessions differed, mouse density could be estimated only for capture sessions when >1 mice were caught (Wilson et al. 2018), and lags were expected between mouse density and its effects on invertebrate populations.

Differences in the temporal trends between the two study blocks were examined by plotting 83% confidence intervals around the predicted mean values. Non-overlapping 83% confidence intervals indicate differences between the study blocks at the 5% significance level (Krzywinski & Altman 2013). The total number of invertebrates caught (per trap), the number of preferred diet taxa invertebrates caught, the number of beetle species caught, the mean beetle length, and the mean wētā size were analysed as response variables. The number of spiders, beetles, wētā caught were also separately analysed, but the caterpillar count data were too sparse to analyse separately. Residual diagnostic plots were inspected for evidence of departures from the assumptions of normality and homogeneity of variance. All count data were square-root transformed prior to analysis to stabilise the variance.

To assess the variation in beetle species composition and abundance between samples collected from the M and

Table 2. The random and fixed effects of the linear mixed models with smoothing splines over time used to model the temporal trends and the covariance structure of the repeated measurements, for a) pitfall trap invertebrate community data, b) leaf-litter invertebrate community data, and c) wētā tunnel tracking data.

Data	Random effects	Fixed effects
Pitfall trap invertebrate community	Temporal splines: overall, study block, transect and pitfall trap Correlated random coefficients: pitfall trap plus pitfall trap by time Random factors: transect, month	Covariates: time, number of trap nights Fixed factor: study block Interaction: study block by time
Leaf-litter invertebrate community	Temporal splines: overall, study block, transect and plot Correlated random coefficients: plots plus plots by time Random factor: transect	Covariates: time, weight of litter sampled Fixed factor: study block Interaction: study block by time
Wētā tunnel tracking	Temporal splines: overall, study block and transect Correlated random coefficients: transect plus transect by time Random factor: season	Covariates: time Fixed factor: study block Interaction: study block by time

Q blocks over the study, classification cluster analysis and ordination techniques were performed within the PATN multivariate analysis package (Belbin 1995). Species with only one specimen in the dataset were omitted from the analysis. The procedures FUSE (agglomerative hierarchical fusion) and SSH (semi-strong hybrid multidimensional scaling) were implemented. Furthermore, a flexible unweighted pair-group method using UPGMA clustering (with $\beta = -0.1$), where equal weight is given to objects, not groups, and the Bray-Curtis association measure, which consistently performed well in data testing (Faith et al. 1987), were selected. A two-dimensional ordination with a stress value of 0.1867 was considered to summarise the data suitably (see Belbin 1995).

Leaf-litter invertebrate community data

Similar to the analysis of the pitfall data, an LMM with smoothing splines was used to model the litter invertebrate data over time (Table 2). The total number of litter-dwelling invertebrates found per transect plot, the number of litter-dwelling spiders, beetles, caterpillars, and beetle species found per transect plot, and the mean beetle length of litter-dwelling invertebrates found per transect plot were analysed. The wētā count data were too sparse to analyse separately. Residual diagnostic plots were inspected for evidence of departures from the assumptions of normality and homogeneity of variance. Transformations were not needed.

Wētā tunnel tracking data

At each sampling time, the proportion of tunnels on a transect tracked by (1) adult Auckland tree wētā and (2) other wētā was calculated. Similar to the analysis of the pitfall data, an LMM with smoothing splines was used to model the tracking tunnel data over time (Table 2). Residual diagnostic plots were inspected for evidence of departures from the assumptions of normality and homogeneity of variance. Transformations were not needed.

Land snails

LMMs were used to assess the effects of study block, year (2011 and 2012), and their interaction, on the number of snails collected and the number of unique snail species found (i.e. species richness) in the litter samples. Random terms for transect nested within block and plot nested within transect were included to take account of the sampling structure. In addition, a random intercept for sampling date and a sampling date by plot spline were included to account for additional temporal variability. Residual diagnostic plots were inspected for evidence of departures from the assumptions of normality and homogeneity of variance. The number of snails collected per plot was natural log + 1 transformed prior to analysis to stabilise the variance, and back-transformed means and exact back-transformed 95% confidence intervals were calculated. The significance of the study block by year interaction was assessed using an F-test, and Fisher's unprotected least significant differences at the 5% level were used to compare means.

Earthworms

LMMs were used to assess the effects of study block, year (2013 and 2015), and their interaction on the mean abundance, biomass (g), and species richness of earthworms collected within the transect plots. Random terms for transect within block and plot within transect were included to take account of the sampling structure. Residual diagnostic plots were inspected for evidence of departures from the assumptions of normality and homogeneity of variance. To normalise the data, the variables (abundance, biomass, and species richness) were natural log transformed prior to analysis. Due to the presence of zeroes, half the minimum non-zero value were added prior to logging. Back-transformed means and exact back-transformed 95% confidence intervals were obtained. The significance of the study block by year interaction was assessed using an F-test, and Fisher's unprotected least significant differences at the 5% level were used to compare means.

Seedlings

LMMs were used to assess the effects of study block, year (2011, 2013 and 2016) and their interaction on the mean litter depth (cm), total density of all seedlings (number m^{-2}), total seedling species richness, and densities of cotyledonary, mixed-leaf, and true-leaf seedlings. The analysis was the same as for the earthworm data except that we also included a power model of order one in the seedling LMMs to accommodate correlations between measurements taken on the same transect plot over the 3 years.

All statistical analyses were performed using Genstat version 19 (VSN International 2017).

