



## Predation of seabirds by invasive rats: multiple indirect consequences for invertebrate communities

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Invasive species are a global problem but most studies have focused on their direct rather than indirect ecological effects. We studied litter and soil-inhabiting invertebrate communities on 18 islands off northern New Zealand, to better understand the indirect ecological consequences of rat (*Rattus*) invasion. Nine islands host high densities of burrowing procerrariid seabirds that transport large amounts of nutrients from the ocean to the land. The other nine have been invaded over the past 50–150 years by rat species that have severely reduced the density of seabirds by preying on eggs and chicks. Invaded islands had lower densities of seabird burrows but deeper forest litter than did the uninvaded islands, indicative of rats reducing disturbance effects of seabirds. However, despite deeper litter on the invaded islands, eight of the 19 orders of invertebrates that we measured were significantly less abundant on invaded islands. Furthermore, three soil-inhabiting micro-invertebrate groups that we measured were significantly less abundant on invaded islands. These differences probably result from rats thwarting transfer of resources by seabirds from the ocean to the land. We also investigated community-level properties of each of three test groups of invertebrates (minute land snails, spiders and soil nematodes) to illustrate this process. Spiders were equally abundant on both groups of islands, but showed lower species richness on the invaded islands. The other two groups showed no difference in species richness with island invasion status, but were more abundant on uninvaded islands. Reduced abundance of soil nematodes on invaded islands provides strong evidence of indirect consequences of seabird reduction by rats, because nematodes are unavailable to rats as prey. We predict that if rats are eradicated from islands, components of below-ground invertebrate dependent on seabird-mediated soil conditions may take considerable time to recover because they require subsequent seabird recolonisation.

Biological invasions are widely regarded as a significant component of global environmental change (Vitousek et al. 1997, Mack et al. 2000). Their effects range from the spread of infectious diseases, to economic effects on crops, ecosystem effects such as those on decomposition and nutrient cycles, and effects on native biodiversity (Simberloff 1990, Vitousek et al. 1997, Mack et al. 2000). In a review of global literature, Gurevitch and Padilla (2004) concluded that the greatest threat posed by invasive species to biodiversity came from alien predators, but that these threats were often overstated. However, Simberloff (2006) warned that a focus on biodiversity underplays the profound effects of invasive species on communities and ecosystems at the process level, especially when these effects are interactive between invaders. The effects of invasive plant species on community- and ecosystem-level properties are relatively well studied (Vitousek and Walker 1989, Simberloff 1990, Ehrenfeld 2003), but fewer studies have

considered the indirect effects of invasive predators on these properties (O'Dowd et al. 2003, Croll et al. 2005, Fukami et al. 2006, Kurlle et al. 2008).

Rats are quintessential invaders that have reached up to 90% of the world's island groups (Atkinson 1985, Martin et al. 2000). They feed on a wide range of plant and animal species, and inhabit environments ranging from sub-polar to tropical (Dickman 1999, Towns et al. 2006). Predation of seabirds by rats has long been implicated in declines and local extinctions of seabird populations (Atkinson 1985, Jones et al. 2008). In theory, loss of seabirds could have a multitude of effects on island ecosystems because seabirds can affect islands in two ways. First, when islands are dominated by seabirds that burrow, physical characteristics and the soil environment are modified for plants, invertebrates and reptiles (Mulder and Keall 2001, Bancroft et al. 2005). Second, through waste and cadavers, seabirds add nitrogen, phosphorus and other minerals of marine origin

(Bancroft et al. 2005) that are then incorporated into terrestrial food webs (Polis and Hurd 1996, Sanchez-Piñero and Polis 2000, Mulder and Keall 2001, Markwell and Daugherty 2002, 2003, Bancroft et al. 2005, Fukami et al. 2006). If these effects of seabirds were disrupted by rat invasions, hitherto unknown subtle and pervasive effects of the invasion could eventuate (Towns et al. 2006).

We studied the indirect effects of invasive species of *Rattus* on the litter and below-ground invertebrate communities on island systems in northeastern New Zealand. These islands are ideal model systems because different islands in the same archipelago have different histories of invasions, each island is a spatially discrete entity (enabling replication of independent ecosystems), and the islands support an extraordinary density of burrowing seabirds (Daugherty et al. 1990, Towns et al. 1997, Mulder and Keall 2001, Fukami et al. 2006). By comparing islands that are rat-free and support high densities of burrowing seabirds with those that have been invaded by predatory rats and support few seabirds, we tested the hypothesis that the abundances and diversity of litter-dwelling macro-invertebrates and soil-dwelling micro-invertebrates should be greatly reduced on invaded islands. First, predation by rats will selectively remove large-bodied invertebrates on invaded islands (Towns et al. 2006). Second, the transfer by seabirds of nutrients from the ocean to land should promote the density and diversity of litter and soil invertebrates on uninvaded islands (Polis and Hurd 1995, Sanchez-Piñero and Polis 2000, Markwell and Daugherty 2002). However, this effect may be counteracted by disturbance effects of seabirds, particularly when they are at high densities (Mulder and Keall 2001).

