Land snail communities respond to control of invasive rats in New Zealand forests

Gary M. Barker

Landcare Research, Private Bag 3127, Hamilton, New Zealand
Present address: PO Box 108, Meeniyan, Victoria 3956, Australia
(Email: barkerg@landcareresearch.co.nz)

Abstract: While invasive rats are demonstrably inimical to indigenous vertebrate species, there has not been unequivocal evidence of benefit to invertebrate communities from management of these invasive mammals in New Zealand forest systems. The present study examined the response of land snail communities to intensive management of ship and Norway rats by sampling paired rainforest blocks, one block of which had been subject to intensive management of rats, while the other block had been without management of invasive rats and thus subject to ambient rodent infestations. Rat tracking index data indicated rat management regimes were generally effective in reducing rat abundance relative to non-treated forest blocks. At the whole community level there was little evidence that forest management regime influenced the structure of land snail communities. However, when only the larger-shelled ($\geq$4 mm maximum shell dimension) component of the communities was considered, strong effects of rat management regime were evident with increased land snail abundances, species richness and functional trait values. These results are discussed in relation to potential direct and indirect of effects of management regimes that reduce rat abundance.

Keywords: conservation; invertebrates; mammal control; New Zealand; Norway rat; *Rattus*; rodents; ship rat

Introduction

Since the Middle Miocene the New Zealand terrestrial biota evolved free of the influence of nonvolant mammals (Worthy et al. 2006). A product of such an evolutionary setting is a biota naïve to the search and prey handling strategies of ground-dwelling mammalian predators (Gibbs 2009, 2010) introduced with human visitation and settlement commencing with predecessors of the Māori about 750 years ago (Wilmshurst et al. 2008). Among the 34 mammals introduced to date are a suite of predators with important ecological impacts in New Zealand indigenous ecosystems, including dogs, cats, stoats, ferrets, weasels, and four rodents that comprise the house mouse, Pacific rat, ship rat and Norway rat (Atkinson 2001; Blackwell 2005). The Pacific rat (*Rattus exulans*) probably accompanied the first travellers to New Zealand and available evidence indicates rapid pervasive colonisation from sea level to the sub-alpine zone (Atkinson 2001). Norway rat (*Rattus norvegicus*) accompanied the first European visitors to New Zealand from 1769 and also extensively colonised the main islands. Ship rat (*Rattus rattus*) introduction was much later, evidently around 1860–1870, but despite earlier dominance by Pacific rat and then Norway rat, it is this species that now predominates in forest systems in mainland New Zealand (Innes 2005). Among the introduced mammals, it is these *Rattus* species that have been considered the most damaging to the New Zealand terrestrial invertebrate biota (Ramsay 1978; Buckley et al. 2015). Nonetheless, while alien mammals are widely recognised as inimical to indigenous vertebrate species, the effects on indigenous invertebrates are still poorly understood. While there are documented cases of extinction in large bodied invertebrates that have been attributed to rodent predation (Kuschel & Worthy 1996; Gibbs 1998; Leschen & Rhode 2002; Leschen et al. 2012; Buckley et al. 2015), for the most part the indigenous invertebrate fauna has suffered

few known extinctions since human colonisation of the New Zealand archipelago (Stringer & Hitchmough 2012). However, it is possible that sustained predation by rodents over several centuries has substantially modified invertebrate community structure, with reduced range and abundance in species whose population dynamics are vulnerable to perturbation through imposition of novel levels and forms of predation and shifts in resource availability (Ramsay 1978). It is even possible that sustained effects of rodents over several centuries has led to high levels of cryptic extinction and new states of equilibria, with predominately disturbance-tolerant species persisting in communities, such that rodent removal is now unlikely to lead to observable ecological release.

Rats are intensively managed at an increasing number of sites throughout mainland New Zealand with the objective of restoration of indigenous communities and ecosystems (Saunders & Norton 2001; Campbell-Hunt 2008; Peters et al. 2015; Russell et al. 2015). While Craddock (1997), Hunt et al. (1998), Green (2002), Rufaut and Gibbs (2003), Watts (2004), Sinclair et al. (2005), King (2007), Ogden and Gilbert (2009), Rate (2009), Ruscoe et al. (2013), Watts et al. (2014) and others have provided information on the response of invertebrates to management of forests to reduce rat abundance, the evidence for rats being important drivers of community structure in contemporary New Zealand forests remains very weak. Watts et al. (2014) suggest five possible reasons for insubstantial change in invertebrate communities in ecosystems released from mammal predation, namely: (i) pest mammal species may not regulate extant indigenous invertebrate populations; (ii) residual mammal species/densities may continue to suppress invertebrate communities; (iii) increased densities in indigenous insectivorous birds, in response to pest mammal control, suppress invertebrate communities; (iv) there may have been insufficient time for changes to develop. The first scenario is perhaps the null hypothesis – that predatory mammals such

as rats have not imposed mortality that cannot be replaced by other regulatory agents (irreplaceable mortality *sensu* Thompson 1955; Morris 1965) sufficient to drive changes in indigenous invertebrate population dynamics and regulation.