Results

Mouse population density and footprint tracking indices

Mouse density fluctuated seasonally in both blocks, with relatively high summer or autumn densities following mouse reproduction in spring and summer (Fig. 1). In QH, density was 9–46 mice per hectare until mice were eradicated in August 2013. In ML, density was apparently zero until summer 2012, when the first mouse was caught there; in MH, density then increased to 6–23 per hectare.

The percentage of tunnels with mouse tracks was positively related to mouse density in the corresponding block and capture session. Density could be estimated only for capture sessions where > 1 mice were caught; at these times tracking rates ranged from 8–92% in M block and 67–100% in Q block. In other sessions, where 0 or 1 mice were caught and density was not estimated, tracking rates were 0–11%.

Further details of mouse population density estimates (mice per hectare) and abundance indices based on the percentage of tunnels with footprints for each block throughout the 5-year study are given in Wilson et al. (2018).

Invertebrates

Invertebrate community assessed with pitfall traps

A total of 42 639 invertebrates were caught in pitfall traps during the study. There was strong statistical evidence that, on mean, the number of preferred diet taxa caught in pitfall traps was lower in QH than in ML (Fig. 2a). In contrast, following the treatment switch, there was strong statistical evidence that the mean number of preferred diet taxa caught in pitfall traps was higher in QL than in MH (Fig. 2a). A similar pattern was observed for the total number of invertebrates caught, the number of spiders, beetles, and wētā caught, and the number of beetle species caught in pitfall traps (Appendices S2–S7).

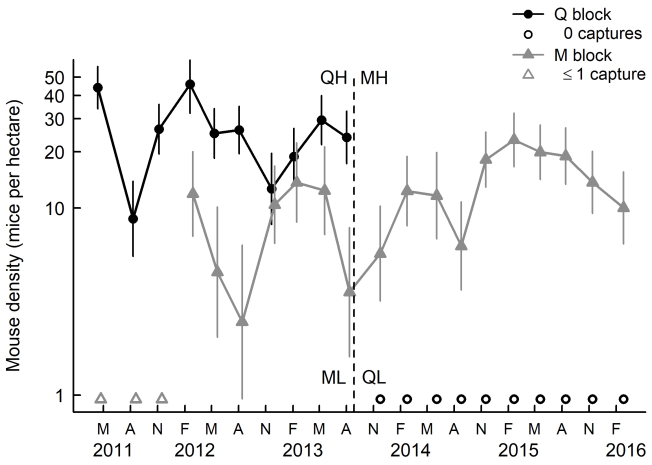

Figure 1. Estimated house mouse population density in Q and M blocks within Sanctuary Mountain Maungatautari. Vertical lines show 95% confidence intervals. Open symbols show trapping sessions when density could not be estimated; i.e. when ≤ 1 mice were captured in M block (triangles) early in the study, and when 0 mice were captured in Q block (circles) after eradication. Timing of the treatment switch in August 2013 is shown with a dashed vertical line. Density is plotted on a logarithmic scale. QH, QL, MH, and ML indicate block–phase combinations; i.e. mouse density treatments (High, Low) that switched between blocks (Q, M) at or around August 2013. Reproduced with permission from Wilson et al. (2018).

On average, beetles with significantly shorter body length were caught in pitfall traps at QH compared with ML, and there was some evidence that the mean length of beetles caught was longer in QL than in MH (Fig. 2b). A similar pattern was observed for mean wētā pronotum width (Appendix S7).

The FUSE classification analysis and SSH ordination indicated a clear separation of four beetle coummunity groups associated with different mouse density treatments in Q and M blocks (Fig. 3). Beetles collected from all pitfall trap transects in low mouse density treatments (ML and QL) had similar species assemblages (Group I; Fig. 3). The transects in the summer immediately after the treatment switch (December 2013–April 2014) were distinct (Group II; Fig. 3), and transects in high mouse density treatments (QH and MH) formed another group (Group III; Fig. 3). Finally, one transect (February 2016) in Q block at low mouse density formed Group IV (Fig. 3), which was characterised by very high beetle abundance.

Leaf-litter invertebrate community

In total, 10 719 invertebrates were sampled from the leaf litter during the study. The mean number of preferred diet taxa leaf-litter invertebrates was lower in QH than in ML (Fig. 4a). Following the treatment switch there was strong statistical evidence that the mean number of preferred diet taxa leaf-litter invertebrates was higher in QL than in MH (Fig. 4a). A similar pattern was observed for the total number of invertebrates caught, the number of beetles, caterpillars and spiders caught, and the number of beetle species sampled from the leaf litter (Appendix S8–S12).

On average, beetles with significantly shorter body length were found in the leaf litter in QH compared with ML. In QL and MH there was no evidence of a difference in beetle lengths between the two study blocks approximately 4 months after the treatment switch (Fig. 4b).

Tracking rates of wētā in tunnels

During the first 2 years of the study (April 2011–July 2013), mean tracking rates of adult Auckland tree wētā were significantly higher in ML (range of predicted means: 36–51%) compared with QH (9–23%; Fig. 5a). In the year after the treatment switch, mean tracking rates of adult Auckland tree wētā were similar in the two blocks. After August 2014, mean tracking rates of adult Auckland tree wētā significantly increased to more than 47% in QL, while in MH the predicted the mean tracking rates was always < 30% (Fig. 5a).

Before the treatment switch, mean tracking rates of other wētā were significantly higher in ML compared with tracking rates in QH (Fig. 5b). Between August 2013 and February 2015 the mean tracking rates of other wētā in the two blocks were similar. After February 2015, mean tracking rates of other wētā were significantly higher in QL than in MH (Fig. 5b).