In this work we studied the effect of rat invasion on total abundances at the order level for most major invertebrate groups. Further, to determine the effects of invasion on invertebrate community composition and diversity at a finer level of taxonomic resolution, we focused on three test

groups which each have a high diversity in our study system: 1) minute land snails, which are almost all grazers of algae, fungi and other encrusting organisms and should therefore respond indirectly to variations in primary production and soil fertility; 2) spiders, which are all predators and should respond to variations in invertebrate prey density; and 3) soil nematodes, which include herbivores and microbe feeders, and should respond to changes in soil conditions.

## Material and methods

### Study sites

We utilized 18 islands in northern New Zealand that have previously been used to study the indirect effects of rat invasion on ecosystem-level properties (Fukami et al. 2006, Wardle et al. 2007) (Supplementary material Table 1). Nine islands (Aiguilles, Goat, Hauturu, Motueka Motu-horopapa, Otata; western Coromandel islands Motukar-amarama, Motuoruhi and Motutapere) have been invaded by rat species (ship rats *Rattus rattus* and Norway rats *Rattus norvegicus*) spread after European contact in the past 50–150 years and support few seabirds. The other nine islands (Poor Knights Islands – Aorangi, Aorangaia, Arch-way and Tawhiti Rahi; Green, Middle, Ohinauiti; Alder-men Islands – Ruamahuanui and Ruamahuaitei) have never been invaded by rats and support very high densities of seabirds (Fukami et al. 2006). The size of the islands ranged from 3 to 300 ha. We only used islands that were uninhabited, contained coastal forest and lacked farm stock. We also constrained the geographic range of the islands to between 35°25'S and 37°12'S in order to overcome variations in the species pool of native forest and seabirds (Mulder et al. 2008). Previous work on these islands showed that the invaded and uninvaded islands do not differ significantly with regard to longitude, latitude, area,

Table 1. Comparisons of relative abundance of orders of macro-invertebrates (mean ± SE) on invaded and uninvaded islands presented as numbers per unit area sampled, and as standardised dry wt of litter, with significant differences in bold. F- and p-values (in parentheses) have been derived from one-way ANOVA. Degrees of freedom for F-values are 1 for treatment and 16 for residual. For data for no. per m<sup>2</sup>, data were transformed by ln(x+1) before analysis by ANOVA; for data for no. per 100 g litter, data were transformed by ln(x+0.01) before analysis by ANOVA.

Taxon	No. m <sup>-2</sup>			No. per 100 g litter		
	Invaded	Uninvaded	F- and p-value	Invaded	Uninvaded	F- and p-value
Oligochaeta	1.9 ± 1.7	0.4 ± 0.4	0.64 (0.442)	0.30 ± 0.23	0.01 ± 0.01	1.26 (0.278)
Gastropoda	224.1 ± 165.5	1748.4 ± 888.5	4.86 ( <b>0.042</b> )	22.3 ± 14.9	116.7 ± 70.2	3.03 (0.100)
Araneae	23.8 ± 8.3	49.7 ± 14.1	2.59 (0.129)	3.20 ± 0.96	2.60 ± 0.45	0.01 (0.950)
Isopoda	25.9 ± 15.7	108.7 ± 43.6	2.49 (0.134)	3.42 ± 2.22	6.52 ± 3.51	1.03 (0.324)
Amphipoda	29.3 ± 14.3	256.7 ± 96.6	5.42 ( <b>0.033</b> )	3.50 ± 1.73	10.65 ± 3.23	2.71 (0.110)
Collembola	270.4 ± 154.5	4338.5 ± 3593.8	4.87 ( <b>0.042</b> )	33.0 ± 18.2	163.8 ± 120.1	2.98 (0.103)
Blattodea	0.30 ± 0.28	0.67 ± 0.45	0.41 (0.533)	0.03 ± 0.03	0.03 ± 0.03	0.03 (0.863)
Thysanura	0.68 ± 0.50	2.30 ± 2.10	0.12 (0.730)	0.07 ± 0.05	0.26 ± 0.23	0.44 (0.516)
Homoptera	1.80 ± 1.0	2.90 ± 0.85	1.40 (0.731)	0.20 ± 0.09	0.20 ± 0.07	0.00 (0.987)
Hemiptera	4.10 ± 1.70	7.60 ± 2.58	0.38 (0.545)	0.52 ± 0.18	0.72 ± 0.33	0.48 (0.779)
Thysanoptera	13.8 ± 6.0	4.3 ± 2.0	0.61 (0.226)	1.79 ± 0.81	0.28 ± 0.11	3.89 (0.066)
Psocoptera	19.5 ± 4.5	546.1 ± 427.8	12.45 ( <b>0.003</b> )	2.50 ± 0.55	52.55 ± 40.44	4.80 ( <b>0.043</b> )
Coleoptera	67.2 ± 30.6	527.8 ± 162.5	16.55 ( <b>&lt;0.001</b> )	8.15 ± 1.82	26.35 ± 5.05	14.73 ( <b>0.002</b> )
Diptera	29.5 ± 12.4	92.9 ± 57.9	2.77 (0.110)	5.54 ± 0.52	9.41 ± 3.05	1.11 (0.307)
Lepidoptera	37.9 ± 13.9	264.8 ± 66.6	20.74 ( <b>&lt;0.001</b> )	4.89 ± 1.71	19.05 ± 6.04	12.51 ( <b>0.003</b> )
Hymenoptera	7.7 ± 2.8	52.2 ± 15.5	20.46 ( <b>&lt;0.001</b> )	0.96 ± 0.10	4.20 ± 1.53	7.73 ( <b>0.013</b> )
Diplopoda	44.4 ± 12.4	222.2 ± 95.2	0.93 (0.348)	3.40 ± 1.25	7.59 ± 5.63	0.12 (0.729)
Chilopoda	1.5 ± 0.7	27.5 ± 11.8	7.02 ( <b>0.012</b> )	0.28 ± 0.13	1.18 ± 0.40	4.38 ( <b>0.050</b> )