In this work, I examine the response of land snail communities to intensive management of ship rats in New Zealand broadleaf rainforests. The hypothesis is that if predation by rats is presently important in the ecology of land snails, rat control should lead to ecological release that in turn should be evident in changes in the structure of land snail communities. This work was undertaken as a prelude to more detailed examination of the impact of predation by rats on the population dynamics of individual land snail species.

Materials and methods

Experimental design

At nine locations in New Zealand, land snail communities were sampled in paired rainforest blocks, one block of which had been subject to intensive management of invasive rats (treated), while the other block had been without management of invasive rats and thus subject to ambient rodent infestations (non-treated). These treated and non-treated blocks were located within 2–6.5 km of each other and of similar topography and vegetation type (see Table S1 in Supplementary Material). All treated forest blocks were under the management of the New Zealand Department of Conservation (DOC) or by local community groups under guidance from DOC, had the objective of native biodiversity restoration, and employed recognized rodent management protocols that involved aerial application of baits containing 1080 (sodium monofluroroacetate) and/or continuous ground baiting with a rodenticide (variously Diphacinone, Racumin, Pindone) and trapping on a grid pattern throughout the forest. Rat populations have been observed to decline rapidly (more than 90%) within 2–3 weeks of aerial 1080 operations (Innes et al. 1995). However, the recovery of rat populations to precontrol levels within 2–5 months of a 1080 control operation has been noted by several authors (e.g. Warburton 1989; Innes & Williams 1991) and thus management of forests to maintain low rat abundance is dependent on ongoing control using trapping and/or rodenticides available at bait stations. The nine locations were selected from a suite of candidate sites at which intensive rat management was being undertaken primarily on the grounds that: (i) management of rats had been in place for at least five years; and (ii) non-treated forest was available in the vicinity that could serve as an appropriate control. The size of the treated forest blocks varied: Trounson 800 ha; Waitakere 1100 ha; Moehau 3000 ha; Te Urewera 1000 ha; Ruakuri 160 ha; Whareorino 300 ha; Boundary Stream 800 ha; Pukawa 50 ha; Takaka 18 ha. The locations collectively provided a gradient of ecosystem productivity, with a range of latitude (35.7264 to 40.9404°S) and elevation (140 to 768 m). Queries of 100 m resolution surfaces interpolated from meteorological station climate data (30-year period 1950–80) (Leathwick & Stephens 1998) indicated varied macroclimatic conditions across the locations, with mean annual temperature ranging from 8.7°C to 14.1°C and mean annual rainfall ranging from 1350 to 2700 mm.

Land snails as a focal taxon

The New Zealand land-snail fauna is well studied and among the most species-rich in the world, with approximately 1400 species (Barker & Mayhill 1999; Barker 2005). The alpha diversity of land snails in forest sites is also very high, with communities of 30–70 species occurring within areas of only a few square metres (Barker & Mayhill 1999; Barker 2005). These patterns of diversity, along with the limited mobility and sensitivity to habitat disturbance (Lydeard et al. 2004; Douglas et al. 2013), and ease of sampling make them an ideal choice among invertebrates for this type of study. Despite recognition of predation by rats as a threatening process in populations of some larger iconic species, the role of rats in structuring land snail communities has not been previously studied in New Zealand forests.

Land snail sampling

Land snail communities were sampled quantitatively at five plots in each treated and non-treated forest block on a single occasion during April–May (autumn) 2008. The plots, each c. 20 x 20 m and separated by at least 100 m, were selected by a random walk within the core of the treated forest (to avoid margins of the treatment areas that may be most strongly affected by rat reinvasion), and a walk through the non-treated block with like elevation, topography and vegetation. Standardised sampling effort was applied per plot through a combination of two complementary approaches to sampling litter-associated land snails on the forest floor (Barker 2005): (i) collections by hand and 'spooning' of litter and humus across the extent of the plot from micro-sites favourable for live animals and the accumulation of 'dead-shell' assemblages. These micro-sites generally comprised the base of trees or rocks, the undersides and upper surfaces on small logs and other woody debris, crevices among talus boulders, and particularly deep accumulations of litter amongst ground cover vegetation and under fallen palm and tree-fern fronds. At the plot level this litter and humus material amounted to 2–4 litres. (ii) Defined area sampling by collection of litter and associated humus from ten 33 cm-diameter circular frames (0.086 m^2) placed randomly within the plot. The high intensity of sampling sought to yield high numbers of specimens per forest block to maximise ability to detect treatment effects on the land snail communities.

The litter and humus collections from both methods were placed directly into cloth bags in the field and on return to the laboratory slowly and completely dried in an oven at 50°C. Dried samples were partitioned by dry sieving, with the coarse fraction retained by a 10 mm mesh examined by eye for larger shells and the fine fraction retained by a 0.5 mm mesh examined under a stereomicroscope. All shells, including those of juveniles, were identified to species with reference to authoritatively-identified material (including vouchers for undescribed species) held in the Museum of New Zealand Te Papa Tongarewa (MNZ) and Auckland Museum. Nomenclature was standardised to that used by Spencer et al. (2009). For all specimens recovered from samples the shell height and width were measured with either an ocular micrometre affixed to a Wild M7A™ stereomicroscope or with General™ callipers. Furthermore, all individuals in the samples were classified as either 'live-collected' or 'dead-collected'; that a particular snail was alive at the time of collection was indicated by the presence of dried animal tissues within the shell.