Land snails

At both blocks, the number of snail species caught per leaf-litter sample decreased from 2011 to 2012 (Table 3), but there is no statistical evidence that this decline differed between ML and QH ($F_{1,63.3} = 2.88$; $P = 0.095$). Furthermore, there is no statistical evidence of any differences in the mean abundance of snails collected from leaf litter samples between years or between study blocks (Table 3).

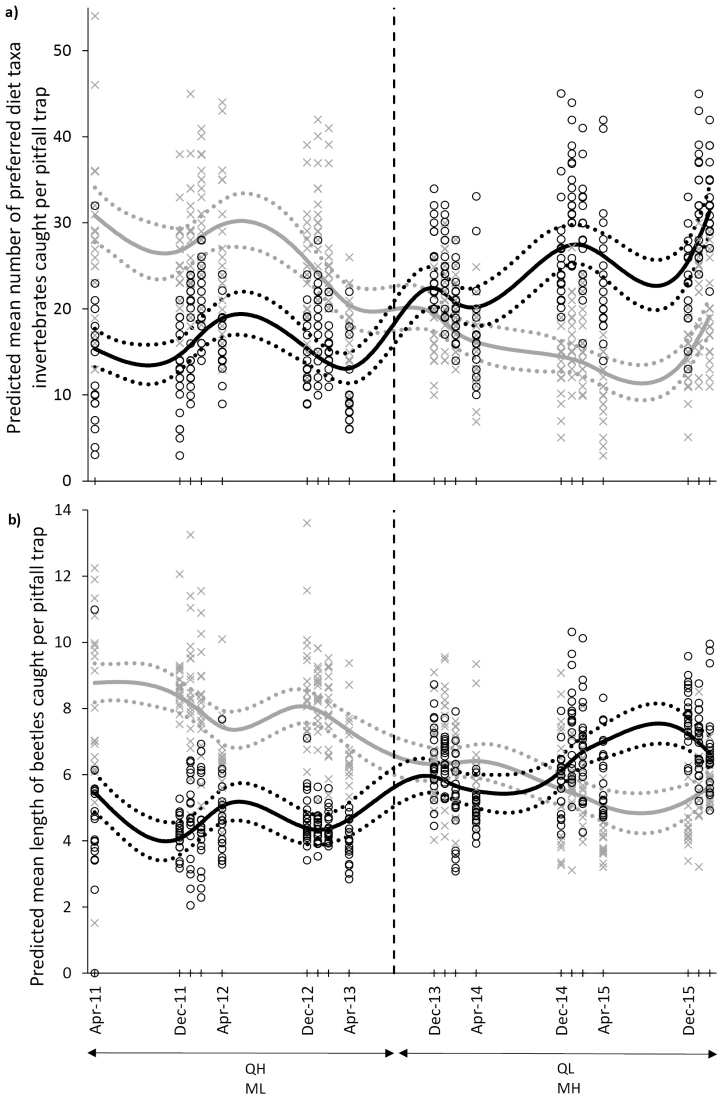

Figure 2. Predicted mean number of a) preferred diet taxa invertebrates and b) mean body length (mm) of beetles caught per pitfall trap at study blocks M (grey solid line) and Q (black solid line) at Sanctuary Mountain Maungatautari. The dashed lines represent 83% confidence intervals around the predicted values. Non-overlapping 83% confidence intervals indicate differences between the study blocks at the 5% significance level. Observed data for block M are plotted with grey crosses and for block Q with black circles. The vertical dashed line denotes the 'treatment switch', where mice were eradicated from Q block and mouse control ceased in M block. The observed data have been jittered, by adding a small amount of random noise, to prevent overplotting.

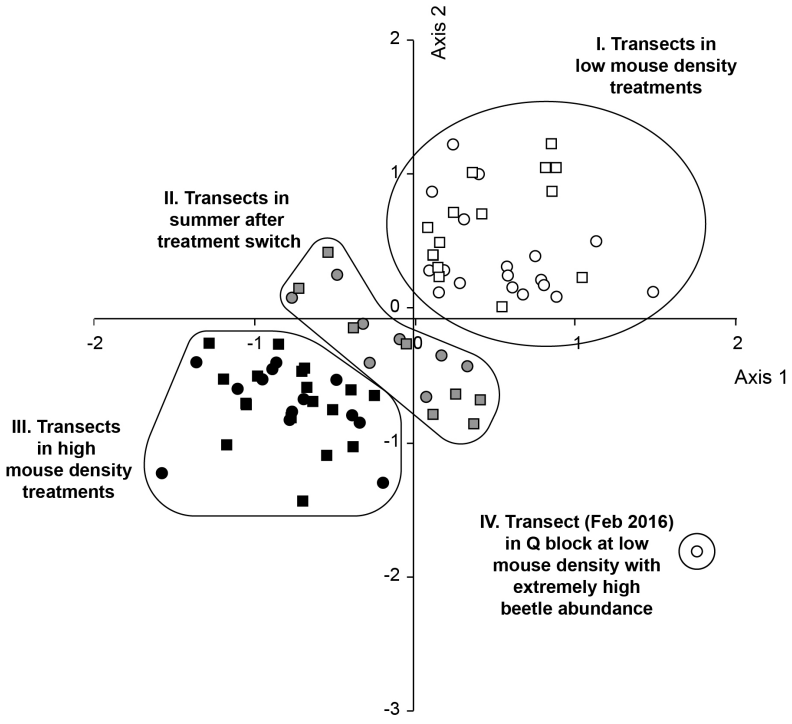

Figure 3. Distribution of beetle taxa caught in pitfall traps in Q and M blocks at Sanctuary Mountain Maungatautari, defined by two-dimensional SSH ordination analyses. See Appendix S1 for beetle species (RTUs). Four groupings with similar beetle species composition identified by the FUSE clustering analysis have been superimposed as hand-drawn polygons around plots: Group I = transects in low mouse density treatments (QL and ML); Group II = transects in the summer (December 2013–April 2014) immediately after the treatment switch; Group III = transects in high mouse density treatments (QH and MH); Group IV = one transect (Feb 2016) in Q block at low mouse density. Circles = Q block, squares = M block. Open symbols = transects in low mouse density treatments, grey symbols = transects in the summer (December 2013–April 2014) immediately following the treatment switch, black symbols = transects in high mouse density treatments.