elevation, distance to mainland, distance to nearest larger island, or distance from plots to shore within islands (Fukami et al. 2006).

Most of the 18 islands are of volcanic origin, ranging from late Miocene and Pliocene rhyolites (Poor Knights Islands, Ohinaiti, Motueka and Aldermen Islands), through Miocene andesites (western Coromandel islands) to Quaternary volcanics (Middle and Green Islands). The only islands known to be of sedimentary origin are Aiguilles, Motuhoropapa and Otata, which are of Permian–Jurassic greywacke and Goat, which is predominantly Miocene sandstone and siltstone (Hayward 1986). We assumed that seabird effects on the soils would over-ride variations in soil properties that result from varying geological origins. Previous studies of seabird effects on a range of soil types in New Zealand support this assumption (Wright 1961, Atkinson 1964, Hawke et al. 1999, Mulder and Keall 2001, Markwell and Daugherty 2003).

### Sampling methods

Potential seasonal effects were mitigated by sampling all 18 islands for litter and soil invertebrates in a roughly north to south sequence over 67 days between February and April (summer–early autumn) 2004. We also switched between uninvaded and invaded islands within sample periods (Supplementary material Table 1). Sampling was from two 10 × 10 m plots on each island. Plots were located in the forested portions of each island on slopes of <30° to ensure potential litter accumulation. Within each plot, seabird burrow densities were counted by systematically working along predetermined belt transects that covered the entire area. Litter depths were obtained from at least 15 random measurements within each plot.

From each plot, a single 2 l sample of surface litter was collected to soil level and stored in a cloth bag. The dimensions of the area from which this 2 l sample was collected were then measured. Invertebrates from this litter were extracted into ethanol within three days of sampling using Tullgren funnels running for seven days. These invertebrates were then sorted, counted, classified to order and identified to presumed species as operational taxonomic units (OTUs) under stereo-microscope. Spiders were classified to species. The dried litter was then checked for land snails, which were removed, counted and identified to species. This litter was then oven-dried (60°C to weight constancy) and weighed. Litter invertebrate abundance and diversity was expressed both per unit litter weight and per unit land area.

A sample of mineral soil was taken from a 0.5 × 0.5 m subplot within each plot to 10 cm depth. Soil microfauna were extracted from a 100 g wet weight subsample of this soil, using the variant of the tray method described by Yeates (1978). Gravimetric moisture content was determined so that data could be expressed on a dry weight basis. Microfauna were counted live at 40× magnification before fixing the suspension by the addition of an equal volume of boiling 8% formaldehyde. Subsequently, an average of 122 nematodes per sample were identified to nominal genus.

### Data analysis

Individual islands served as the units of replication, and for all response variables values from the two plots on each island were averaged prior to data analysis to yield a single data value for each island. For each invertebrate group, one way analysis of variance (ANOVA) of abundance was used to determine the statistical significance of differences between invaded and uninvaded islands. Where invertebrate groups showed differences in abundance according to rat history, we tested for rat effects mediated through seabird density by regressing invertebrate abundance against seabird burrow density across all islands. The regressions were repeated for uninvaded islands to test for the effects of seabirds alone. For each of the three invertebrate groups for which we had compositional data (spiders, land snails and nematodes), we also determined taxonomic richness (number of species for spiders and snails, and number of genera for nematodes) and the Shannon–Wiener diversity index for each island. For the 18 islands, community structure for each of these three groups was also analyzed using principal components analyses (PCA). ANOVA was used to determine the significance of differences between invaded and uninvaded islands for taxonomic richness, the Shannon–Wiener index, and the main PCA axis scores (PCI and PCII) summarizing community structure, for each of the three groups. Data were transformed as necessary to satisfy the assumptions of parametric data analysis.