Index of rat abundance

The relative abundance of rats in the treated and non-treated forest blocks was monitored using animal tracking tunnels

(King & Edgar 1977; Gillies & Williams 2013) following the national guidelines (see Gillies & Williams 2013 for version chronology and current guidelines). The technique employs a 'run through' tunnel containing two pieces of card either side of a pad coated or soaked with ink. As an animal passes through the tunnel it picks up the ink on its feet, then as it departs from the tunnel it leaves a set of footprints on the cards. Tracking tunnels were set on randomly orientated lines, and animal visitations recorded as the average percentage of tunnels containing rat tracks – hence forth referred to as rat tracking index (RTI). RTI provides only a coarse index of relative abundance of rats; it is not a direct measure of population density as the index can be influenced by variation in activity. The technique is best suited for providing simultaneous comparisons of the relative abundance of rats between similar habitat areas and gross changes in relative abundance over time at a single site. Sources of RTI data are given in Table S3 in Supplementary Material.

Analyses

To avoid issues of pseudoreplication, data for the five plots were pooled to provide a single, robust estimate of land snail community structure within treatment blocks within each location. Abundance was expressed as the total number of snail individuals recovered for the five plots. The functional composition of land snail communities was expressed using aggregate, abundance-weighted shell size trait values (Shipley et al. 2006):

$$T = \sum_{i=1}^{S} x_i a_i \tag{1}$$

where: x_i is the trait value for species i, a_i is its abundance and S is species richness of the community. The functional trait used was shell maximum dimension (mm) (see Table S2 in Supplementary Material) and the aggregate, abundance-weighted values for T referred to community-level functional trait values.

The completeness of land snail community sampling was evaluated in EcoSim7.44 (Gotelli & Entsminger 2004) using Chao1 (Chao 1984; Chao et al. 2005) (and its standard deviation; Chao 1987), a nonparametric richness estimator that has been shown to give reliable estimate, even from relatively small sample sizes (Colwell & Coddington 1994). For 1000 permutations of the data, Chao1 estimates the number of species missed during sampling using the number of singletons and doubletons observed and adds this number to the observed number of species to obtain an estimated total number of species. Percentage sample completeness was calculated as:

$$C = 100 \cdot \frac{S_{Obs}}{S_{Chao1}} \tag{2}$$

where: S_{Obs} is the observed sample species richness, and S_{Chao1} the Chao1 estimate. Representativeness of the samples for the block-level communities was assessed using sample- and individual-based species richness accumulation curves in EcoSim7.44. Turnover in community composition within and between treatment blocks at each location was estimated as Bray-Curtis (Bray & Curtis 1957) dissimilarity:

$$BC = \sum_{i=1}^{P} |x_{ij} - x_{ik}| / \Sigma_{i=1}^{p} x_{ij} + x_{ik} \tag{3}$$

where x_{ij} and x_{ik} are the abundances for the ith species in the jth and kth sample ($i = 1, 2, ..., p; j = 1, 2, ..., n; k = 1, 2, ..., n$).

Null model analysis Monte Carlo permutation using EcoSim 7.44 was applied to assess the significance of differences in land snail abundance and community-level functional trait values, and RTI values of rat abundance, between paired treated and non-treated blocks within locations and, where appropriate, treated and non-treatment blocks across all locations. The null model randomizes values between treated and non-treated blocks, with the permutation procedure repeated 1000 times. P-values were calculated as the proportion of simulations giving a value for the test statistic that departed from the observed. Observed paired differences were expressed relative to expected values using Standardized Effect Size (SES) (Gotelli & McCabe 2002; Leprieur et al. 2012), which is an extension of the familiar z-score for testing if an individual deviates significantly from the population mean:

$$SES = \frac{x_{Obs} - x_{Exp}}{\sigma_{Exp}} \tag{4}$$

where x_{Obs} is the mean value obtained from the observed data, x_{Exp} is the mean of the randomisations and σ_{Exp} is the standard deviation across those randomizations.

The potential importance of individual species was simply identified as those contributing $\geq 10\%$ to any differences between treated and non-treated blocks. Setting the observed values for the species in question to its average across treated and non-treated blocks within location and rerunning the Monte Carlo permutations confirmed that these differences between blocks for these species were the primary driver for rejection of null models.

Null models were also used to compare species richness between paired treated and non-treated blocks within locations. Species richness computed as Chao1 (see above) was used to calculate SES as in Equation 2, but where x_{Obs} is the value obtained from the treated block, and x_{Exp} and σ_{Exp} is the value and its standard deviation obtained from the non-treated block.

All analyses were computed for entire communities and for that subset of species whose maximum shell dimension was estimated at ≥ 4 mm (as indicated by examination of extensive specimen series in MNZ), and as such hypothesised as that component of communities most vulnerable to predation by rats due to their larger size.