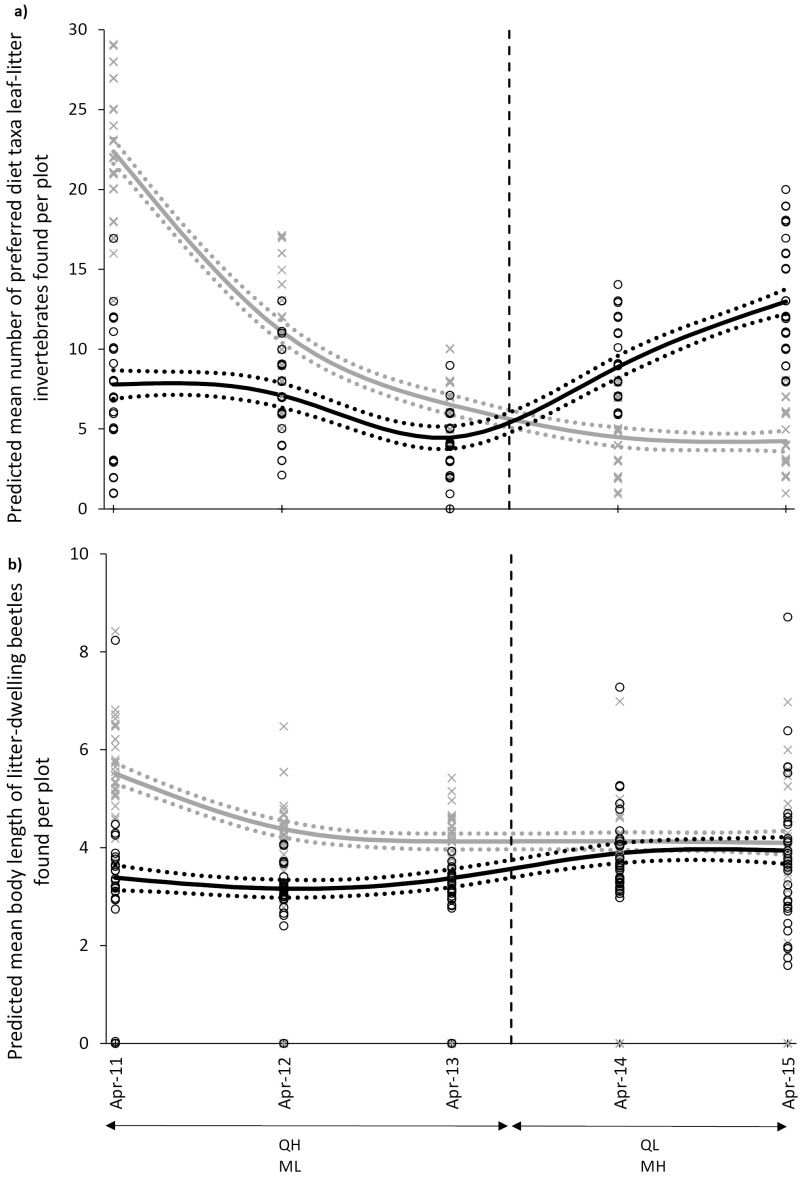

Figure 4. Predicted mean number of a) preferred diet taxa leaf-litter invertebrates and b) mean body length (mm) of litter-dwelling beetles collected per plot at study block M (grey solid line) and Q (black solid line) at Sanctuary Mountain Maungatautari. The dashed lines represent 83% confidence intervals around the predicted values. Non-overlapping 83% confidence intervals indicate differences between the study blocks at the 5% significance level. Observed data for block M are plotted with grey crosses and for block Q with black circles. The vertical dashed line denotes the 'treatment switch' where mice were eradicated from Q block and mouse control ceased in M block. The observed data have been jittered, by adding a small amount of random noise, to prevent overplotting.

Table 3. Means and 95% confidence intervals for the number of snails collected and the number of unique snail species found in litter samples at study blocks M and Q in 2011 and 2012. For each variable, means without a letter in common are statistically different at the 5% level.

Year	Block–treatment combination	Number of species		Abundance*	
		Mean	95% CI	Mean	95% CI
2011	ML	15.6 c	(12.60, 18.66)	35.3 a	(17.23, 71.47)
	QH	11.1 b	(8.07, 14.22)	24.6 a	(11.79, 50.30)
2012	ML	7.2 ab	(4.13, 10.20)	15.4 a	(7.20, 31.63)
	QH	5.5 a	(2.40, 8.52)	10.3 a	(4.66, 21.59)

* The means and 95% confidence intervals are back-transformed from the ln+1 scale.

Earthworms

There was strong statistical evidence of an interaction between study block and year on the mean log-transformed abundance ($F_{1,70.8} = 9.82$; $P = 0.003$), biomass ($F_{1,70.9} = 7.92$; $P = 0.006$) and species richness ($F_{1,71.3} = 7.53$; $P = 0.008$) of earthworms collected, indicating that earthworm populations at the two study blocks responded differently over time. The mean number of earthworms, biomass, and species richness per plot increased in Q block from 2013 to 2015 (QL) with a decreasing mouse population, but there was no evidence of a change over time at M block (Table 4).