We used path analysis (Wright 1934) to inform hypotheses about mechanisms underlying seabird–invertebrate relationships (see Schemske and Horvitz 1988 and Mitchell 1993 for ecological examples). The analyses were applied to all invertebrate groups that showed significant relationships with island invasion status and burrow density. We also included litter depth, soil moisture, pH and total nitrogen as potential mechanisms through which seabirds may indirectly affect invertebrate groups on our study islands (Fukami et al. 2006, Mulder et al. 2008). When applied at island level, we had too few data points ( $n = 9$  for each treatment (uninvaded and invaded)) for any relationships to be interpreted usefully by path analysis. We therefore used plot-level data (by treating each of the two plots on each island as separate data points) which resulted in a sample size of 18 for each treatment. This prevented us from performing path analysis for the below-ground samples comprising Nematoda, Rotifera and Enchytraeidae, which were obtained from only one sample per island. Analyses by plot rather than by island meant that we could not guarantee independence of samples, especially on the smaller islands. We therefore treated the results simply as a means of generating additional hypotheses and confirming trends identified through regression approaches without assigning levels of significance to path coefficients.

We performed path analysis to test several expectations. We expected that on uninvaded islands seabirds would have direct effects on the litter and soil environments by reducing soil pH, soil moisture and litter depth, but increasing soil nitrogen. We also expected that grazing species such as Gastropoda would respond positively to elevated soil nitrogen, but negatively to low pH, while litter inhabiting groups such as Amphipoda and Collembola would respond negatively to litter disturbance. On invaded islands, we

expected rats to suppress seabirds, thereby having the indirect effect of raising soil pH and lowering soil nitrogen concentration, reducing litter disturbance, and raising soil moisture levels.

## Results

### Rat history and seabird effects

On uninhabited islands, all of which were occupied by seabirds, only one plot on Ohinaiti out of the 18 sampled (5.6%) lacked seabird burrows. Mean burrow density was 37.65 per plot, which is equivalent to 3765 ha<sup>-1</sup>. The highest burrow density was on Green Island, where the two plots combined had an equivalent density of 10 150 ha<sup>-1</sup>.

On rat-invaded islands, only six plots (33.3%) contained seabird burrows. Mean burrow density on invaded islands was 1.33 per plot; considerably lower than on uninhabited islands ( $F = 41.5$ ,  $p < 0.001$ ). The highest burrow density recorded on invaded islands was nine burrows in one plot on Otata at a density equivalent to 900 ha<sup>-1</sup>. Litter depth was weakly negatively correlated with burrow density across all islands ( $r^2 = 0.215$ ,  $p = 0.053$ ). However, when only uninhabited islands were considered, litter depth strongly decreased with increased burrow density (Fig. 1a).

### Litter macro invertebrates

We found no relationship between total litter invertebrate abundance (standardized for dry weight of litter sampled) and burrow density either across all islands ( $r^2 = 0.141$ ,