The results for the rat management regime effects presented below are based entirely on the 'live-collected' component of samples as this treatment of samples is less controversial than analyses based on counts that include shells of animals that had died prior to sampling (see Sólymos et al. 2009; Schilthuizen 2011; Yanes 2011; Albano 2014 for discussions). However, it should be noted that: (i) in the moist rainforest environments of New Zealand most shells of dead land snail species degrade rapidly and in most situations are entirely decomposed within 3–6 months (GM Barker, unpubl. data). Thus counts that combine both shells from prior mortality events and 'live-collected' individuals can effectively integrate short-term temporal variability in species occurrence; (ii) in the present work, results are consistent between analyses based entirely on 'live-collected' and those on composite samples (see Tables S3 and S4 in Supplementary Material). On average 73.4% (range 62–82%) of individuals obtained in samples were 'live-collected'. The percentage of 'live-collected' individuals did not vary between treated and non-treated blocks (Table S4).

Results

Adequacy of land snail sampling

Sampling yielded 126 347 land snail specimens, representing seven families and 254 species (Table S3). All but two species were native to the sampled locations. The number of individuals in samples for each treatment block averaged 7020 (range 3389–11 009) for 'dead-collected' plus 'live collected' snails, and 5270 (2583–8404) for 'live collected' snails (Table S4). Sample- and individual-based species accumulation curves (see Figure S1 in Supplementary Material) exhibited asymptotes in species richness. Such large sample sizes provided for 99% completeness, as estimated as the ratio of observed to Chao1 species richness. The ratio of individuals to species averaged 83.6 (32.9–126.5) and thus far exceeded the minimum of 10 recommended specifically for samples from land snail communities by Cameron and Pokryszko (2005). This ratio did not vary significantly between treatment blocks (SES -0.363, P=0.484). Bray-Curtis dissimilarity between sites within treatment blocks averaged 0.162 (Table S4). The sampling was thus representative of the community within forest blocks at the nine locations, and our estimates robust to within-treatment community composition and comparisons across the two treatments.

Effects of forest management regimes

Analyses based on all sampled 'live collected' individuals (Table 1) indicated an absence of treatment effects on land snail abundance. Similarly, analyses restricted to species with specific maxima in shell dimension <4 mm indicated an absence of treatment effects on abundance (data not presented). Chao1 estimates of species richness tended to be higher in the forest blocks under management to reduce rat abundances, and indeed null models were rejected for four locations (Trounson, Wharerino, Pukawa, Takaka) indicating land snail species richness differed between treatments more than expected by chance. Across all locations, and at the Trounson location, the null models rejected the hypothesis that size of land snail individuals, as measured by mean shell maximum dimension, was independent of forest block management. For the remaining eight locations the observed trend was for a larger mean size of individuals in the forest blocks where rats were managed, but the null models could not be rejected. The community-level functional trait values tended to be higher for land snails in forest blocks where rats were managed, but null models consistently indicated chance effects could not be rejected.

A total of 78 species with specific maxima in shell dimension ≥4 mm were identified across the nine locations. When only these larger species were considered, forest block treatment effects were much more apparent (Table 2) than when including all species in the analyses. The null models were rejected and the pattern of community structure was consistent with predictions that management to reduce abundance of rats led to more abundant, and more species rich, larger-shelled land snail communities. Averaged across locations, larger-shelled species were 96% more abundant, the mean size of individuals increased by 11.5%, and community-level functional trait values increased by 117.8% in managed forest blocks relative to the non-treated blocks. Chao1 estimates indicated managed forest blocks, on average, contained an additional 2.6 species relative to the non-treated forest blocks, although this was not statistically significant.

Table 3 summarises data for those species in the larger-snail category that exhibited the greatest numerical and functional trait responses to forest block treatment. Several species of land snail of concern to conservation managers occurred at the sampled locations, including the Rhytididae *Amborhytida*

Table 1. Whole community-level abundance, richness and functional trait values for 'live collected' land snails sampled in paired forest blocks at nine locations where ship rat and Norway rat were either intensively managed (T) or not (NT), with SES estimated from null models.

Location	Abundance			Species richness[1]			Mean shell maximum dimension (mm)			Community-level functional trait values		
	T	NT	SES	T	NT	SES	T	NT	SES	T	NT	SES
Trounson	4397	4546	-0.691 P=0.142	68.0	63.2	**6.517 P<0.001**	2.00	1.63	**-1.546 P=0.042**	8813	7398	0.007 P=0.674
Waitakere	6081	6009	-0.844 P=0.162	116.0	115.7	0.095 P=0.867	2.27	1.89	-0.578 P=0.206	13800	11370	-0.083 P=0.647
Moehau	4569	4793	-0.494 P=0.273	84.2	82.0	0.221 P=0.657	2.02	1.60	-0.785 P=0.074	9242	7680	-0.135 P=0.369
Te Urewera	4477	4397	-0.772 P=0.164	66.0	65.0	1.000 P=0.357	1.90	1.57	-0.835 P=0.213	8689	7007	-0.067 P=0.630
Ruakuri	7456	7850	-0.884 P=0.151	92.5	91.5	0.970 P=0.327	2.07	1.70	-1.145 P=0.067	15422	13340	-0.565 P=0.401
Wharerino	7792	8404	-0.977 P=0.189	89.7	84.7	**3.831 P<0.001**	1.82	1.58	-1.006 P=0.085	14156	13289	-0.947 P=0.195
Pukawa	5421	6025	-0.678 P=0.282	83.0	77.5	**4.158 P<0.001**	2.00	1.75	-0.591 P=0.339	10830	10531	-0.792 P=0.069
Boundary Str.	3650	3547	-0.713 P=0.175	66.0	65.2	0.171 P=0.764	1.59	1.41	-0.157 P=0.603	5793	4984	-0.533 P=0.405
Takaka	2583	2877	-0.474 P=0.451	97.9	90.4	**8.636 P<0.001**	2.29	2.02	-0.654 P=0.132	5923	5820	-0.707 P=0.084
All locations	5158	5383	-0.631 P=0.205	84.8	81.7	-0.569 P=0.309	2.00	1.68	**5.469 P=0.003**	10296	9046	-0.243 P=0.425