Seedlings

There was weak statistical evidence of an interaction between study block and year on the mean log-transformed density of seedlings (number m^{-2}; $F_{2,92.5} = 2.82$; $P = 0.065$). In Q block,

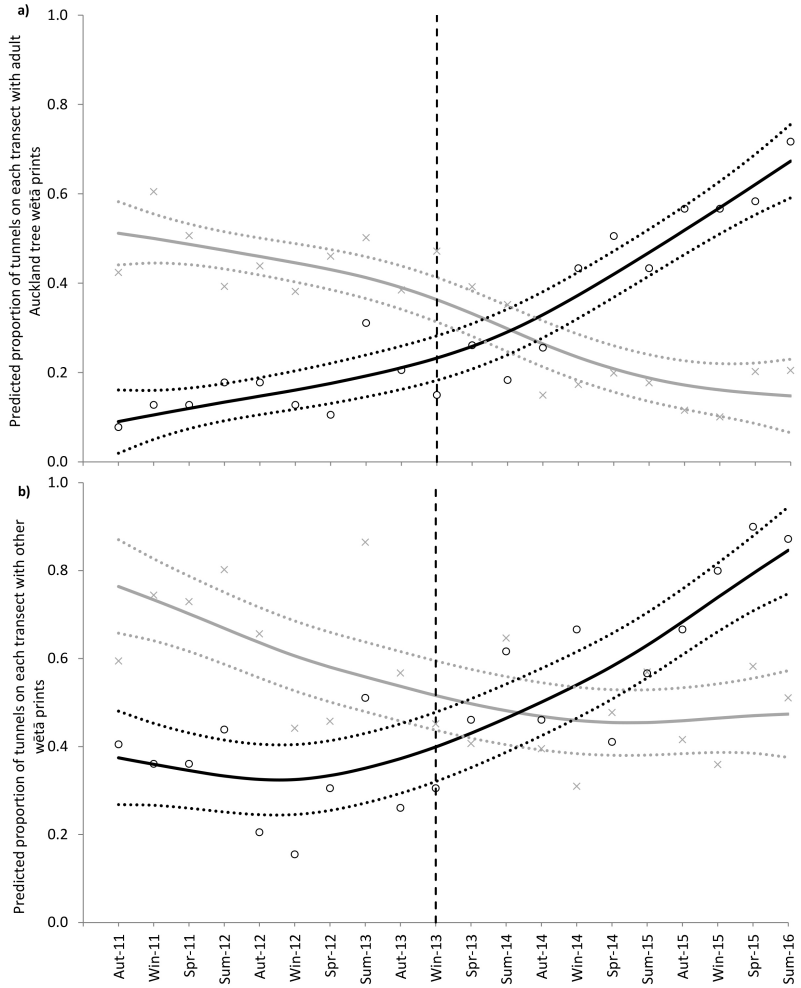

Figure 5. Predicted proportion of tunnels on each transect tracked by a) adult Auckland tree wētā and b) other wētā at study block M (grey solid line) and Q (black solid line) at Sanctuary Mountain Maungatautari. The dashed lines represent 83% confidence intervals around the predicted values. Non-overlapping 83% confidence intervals indicate differences between the study blocks at the 5% significance level. Observed data for block M are plotted with grey crosses and for block Q with black circles. The vertical dashed line denotes the 'treatment switch', where mice were eradicated from Q block and mouse control ceased in M block. The observed data have been jittered, by adding a small amount of random noise, to prevent overplotting.

Table 4. Back-transformed means and exact back-transformed 95% confidence intervals for the number, total weight (g) and number of unique recognised taxonomic units of earthworms collected per plot at study blocks M and Q in 2013 (3 months after treatment switch) and 2015. For each variable, means without a letter in common are statistically different at the 5% level.

Year	Block–treatment combination	Abundance		Biomass (g)		Species richness	
		Mean	95% CI	Mean	95% CI	Mean	95% CI
2013	MH	1.1 b	(0.51, 2.09)	0.13 b	(0.041, 0.380)	0.68 b	(0.363, 1.117)
	QL	0.3 a	(−0.02, 0.75)	0.01 a	(−0.001, 0.044)	0.19 a	(0.005, 0.445)
2015	MH	1.4 bc	(0.66, 2.50)	0.17 b	(0.054, 0.487)	0.99 bc	(0.586, 1.536)
	QL	2.9 c	(1.64, 5.01)	0.31 b	(0.103, 0.883)	1.40 c	(0.885, 2.098)

the density of seedlings was higher in 2016 (QL) than in 2011 (QH) and 2013 (Table 5). Conversely, there was no evidence of any differences in M block. For both mean litter depth and log-transformed species richness, there was no statistical evidence of an interaction between study block and year ($F_{2,116.5} = 1.26$; $P = 0.288$, $F_{2,95.8} = 0.54$; $P = 0.584$, respectively), nor was there any statistical evidence that these means differed over time at either study block (Table 5).

There was strong statistical evidence of an interaction between study block and year on the mean log-transformed density of cotyledonary seedlings per plot ($F_{2,96.0} = 4.10$; $P = 0.020$), indicating that cotyledonary seedling densities on Q and M blocks responded differently over time. In both study blocks cotyledonary seedling density decreased from 2011 to 2013 and then increased from 2013 to 2016 (Table 6). However, these changes were greater for Q block, where the mouse population increased between 2011 and 2013 and decreased between 2013 and 2016.