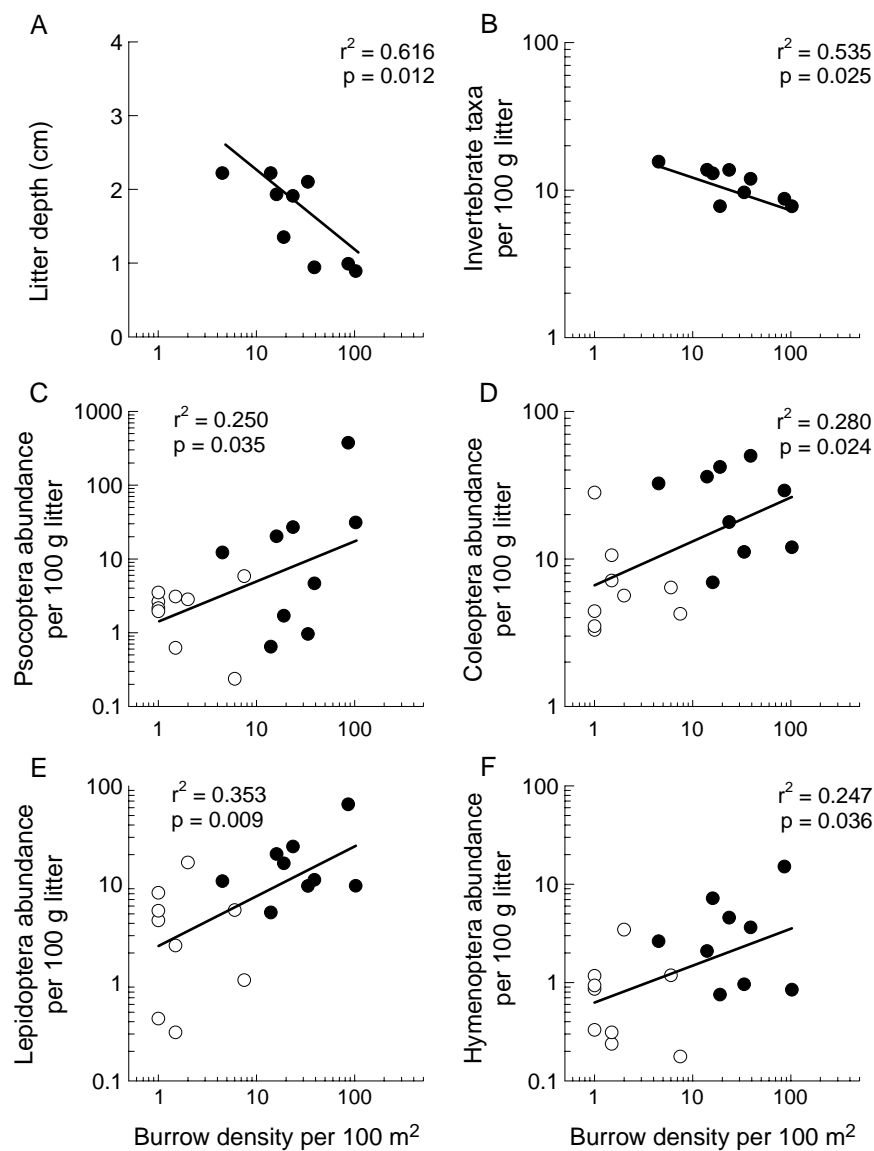


Figure 1. Relationships between burrow density (n+1) for the nine uninhabited islands and (A) mean litter depth; (B) species richness (OTUs) of litter dwelling invertebrates; and relationships between burrow density (n+1) for all 18 islands and (C) Psocoptera abundance; (D) Coleoptera abundance; (E) Lepidoptera abundance; and (F) Hymenoptera abundance. Uninhabited islands = filled symbols; invaded islands = empty symbols.

$p = 0.125$ ) or for uninvaded islands ( $r^2 = 0.120$ ,  $p = 0.360$ ). Furthermore, there was no relationship between litter invertebrate taxonomic richness (OTUs) and burrow density for standardized samples when all islands were combined ( $r^2 = 0.055$ ,  $p = 0.351$ ). Similarly, there was no significant difference in the number of OTUs of litter-dwelling invertebrates per 100 g litter from uninvaded islands (mean = 10.30) compared with invaded islands (mean = 9.81,  $F = 0.202$ ,  $p = 0.659$ ). In contrast, there was a decline in litter invertebrate OTUs with increased burrow density on uninvaded islands (Fig. 1b).

Eight orders of litter-dwelling macro-invertebrates were significantly more abundant on uninvaded islands when data were expressed on a per land area basis (Table 1). Five of the orders also had significantly greater abundances on uninvaded islands when data was expressed per unit litter weight (Table 1). However, there was no relationship across islands between seabird burrow density and abundances of Amphipoda ( $r^2 = 0.016$ ,  $p = 0.617$  for all islands;  $r^2 = 0.300$ ,  $p = 0.127$  for only uninvaded islands), Collembola ( $r^2 = 0.060$ ,  $p = 0.329$  for all islands;  $r^2 = 0.012$ ,  $p = 0.780$  for uninvaded islands) or Chilopoda ( $r^2 = 0.064$ ,  $p = 0.313$  for all islands;  $r^2 = 0.071$ ,  $p = 0.489$  for uninvaded islands). However, Psocoptera, Coleoptera, Lepidoptera (almost all larvae) and Hymenoptera all showed strong significant relationships with burrow density when all 18 islands were considered (Fig. 1c–f). When only the nine uninvaded islands were considered, no relationship with burrow density was found for Psocoptera ( $r^2 = 0.174$ ,  $p = 0.264$ ), Coleoptera ( $r^2 = 0.033$ ,  $p = 0.642$ ), Lepidoptera ( $r^2 = 0.124$ ,  $p = 0.353$ ), or Hymenoptera ( $r^2 = 0.003$ ,  $p = 0.896$ ).