1. Chao1 estimate.

dunniae (Gray, 1840), *Amborhytida forsythi* (Powell, 1952), *Paryphanta busbyi busbyi* (Gray, 1850), *Rhytida oconnori* (Powell, 1946), and *Powelliphanta hochstetteri* (L. Pfeiffer, 1862). Because of their low abundance in the samples, these species generally contributed little to sample sizes and thus to null model testing, but observed abundances and species-level functional trait values were in all cases higher in the treated than in the non-treated forest blocks (abundancies: 83.7 vs 30.7; functional trait values 374.7 vs 128.0, respectively).

Effort expended to assess residual rat abundance in treated forest blocks and ambient rat abundance in non-treated comparison blocks, varied greatly among locations, reflecting the desired outcomes and management objectives of the projects at the respective locations. No RTI data were available for the Takaka location. Available RTI data for the remaining eight locations ranged from a single assessment at Pukawa to 60 assessments over 13 years at Boundary Stream (Table 4). Despite the limitations of sample sizes, the high effectiveness of the rat management regimes in the treated forest blocks was indicated, with 78–100% reduction in RTI relative to the non-treated blocks (Table 4). Null models were rejected, indicating differences in RTI between treated and non-treated forest blocks were not due to chance effects. Nonetheless, the RTI of non-treated forest blocks could not be taken as a reliable indicator of ecosystem differences among locations in rat abundance as monitoring frequency and timing were not standardised and thus variably accommodated marked seasonal fluctuations in rat densities. Against this background, no relationship could be detected between RTI in the non-treated forest blocks and SES for treatment contrasts of land snail abundance and community-level functional trait values within locations.

Discussion

As is typical of New Zealand forest systems, the ground-dwelling land snail communities at the sampled locations were highly species rich (alpha diversity 49–71 species; block-level diversity 65–116 species), strongly dominated by minute species (<4 mm) and with a significant component of immature individuals (community mean shell size 1.38 to 2.30 mm), but including a few larger species with shells 30–35 mm (exceptionally to 80 mm) in maximum dimension. The stronger treatment effect seen in the larger-shelled (≥4 mm) component of the land snail communities provide some positive evidence in favour of release from predation by rats as a mechanism for ecological response in communities of larger-sized land snails. RTI data confirmed that the management regimes imposed in the treated forest blocks were effective in reducing rat abundance. The RTI data also indicated considerable variation in rat abundance in non-treated forests across the locations included in the study, but variable numbers of RTI assessments and inconsistencies in the seasonal spread of those assessments within locations limited ability to detect a relationship between ecosystem-level rat carrying-capacity and effects on land snail communities. Thus, the exact mechanism(s) by which land snail communities might have been impacted by the contrasting management regimes at these locations is as yet unclear as both direct and indirect effects are possible.

The treated forest blocks used in the present study varied greatly in size – 18 to 3000 ha – and thus may have differed in the level and importance of rat reinvasion from neighbouring non-treated forests and other habitat. These forest block area effects were likely most significant at Takaka. Being surrounded by a huge non-treated area of beech forest, the 10 ha treated block at Takaka was likely overwhelmed by rats during irruptive periods associated with beech masts (King & Moller

Table 2. Abundance, richness and functional trait values for 'live collected' larger land snails (adult shell size ≥4.0 mm) sampled in paired forest blocks at nine locations where ship rat and Norway rat were either intensively managed (T) or not (NT), with SES estimated from null models.