The mean log-transformed density of mixed-leaf seedlings per plot exhibited a similar pattern over time to cotyledonary seedlings (Table 6). However, there was no evidence that the density of mixed-leaf seedlings in Q and M blocks responded differently over time (the interaction between study block and year was not statistically significant; $F_{2,136.9} = 1.83$; $P = 0.164$).

At both Q and M blocks the mean log-transformed density of true-leaf seedlings was lower in 2016 than in 2011 and

Table 5. Means and 95% confidence intervals for the total density of all seedlings (number per m^2), mean litter depth (cm), and total seedling species richness per transect plot at study blocks M and Q in 2011, 2013 and 2016. For each variable, means without a letter in common are statistically different at the 5% level.

Year	Block–treatment combination	Total density*		Mean leaf litter		Species richness*	
		Mean	95% CI	Mean	95% CI	Mean	95% CI
2011	ML	7.6 ab	(4.98, 11.32)	3.5 ab	(2.65, 4.30)	3.1 ab	(2.38, 3.88)
	QH	13.4 b	(9.00, 19.91)	3.2 ab	(2.39, 4.03)	3.9 ab	(3.09, 4.94)
2013	ML	5.7 a	(3.72, 8.61)	3.1 ab	(2.32, 3.94)	2.8 a	(2.17, 3.56)
	QH	8.1 ab	(5.36, 12.17)	2.9 ab	(2.08, 3.71)	3.7 ab	(2.90, 4.68)
2016	MH	7.5 ab	(4.96, 11.29)	3.6 b	(2.90, 4.27)	3.0 a	(2.30, 3.76)
	QL	20.9 c	(13.87, 31.40)	2.4 a	(1.73, 3.16)	4.5 b	(3.54, 5.75)

*The means and 95% confidence intervals are back-transformed from the ln + 0.5 scale.

Table 6. Back-transformed means and exact back-transformed 95% confidence intervals for the densities of cotyledonary, mixed-leaf and true-leaf seedlings per transect plot at study blocks M and Q in 2011, 2013 and 2016. For each variable, means without a letter in common are statistically different at the 5% level.

Year	Block–treatment combination	Cotyledonary		Mixed-leaf		True-leaf	
		Mean	95% CI	Mean	95% CI	Mean	95% CI
2011	ML	1.03 b	(0.653, 1.528)	0.97 bc	(0.469, 1.739)	4.48 b	(2.873, 6.843)
	QH	3.15 c	(2.257, 4.340)	2.68 cd	(1.592, 4.323)	4.70 b	(3.031, 7.154)
2013	ML	0.50 a	(0.255, 0.827)	0.12 a	(0.000, 0.442)	5.11 b	(3.300, 7.772)
	QH	0.62 ab	(0.343, 0.998)	0.27 ab	(0.005, 0.675)	6.67 b	(4.357, 10.096)
2016	MH	2.54 c	(1.791, 3.530)	3.50 de	(2.128, 5.573)	0.93 a	(0.468, 1.606)
	QL	6.44 d	(4.602, 8.945)	8.04 e	(5.016, 12.717)	1.70 a	(0.979, 2.783)

2013. However, there was no evidence that the density of true-leaf seedlings at two study blocks responded differently over time (the interaction between study block and year was not statistically significant; $F_{2,134.3} = 1.31$; $P = 0.272$).

Fungi

No mice were filmed visiting fruiting bodies of known edible and other mushrooms in the 48 hr during which they were presented.

Fungal DNA was amplified successfully from 14 of 54 examined faecal pellets, but good-quality DNA sequence data were obtained from only three of these. When the DNA sequence data were compared with the data from GenBank (a repository of DNA sequences) via BLAST searches, the sequences were found to correspond to species from Polyporaceae (bracket fungi) or corticioid fungi (crust fungi). None of the sequences corresponded to fleshy mushrooms.

Several kinds of fungal spores were observed in 12 of 17 pellets examined microscopically, but most were in small numbers. These were typical of fleshy fungi, bracket fungi, and arbuscular mycorrhizal fungi. Several spores from plant pathogens, including rusts and hyphomycetes, were also observed.

Discussion

Impacts of mice on biodiversity

As expected, our data provide strong evidence that mice may reduce ground-dwelling invertebrate abundance, particularly preferred diet taxa such as wētā. The treatment switch between the two study blocks confirmed this inference. In addition, the number, biomass, and species richness of earthworms increased in Q block from 2013 to 2015 (QL) with a decreasing mouse population, but did not change over time at M block.

There are three important contextual perspectives when considering mouse impacts measured in this project. First, the indigenous biota we examined at Maungatautari have already survived c. 750 years of rodent predation and at least 150 years of impacts of other introduced mammals. Kiore (*Rattus exulans*) would have done the most damage to New Zealand invertebrates, being the first and smallest (mean weights 70–130 g at different locations; King & Forsyth 2021) rat to be introduced (c. 1280 AD; Wilmshurst et al. 2008). Therefore, in this comparatively brief research project we looked for rapid responses from the relatively resilient fauna that has already survived for centuries in the presence of mammalian predators (Gibbs 2010). Second, the impacts of mice on invertebrates and birds at Maungatautari are likely to be small compared with the combined impacts of the larger mammalian predators and browsers/tramplers, such as stoats, ship rats and Norway rats, brushtail possums, hedgehogs (*Erinaceus europaeus*), feral cats, feral goats (*Capra hircus*), red deer (*Cervus elaphus*),

and pigs (*Sus scrofa*; King 2005) that have been removed successfully. Abundant mice may be more damaging to lizards that routinely use small crevices as refuges, because the smaller mice can access spaces unavailable to larger rodents, mustelids and cats (Tingley et al. 2013; Norbury et al. 2014). Third, if mice can also be eradicated, and extirpated bird and lizard fauna can be at least partially restored by translocation, then there may be even greater predation pressure on invertebrates from these native predators (Sinclair et al. 2005; Watts et al. 2014). The primary objective of restoration in New Zealand sanctuaries is to restore pre-human ecological interactions and processes (Lee et al. 2005) as much as possible, and not to increase the abundances of all taxa.