We identified a total of 37 species of Gastropoda (land snails) from the litter samples. Of these, two are predators of other molluscs. One of them, *Rhytida greenwoodi*, was found on two invaded islands and the other, *Delos coresia*, was on one uninvaded island and four invaded islands. The most species-rich island was Ohinauiti, an uninvaded island from which we extracted 12 species. Species richness and Shannon–Wiener diversity indices for Gastropoda did not differ significantly between invaded and uninvaded islands (Table 2). Gastropod abundance showed no relationship with burrow density when all 18 islands were considered ( $r^2 = 0.0002$ ,  $p = 0.958$ ), but a strong negative relationship was detected when only the nine uninvaded islands were used (Fig. 2b). Gastropod species richness declined sharply with burrow density when all 18 islands were used (Fig. 2a), but this relationship was much weaker when only the nine uninvaded islands were considered ( $r^2 = 0.376$ ,  $p = 0.079$ ). There were also differences in gastropod community

composition between invaded and uninvaded islands according to PCA (Table 3, Fig. 3a).

A total of 26 species of Araneae (spiders) were identified from litter samples, with the most species-rich islands (each with seven species) being Ohinauiti (an uninvaded island) and Motutapere (an invaded island). Of the species identified, only eight (31%) were strictly litter inhabiting, with the remainder from other habitats, including foliage and burrows. Spider abundance was not significantly related to seabird burrow density either across all 18 islands ( $r^2 = 0.004$ ,  $p = 0.806$ ) or across the nine uninvaded islands ( $r^2 = 0.235$ ,  $p = 0.186$ ). Species richness of spiders was not related to burrow density when all 18 islands were considered ( $r^2 = 0.006$ ,  $p = 0.786$ ), but declined with increasing burrow density when only the nine uninvaded islands were used (Fig. 2c). However, species richness and Shannon–Wiener diversity indices for spiders were significantly higher on uninvaded islands than invaded islands (Table 2). There was no difference in community composition of spiders between invaded and uninvaded islands according to PCA (Table 3).

### Soil micro-invertebrates

Rotifera, Enchytraeidae and Nematoda were more abundant on uninvaded than invaded islands (Table 4). Rotifers showed no relationship between abundance and burrow density, either across all 18 islands ( $r^2 = 0.172$ ,  $p = 0.087$ ) or across the nine uninvaded islands ( $r^2 = 0.054$ ,  $p = 0.548$ ). In contrast, the abundance of enchytraeids was strongly related to burrow density both when all 18 islands were combined (Fig. 4a), and when the nine uninvaded islands were considered ( $r^2 = 0.685$ ,  $p = 0.006$ ).

Nematode abundance was also positively related to burrow density when all islands were considered (Fig. 4b), but not when only the nine uninvaded islands were used ( $r^2 = 0.174$ ,  $p = 0.264$ ). A total of 56 taxa of soil nematodes were identified, but taxonomic richness and the Shannon–Wiener diversity index for nematodes did not differ significantly between invaded and uninvaded islands (Table 3). Similarly, there was no relationship between nematode taxonomic richness and burrow density when all 18 islands were considered ( $r^2 = 0.002$ ,  $p = 0.877$ ), although there was a weak (non significant) decline when only the nine uninvaded islands were used ( $r^2 = 0.346$ ,  $p = 0.096$ ). There were significant differences in community composition between invaded and uninvaded islands according to PCA (Table 3, Fig. 3b).

Table 2. Taxonomic richness and Shannon–Wiener diversity indices (mean  $\pm$  SE) for test groups of invertebrates on uninvaded and invaded islands, with significant differences in bold. F- and p-values derived from oneway ANOVA. Degrees of freedom are 1 for treatment and 16 for residual.

Diversity measure	Taxon	Invaded	Uninvaded	F- and p-value
Richness	Gastropoda (species)	6.11 $\pm$ 1.27	6.22 $\pm$ 1.13	0.01 (0.949)
	Araneae (species)	2.44 $\pm$ 0.50	4.33 $\pm$ 0.61	5.81 ( <b>0.028</b> )
	Nematoda (genera)	18.11 $\pm$ 2.58	19.67 $\pm$ 2.36	0.20 (0.663)
Shannon–Wiener index	Gastropoda (species)	1.94 $\pm$ 0.10	1.57 $\pm$ 0.25	1.01 (0.329)
	Araneae (species)	0.78 $\pm$ 0.18	1.55 $\pm$ 0.17	9.76 ( <b>0.007</b> )
	Nematoda (genera)	3.44 $\pm$ 0.36	3.59 $\pm$ 0.22	0.11 (0.748)