Location	Abundance			Species richness			Mean shell maximum dimension (mm)			Community-level functional trait values		
	T	NT	SES	T	NT	SES	T	NT	SES	T	NT	SES
Trounson	691	347	**3.833** **P=0.011**	22.0	20.0	**11.428** **P<0.001**	5.37	4.54	**6.567** **P<0.001**	3709	1576	**4.424** **P=0.005**
Waitakere	1326	715	**3.909** **P=0.012**	32.0	30.3	**2.651** **P=0.006**	4.75	4.38	**4.127** **P=0.008**	6298	3132	**6.479** **P<0.001**
Moehau	755	249	**4.178** **P=0.005**	27.5	28.0	**0.113** **P=0.904**	4.85	3.92	**4.431** **P=0.005**	3659	975	**10.108** **P<0.001**
Te Urewera	790	388	**3.580** **P=0.015**	18.0	17.0	**2.439** **P=0.026**	4.58	4.04	**4.072** **P=0.011**	3618	1568	**6.629** **P=0.002**
Ruakuri	1393	657	**4.348** **P=0.008**	32.0	31.3	**1.175** **P=0.325**	4.82	4.50	**4.155** **P=0.009**	6718	2957	**6.107** **P<0.001**
Wharerino	1023	577	**2.804** **P=0.029**	37.0	33.0	**11.268** **P<0.001**	4.79	4.44	**4.342** **P=0.008**	4900	2564	**4.157** **P=0.009**
Pukawa	886	392	**7.286** **P<0.001**	28.0	25.0	**7.792** **P<0.001**	5.12	4.83	**3.510** **P=0.013**	4538	1892	**8.155** **P<0.001**
Boundary Str.	334	134	**3.517** **P=0.012**	22.0	16.0	**14.634** **P<0.001**	4.86	4.46	**4.421** **P=0.006**	1624	597	**4.667** **P=0.006**
Takaka	665	545	**-0.345** **P= 0.475**	33.0	27.0	**25.000** **P<0.001**	4.47	4.04	**4.696** **P=0.004**	2974	2200	**0.322** **P=0.243**
All locations	874	445	**5.311** **P=0.005**	27.9	25.3	**-0.184** **P=0.368**	4.85	4.35	**6.401** **P=0.002**	4226	1940	**7.455** **P=0.002**

Table 3. Abundance and functional trait values among those larger-shelled land snail species (adult shell size ≥4.0 mm) most responsive to intensive management of invasive rats as indicated by sampling in paired forest blocks at nine locations where rats were either intensively managed (T) or not (NT).

Location	Species contributing most to treatment differences in community-level abundance Species	T	NT	Species contributing most to treatment differences in community-level functional trait values Species	T	NT
Trounson	*Phrixgnathus sciadium*	56	11	*Phenacohelix ziczac*	227.9	44.3
	Flammulina perdita	66	22	*Phrixgnathus sciadium*	280.8	45.3
	Liarea turriculata	73	27	*Flammulina perdita*	391.6	107.2
	Liarea egea	63	32	*Liarea egea*	339.0	155.4
	Allodiscus dimorphus	84	37	*Liarea turriculata*	595.6	198.1
				Allodiscus dimorphus	591.8	234.3
Waitakere	*Phenacohelix giveni*	140	48	*Rhytida greenwoodi*	469.5	152.5
				Phenacohelix giveni	626.2	191.0
				Allodiscus dimorphus	557.2	354.6
Moehau	*Phenacohelix giveni*	127	0	*Phenacohelix giveni*	581.8	0.0
	Phrixgnathus poecilosticta	147	78	*Thalassohelix zelandiae*	278.8	29.4
				Rhytida greenwoodi	307.0	54.2
Te Urewera	*Flammulina perdita*	55	6	*Rhytida greenwoodi*	216.7	16.1
	Laoma mariae	44	13	*Flammulina perdita*	333.0	31.1
	Phenacohelix giveni	88	51	*Laoma mariae*	279.4	58.2
	Charopa coma	113	54	*Thalassohelix zelandiae*	242.1	80.7
				Phenacohelix perplexa	340.9	170.4
				Charopa coma	471.5	205.3
Ruakuri	*Flammulina crebriflammis*	126	30	*Flammulina crebriflammi*	596.7	129.6
	Suteria ide	184	62	*Allodiscus dimorphus*	430.5	177.3
	Cavellioropa moussoni	153	67	*Cavellioropa moussoni*	563.0	233.4
				Suteria ide	1180.1	313.2
Wharerino	*Flammulina perdita*	76	23	*Rhytida greenwoodi*	252.8	72.2
	Cavellia colensoi	93	33	*Flammulina perdita*	464.8	102.5
				Cavellia colensoi	427.0	131.4
				Allodiscus dimorphus	493.9	329.2
Pukawa	*Flammulina perdita*	63	16	*Flammulina perdita*	393.6	82.2
	Phenacohelix rusticus	105	27	*Phenacohelix rusticus*	408.2	89.6
	Flammulina zebra	76	29	*Laoma mariae*	308.9	111.9
	Suteria ide	94	30	*Flammulina zebra*	388.9	135.0
				Suteria ide	620.7	139.8
				Rhytida greenwoodi	397.2	198.6
Boundary Str.	*Charopa coma*	25	4	*Therasia traversi*	208.5	16.7
	Therasia traversi	25	7	*Charopa coma*	129.7	25.3
	Phenacohelix giveni	71	22	*Phenacohelix giveni*	337.6	82.1
Takaka	*Phacussa prousei*	30	0	*Phacussa prousei*	109.6	0.0
	Phenacohelix pilula	22	5	*Rhytida oconnori*	110.4	0.0
	Charopa coma	29	9	*Flammulina perdita*	159.8	16.0
	Cavellioropa moussoni	90	116	*Charopa coma*	145.6	33.9
				Thalassohelix igniflua	124.2	41.4
				Rhytida patula	280.9	206.0
				Charopidae sp. 161 (M.126641)	164.2	295.5
				Cavellioropa moussoni	283.6	414.1

1997; Studholme 2000) and diminished our ability to detect rat management regime effects on the land snail community. On the other hand, being at high elevation Takaka had few rats present except following beech masts.