In New Zealand, invertebrates, particularly litter-dwelling caterpillars, beetles, spiders, and ground wētā, are often present in the diet of mice in a wide range of habitats, implying that these are significant food items (see Murphy & Nathan 2021). Studies have estimated that the proportion of the total biomass of invertebrates (excluding earthworms, which potentially have not been effectively surveyed) harvested daily by mice ranges from 0.7% to 2.9% (Rowe-Rowe et al. 1989; Crafford 1990; van Aarde et al. 1996). A more recent estimate by Innes et al. (2010) suggests that in the presence of other mammals, mice at typical low density (i.e. < 6 ha^{-1}, Wilson et al. 2018) consume c. 9 g of invertebrates per hectare per night in North Island podocarp–broadleaved forest. The amount consumed by mice alone at high densities is likely to be higher. Therefore, it is not surprising that studies in New Zealand have implicated mice in the decline of invertebrate populations (Bull 1967; Ramsay 1978; Brignall-Theyer 1998). For example, mouse predation has been cited as the most likely cause of the extinction of two insect species, a predatory carabid beetle (*Loxomerus* sp.) and an unidentified wētā species, on Antipodes Island (Marris 2000).

There have been few studies examining the impact of mice on invertebrate communities in New Zealand, particularly in forest ecosystems. One exception is a survey on Allports Island, which found that of the invertebrate species commonly found in pitfall traps, eight were caught in significantly larger numbers on the island after mice were eradicated in 1989 (M. Fitzgerald, pers. comm.; data also mentioned in Murphy & Nathan 2021). In addition, a staphylinid beetle not caught on the island in 1986 was abundant by 1997/1998.

More studies have been carried out in coastal lowland vegetation of the sub-Antarctic islands. For example, a comparison of invertebrates on islands with and without mice in the South Indian Ocean suggested that predation by mice caused a reduction in the mean body size of medium- to large-sized invertebrate taxa, significant negative effects on populations of some invertebrate species, and disruption of the mating strategies of weevils (Crafford & Scholtz 1987; Crafford 1990; Chown & Smith 1993). In New Zealand, evidence suggests that mice on the Antipodes Islands had a markedly harmful effect on the diversity and abundance of the invertebrate fauna, with two species apparently exterminated by mouse predation and at least two others on the brink of extinction (Marris 2000). In contrast, mouse-free exclosures on Marion Island did not reveal effects of mice on any of eight invertebrate prey groups' abundance or biomass, nor on community structure (diversity and composition; van Aarde et al. 2004). Despite these studies being in differing ecosystem types, collectively they show that at some locations mice may limit invertebrates, either directly by predation, or indirectly by competition for food such as seeds, fruits, and other invertebrates.

Our ordination analyses showed that pitfall-trapped beetle community composition could be separated into three groups, associated with high and low mouse density treatments and the period immediately following the treatment switch. In another fenced New Zealand sanctuary, Zealandia, Watts et al. (2014) found that there were winners and losers in the beetle community after mammal eradication, with larger taxa benefiting from mammal eradication. More recently at Maungatautari, Watts et al. (2020b) found that beetle taxa with a roaming predatory lifestyle may be particularly vulnerable to mammal predation. In the present study, a fourth group on the ordination consisted of one outlying plot (February 2016) collected from Q block at low mouse density. This plot had very high beetle abundance (more than twice as many as any other plot), mainly *Saphobius inflatipes* (Scarabaeidae) and *Sepedophilus* spp. (Staphylinidae). The reason for this increase in numbers is unknown.

Our finding of higher tracking rates of adult Auckland tree wētā and other wētā in low mouse density treatments may indicate that wētā populations responded to reduced predation (e.g. Krebs et al. 1995; Banks et al. 1998; Banks 2000) and/or competition (Caut et al. 2007; Trewby et al. 2008; Ruscoe et al. 2011) by mice. Wētā are not only within the preferred prey size range of mice but are also mobile and may be particularly attractive to mice because their movements are readily detectable. The increase in wētā tracking rates occurred relatively rapidly (i.e. adult Auckland tree wētā within 12 months and other wētā within 14 months) after mouse eradication from the Q block. Watts et al. (2011) also observed dramatic increases in wētā pitfall captures, wētā tracking rates, and the density of wētā footprints per tracking card within 2 years after mammals were initially eradicated from a 61 ha fenced exclosure on Maungatautari. This increase may reflect changes in wētā abundance following mammal eradication, but could also be a result of behaviour changes. For example, four years after kiore were eradicated from Nukuwaiata (Chetwode Islands), Wellington tree wētā (*Hemideina crassidens*) spent more time on the ground (Rufaut & Gibbs 2003). Watts et al. (2020b) analysed another four summers of wētā response data from Maungatautari and found that when most mammals were eradicated and mice were controlled to low numbers, wētā abundance was similar within the 61 ha fenced exclosure and outside the exclosure but inside the main sanctuary fence. However, wētā numbers declined in the following 2 years outside that exclosure as mouse abundance increased (Watts et al. 2020b).