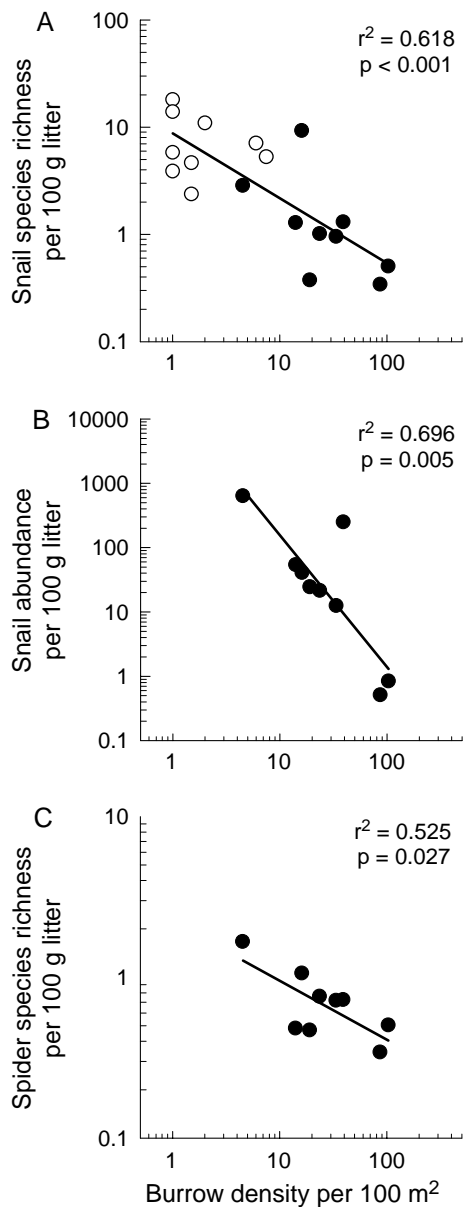


Figure 2. Relationships between burrow density ( $n + 1$ ) and (A) Gastropoda species richness across all 18 islands; (B) Gastropoda abundance on the nine uninvaded islands; and (C) Araneae species richness on the nine uninvaded islands. Uninvaded islands = filled symbols; invaded islands = empty symbols.

### Path analysis

The results of the path analysis are depicted in Fig. 5; because of lack of independence among data points we have treated the results as a means of generating additional hypotheses without assigning levels of significance to path coefficients. All paths tested are included on Fig. 5a–b, but only those with path coefficient  $> 0.4$  have been weighted to indicate strength of the relationships. Had our samples been independent, a path co-efficient of 0.4 would have been significant at the  $p = 0.10$  level.

On uninvaded islands (Fig. 5a), these analyses showed negative relationships between seabird burrow density, soil pH and the abundance and species richness of Gastropoda.

Amphipoda appeared to be negatively affected by soil pH but positively by total nitrogen, which also positively influenced Coleoptera and Chilopoda. Litter depth positively influenced the abundance of Psocoptera and Hymenoptera. Regardless of island invasion status there was an unexpected positive relationship between Hymenoptera and Lepidoptera, which may indicate a parasite–prey relationship. On invaded islands (Fig. 5b), the relationship between soil nitrogen concentration and abundance of Amphipoda was maintained, along with overall species richness and the abundance and diversity of Gastropoda. However, the strong influence of soil pH was less apparent as was the suppressing effect of seabirds. On both sets of islands we found a relationship between total N and the abundance of many groups of litter invertebrates. However, against expectations, this was not reflected in a similar relationship with seabird activity.

### Discussion

The effects of invasions by rats on islands inhabited by burrowing seabirds can only be understood if we know how such systems function in the absence of rats. Seabird dominated islands are disturbance-driven systems that are also subsidised by the nutrients imported by seabirds (Polis and Hurd 1995, 1996, Sanchez-Piñero and Polis 2000). This was exemplified in previous work on our study islands, where Fukami et al. (2006) and Mulder et al. (2008) found high total concentrations of soil carbon, nitrogen and phosphorus, low nutrient availability (ratios of mineral N to total N and Olsen P to total P), and a high marine-derived nutrient signature ( $\delta^{15}\text{N}$ ) in foliage on islands inhabited by seabirds. The beneficial effects of this resource subsidy on belowground invertebrates could potentially be offset by the physical effects of the birds on the soil environment. For example, as seabird activity increases there can be lower soil moisture content (Mulder et al. 2008), increased soil instability, increased trampling, greatly reduced pH (Gilham 1956, Mulder and Keall 2001, Bancroft et al. 2005, McKechnie 2006) and reduced ground cover by surface litter (this study). The importance of nutrient subsidies driven by high seabird density appeared to be demonstrated indirectly in our study through positive linear relationships between burrow density and the abundances of particular groups of invertebrates. In litter these were Psocoptera, Coleoptera, Lepidoptera and Hymenoptera and in soil they were Enchytraeidae and Nematoda. These relationships were also supported for litter invertebrates by path analysis. However, perhaps because of low sample sizes, a direct relationship between seabird activity and nutrient subsidy (total N) on uninvaded islands was not supported by path analysis. Nonetheless, this effect was demonstrated in other studies on these islands (Fukami et al. 2006, Mulder et al. 2008), and is supported in our study by path analysis if data for invaded and uninvaded islands are combined.