Potential direct effects of rodents

There have been numerous studies of rodent diet, including that of ship rat (e.g. Norman 1970; Daniel 1973; Clark 1982; Gales 1982; Sugihara 1997; Cole et al. 2000; Innes 2005; Sweetapple & Nugent 2007; Pisanu et al. 2011). However, despite land snails being known to be predated by ship rat (e.g. Allen 2004; Towns et al. 2006; Chiba 2007; Meyer &

Shiels 2009), and indeed predation by ship rats and other *Rattus* species recognized as a key threatening process (e.g. Meads et al. 1984; Sherley et al. 1998; Bennett et al. 2002; Brescia et al. 2008), the presence of land snails in *Rattus* stomach and faecal samples has been infrequently reported and as a consequence land snails are often considered as an insignificant dietary component. The limitation of stomach and faecal analyses is well recognized (e.g. Caut et al. 2008; Liat 2009) and in the case of land snail prey their inclusion in the diet of *Rattus* may be overlooked because shells may be fragmented and discarded during the predation event and thus not ingested, of rapid digestion of digested soft tissues,

Table 4. RTI for ship rat and Norway rat abundance monitored in paired forest blocks at nine locations where rats were either intensively managed (T) or not (NT), with SES estimated from null models, and level of rat control achieved.

Location	Number of RTI assessments	Mean RTI (range)		SES[1]	Level of rat control % reduction in RTI
		T	NT		
Trounson	11	3.2 (0-16)	19.9 (7-32)	**23.904, P<0.001**	84
Waitakere	15	7.0 (0-37)	41.7 (12-70)	**61.394, P<0.001**	83
Moehau	9	11.6 (0-29)	75.4 (62-90)	**63.730, P<0.001**	84
Te Urewera	39	15.3 (0-54)	69.5 (42-100)	**80.465, P<0.001**	78
Ruakuri	2[2]	0	35 (30-40)		~100
Wharerino	12	3.9 (0-22)	61.8 (30-90)	**94.086, P<0.001**	94
Pukawa	1[3]	0	27		~100
Boundary Str.	52	3.1 (0-42)	31.2 (3-60)	**43.539, P<0.001**	90
Takaka	0[4]			No data	

1. Analyses based only on those assessments in which rat tracking rate estimates were made within the same calendar month for treated and non-treated blocks within the location.
2. Only two RTI assessments, and these not undertaken concurrently in treated and non-treated blocks.
3. Single RTI assessment. Absence of rat tracks in tunnels in treated block indicating very low rat abundance was supported by several other assessment methods (King & Scurr 2013).
4. No RTI assessments. Monitoring in treated block confined to rats taken in kill traps. No monitoring of rats in non-treated block.

and the presence of few post-gastric diagnostic residues. Land snail radular teeth and jaws provide useful post-gastric diagnostic items in diet analyses (e.g. South 1980), but are generally overlooked because of their small size or they are simply not recognized.

That rats may be differentially affecting land snails of different body sizes has important consequences for conservation management, and so it is important to understand the underlying mechanisms. Rats predate on items across a broad prey size range, but, in general, information is lacking on the level of intake of prey below c. 10 mm, especially for soft-bodied prey. The threshold 4 mm maximum shell dimension used to partition the communities based on potential vulnerability was somewhat arbitrary in the absence of definitive information of accepted and preferred size of prey items. Nonetheless, it should be recognized that snails as prey would assume a larger size when active than indicated by the shell maximum dimension, as the animals extend their head/ foot from the shell aperture for locomotor activity. For example, a species with a shell diameter of 4 mm may assume a length of c. 8 mm when actively moving about during foraging and other activities.

The higher potential vulnerability of the larger snails assumed in this study was based on the expectation that these snails are more apparent to searching predators, in part because snail nocturnal activity occurs on the surface of the litter mass. In contrast, micro-snails are primarily active within the litter mass. Whether rats reject micro-snails as diet items because of the small return on search and handling effort is not known. The absence of an effect of rat management regime on micro-snails may be related to their inherently higher rate of increase, compared to larger-bodied snails, because of higher densities and shorter generation times. Nonetheless, *per capita* rate of increase in many micro-snails may be low as fecundity is constrained by the low shell volume necessitating production of eggs either singly or in small clutches (Heller 2001). While at least some larger New Zealand land snails are considered *K*-selected species (Barker 2005) in being long-lived and producing a few large, well-resourced eggs, there is currently little information on the life-history strategies for the great majority of New Zealand land snails.

Potential indirect effects

That responses evidently occurred in relatively small-sized snails raises the possibility that effects were indirect, either mediated through the activity of ship rat or through some secondary effect of the rat management regimes.