We observed no significant changes in earthworm biomass, abundance, and diversity in M block. In contrast, in Q block, which started with high numbers of mice, earthworm biomass, abundance, and diversity increased once mouse density was reduced after the treatment switch, suggesting that earthworm populations were in the early stages of recovery after years of sustained mouse predation. A further unexpected and unwelcome observation in Q block was the apparently faster recovery of invasive earthworm species (e.g. *Octolasium cyaneum* and *Eisenia japonica*) populations in both abundance and biomass, when compared to native species (e.g. *Deinodrilus agilis* and *Megascolides raglani*) populations. However, this result was not statistically tested and requires further investigation.

We did not detect a significant impact of mice on land snails, seedlings or fungi at Maungatautari, although all are likely to be minor diet items, and the faecal pellets examined for fungi were not collected at the time of key autumn fruiting.

It is possible that there were mouse effects on land snails that went undetected because the sampled communities were in a poor condition as a legacy of prior long-term mammalian predation (before the present study) or some other earlier disturbance. There was low snail species richness (6–16 species vs expected 40–70), low abundance (26–49 vs expected 100–1000 per litter sample), and low mean size (1.5–1.7 mm vs expected 2–5 mm).

Limitations of the study design

Although we believe the trends we observed to be meaningful, we wish to draw attention to one unavoidable shortcoming in our study design. As there was no replication of the treatment switch the analysis is descriptive. That is, we cannot conclude that the differences in the mouse control regimes caused differences between study block M and Q; although they were likely to be a major contributor, we have no objective way of assessing this. Therefore, this limitation restricts inference about the cause of differences between the blocks and the significance of this research to other geographical locations. Our design was improved by (1) the high number of replicates in invertebrate samples, chosen to overcome considerable spatial and temporal variation, (2) no significant differences in vegetation composition between the two blocks (Wilson et al. 2018), and (3) the treatment switch mid-way through the study. Hence, our results are robust and illustrate clear differences between the block-treatment combinations, although we are not able to show that the differences were caused by our experimental manipulations of mouse population density.

Implications of mice alone in fenced sanctuaries

In addition to their predation impacts, mice may interfere with monitoring and pest control devices targeting other species, create burrows that jeopardise pest fence integrity, and annoy visitors and volunteers (Wilson et al. 2018). Mice may attract predators into ecosanctuaries, or alternatively they may beneficially divert predators such as weasels away from valued endemic prey until they can be captured or killed. These non-exclusive hypotheses deserve study.

Our research suggests that mice limit populations, diversity, and body size of some indigenous invertebrate groups, particularly those in the preferred diet taxa and some larger native invertebrates (e.g. tree wētā), which remain on the New Zealand mainland despite the long history of predation by introduced mammals. An increasing number of studies show that introduced rodents have a negative effect on wētā populations in New Zealand (Watts et al. 2017). From a conservation perspective it is encouraging that in our study wētā tracking rates responded rapidly to the experimental reduction in mouse abundance at Maungatautari, and that these large invertebrates remain on the New Zealand mainland after more than a century of predation by pest mammals.

Our results add to the complex and growing body of knowledge that regional and district councils, ecosanctuary trusts, and the Department of Conservation use to manage sanctuaries similar to Maungatautari. Overall, there is substantial biodiversity gain from eradicating the full suite of pest mammals despite mice remaining afterwards. Mice may be catastrophic, however, in ecosanctuaries that focus on the recovery of lizards (e.g. Otago skinks, *Oligosoma otagense*, Norbury et al. 2014) or invertebrates (e.g. wētā, Watts et al. 2020b). Nevertheless, we look forward to improvements in mouse control tools to enable the future eradication of mice from large, rugged forest reserves such as Maungatautari.

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Author contributions

All authors except VC designed components of the study and conducted field research. VC undertook the data analysis, and all authors contributed to data interpretation and the writing of the manuscript.

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Supplementary material

Additional supporting information may be found in the supplementary material file for this article:

Appendix S1. Beetle species (RTUs) caught in pitfall traps in Q and M blocks within Sanctuary Mountain Maungatautari.

Appendix S2. Comparison of the pitfall-trapped invertebrates between Q and M blocks: Predicted mean total number of invertebrates caught.

Appendix S3. Comparison of the pitfall-trapped invertebrates between Q and M blocks: Predicted mean total number of beetles caught.

Appendix S4. Comparison of the pitfall-trapped invertebrates between Q and M blocks: Predicted mean total number of wētā caught.

Appendix S5. Comparison of the pitfall-trapped invertebrates between Q and M blocks: Predicted mean total number of spiders caught.

Appendix S6. Comparison of the pitfall-trapped invertebrates between Q and M blocks: Predicted mean total number of beetle species caught.

Appendix S7. Comparison of the pitfall-trapped invertebrates between Q and M blocks: Predicted mean pronotum length of wētā caught

Appendix S8. Comparison of the leaf litter dwelling invertebrates between Q and M blocks: Predicted mean total number of litter-dwelling invertebrates found.

Appendix S9. Comparison of the leaf litter dwelling invertebrates between Q and M blocks: Predicted mean number of litter-dwelling beetles found.

Appendix S10. Comparison of the leaf litter dwelling invertebrates between Q and M blocks: Predicted mean number of litter-dwelling caterpillars caught.

Appendix S11. Comparison of the leaf litter dwelling invertebrates between Q and M blocks: Predicted mean number of litter-dwelling spiders found.

Appendix S12. Comparison of the leaf litter dwelling invertebrates between Q and M blocks: Predicted mean number of litter-dwelling beetle species found.

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