Introduced animals can exert indirect effects through trophic cascades and habitat modifications (O'Dowd et al. 2003; Sanders et al. 2003; Croll et al. 2005; Green et al. 2011), including effects on the microorganisms that drive decomposition processes (e.g. Fukami et al. 2006; Eisenhauer et al. 2011; Peay et al. 2012). As a consequence, attribution of responses is particularly problematic when the pest under management, such as ship rat, is an omnivore since its removal may lead to numerous changes in ecosystem properties additional to release from predation. The great majority of the land snail species studied here were detritivores, feeding on decaying plant material and the associated decomposer microorganisms. The few predatory land snail species present fed on either these detritivore snails or other invertebrates of the decomposer web, such as earthworms. It is thus possible that the responses documented in this study were due in part to changes in the resource base when ship rats were reduced in abundance.

Interpretation is further complicated if multiple pest species are controlled (Veltman 2000) and if regard is not given to the whole-community context of the species removal (Zavaleta et al. 2001), including such possible outcomes as meso-predator release (e.g. Rayner et al. 2007; Harper & Cabrera 2010; Ruscoe et al. 2011). At the majority of locations included in the present study, several pest mammals – including mustelids, deer, pigs, and possums – were under management in addition to ship rats. Reduced abundance of these mammal species may have affected the land snail communities. For example, Wardle et al. (2001) demonstrated that fences to exclude browser mammals such as deer led to marked changes in communities of most groups of litter-dwelling meso- and macro-faunas, including land snails, mediated primarily by changes in the disturbances of the litter layer and ground-cover vegetation. The forest blocks sampled in the present study exhibited no obvious differences in vegetation composition or litter composition and depth – unlike the long-fenced exclosures

sampled by Wardle et al. (2001) – and any differential effects of deer and possums might be excluded from consideration. Nonetheless, in-depth assessments of neither deer and possum numbers nor vegetation condition were made and therefore such mechanisms of effect cannot be entirely excluded. Differences in abundances and herbivory of deer and possum may have meant some sites were more responsive to rat management rimes than others. It is also unclear as to the level of effect the rat management regimes had on abundance of mammals such as house mouse and hedgehog, both of which predate on invertebrates, including land snails (Allen 2004), and are pervasive in New Zealand forests.

Conclusion

Previous studies have not yielded unequivocal evidence of benefit to invertebrates from management of rodents in New Zealand forest systems, although no previous studies have specifically examined the benefits to land snail communities. The evidence for response in the land snail communities to management of ship rat and Norway rat to low levels argues for a reassessment of both the ecological importance of these invasive mammals in New Zealand forest systems and how we might best resolve their impact on invertebrates.

The present study indicated that measuring invertebrate community responses to the removal or reduction of a pest mammal can give some indication of the strength of interactions between the species involved. However, the complexities of multi-trophic community dynamics may mask important effects on component groups of species and the mechanisms driving such responses may be invisible, unless the pest control is conducted as an experimental setting and accompanied by detailed ecological research. When assessing effects of disturbance such as predation by rats, or conversely ecological release when that disturbance is removed, consideration must be given to the dependency of population dynamics in indigenous species on the level of irreplaceable mortality (Thompson 1955; Morris 1965; Buonaccorsi & Elkinton 1990; Schneider 2011) imposed by the predatory activities of rats. That is, it is critical to establish if rats impose mortality that cannot be compensated for by variation in the intensity of contemporaneous or subsequent mortality factors operating in the populations. As a research approach, rather than determining community-level responses, it may be more informative to determine the dynamics of populations of individual indigenous species through analyses of life tables and regulatory or density dependent actions of individual mortality factors, under forest management regimes that provide contrasting abundances of rats. A stratified subset of indigenous species might be selected to span the range of potential vulnerabilities to rodent predation and to rodent perturbations of other ecosystem processes.

In respect to land snails, most current conservation efforts in New Zealand focus on large sized species. This approach has been justified on the demonstrated high risk to exotic predatory mammals in the larger species and the perceived much lower risk in micro-snails. The present work is the first real data available on the topic of risk in the micro-snail component of the communities. While the precise mechanisms await clarification, this study indicates a much lower risk in the micro-snails and thus supports current practice.

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Supplementary Material

Additional supporting information may be found in the online version of this article:

Table S1. Forest sites sampled in New Zealand, with information on location, treatment, NZMG coordinates, elevation, and vegetation.

Table S2. Land snail species recorded in samples from forest blocks at nine locations in New Zealand, with family, biostatus, and shell size.

Table S3. Sources of data on rat tracking index (RTI) for ship rat and Norway rat abundance monitored in paired forest blocks at nine locations where rats were either intensively managed (T) and not (NT).

Table S4. Community-level metrics for land snails sampled in paired forest blocks at nine locations in which rats were either intensively managed (T) and not (NT).

Table S5. Whole community-level diversity and functional traits for all (empty and 'live collected') land snails sampled in paired forest blocks at nine locations in which rats were either intensively managed (T) and not (NT), with Standardized Effect Size estimated from null models.

Figure S1. Individual-based rarefaction curves showing the cumulative number of 'live-collected' land-snail species at nine locations in which rats were either intensively managed (T) and not (NT).

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