The negative effects of high disturbance by seabirds were indicated by groups such as Gastropoda (snails), which were most abundant on uninvaded islands. However, within the uninvaded islands snail abundance declined sharply with increased seabird density. This non-linear relationship was

Table 3. Oneway ANOVA results for the effects of invasion on the two primary ordination axes (axis 1 and axis 2) derived from principal components analysis (p values in parentheses), summarizing the community structure for each of three test groups of invertebrates, and the proportion of total variation in the data set explained by each axis. Significant differences are in bold. Degrees of freedom are 1 for treatment and 16 for residual.

Taxon	F- and p-value		% of variation explained by axis	
	Axis 1	Axis 2	Axis 1	Axis 2
Gastropoda	4.94 ( <b>0.040</b> )	1.79 (0.201)	18.2	13.9
Araneae	1.31 (0.269)	0.41 (0.532)	22.6	16.0
Nematoda	7.80 ( <b>0.013</b> )	1.91 (0.187)	13.5	11.6

also supported by path analysis, which identified increased abundance of snails with increasing soil N on invaded islands as a positive effect of seabird presence. Increased seabird density had little measurable effect on abundance of most other groups of invertebrates, but had strong negative effects on species richness of all litter-dwelling macrofauna, snails, and nematodes. These examples indicate that a relatively restricted subset of the total species is able to tolerate very high levels of disturbance by seabirds, which is consistent with several studies showing diversity of soil associated invertebrates to be generally adversely affected by soil disturbances (Wardle 1995, 2002).

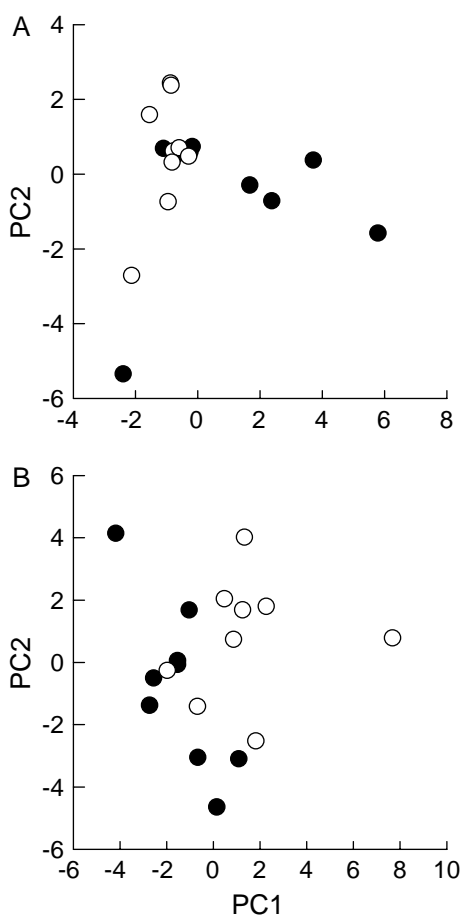


Figure 3. Results from principal components analysis (PC1 vs PC2) of (A) Gastropoda and (B) Nematoda species on uninhabited (filled symbols) and invaded (empty symbols) islands. Statistical analyses are shown in Table 3.

When rats invade, some species of seabirds are extirpated and others are heavily suppressed (Jones et al. 2008). We found that these invasions can have widespread implications. In our study, eight groups of litter-dwelling invertebrates were significantly more abundant per unit area on uninhabited islands than on those invaded by rats, and five were more abundant per unit litter mass. Furthermore, rotifers, enchytraeids and nematodes, which live below the soil surface and are inaccessible to rats, were less abundant on the invaded islands. Despite the presence of seabird burrows on five invaded islands, regressions of invertebrate abundance and diversity against burrow density on invaded islands showed no relationship for any group. These results support our hypothesis that the abundance of litter and soil-dwelling invertebrates should be reduced on islands that have been invaded by rats through suppression of the seabird influence. Two sets of potential consequences for below-ground invertebrates can arise when islands inhabited by burrowing seabirds are invaded by predators such as rats, and these may help to explain our results. The first is the direct effect of predation by rats on selected invertebrate species accessible at the surface. The second results from predation of rats on seabirds, and this could have both positive and negative consequences for invertebrates. Reduced seabird abundance reduces litter and soil disturbance and increases litter residence time and depth, which should be an advantage to many species. However, seabird abundance also thwarts nutrient transfer from the ocean to the land, which can have negative multi-trophic effects in the soil food web (Fukami et al. 2006).

Consistent with possible direct effects of rats through predation (Campbell et al. 1984), we found lower densities of potential prey sources such as Lepidoptera larvae, Coleoptera and Chilopoda on invaded islands. Chilopods (centipedes) are relatively large and distinctive predators of other invertebrates. However, despite islands invaded by rats having greater litter depth and reduced environmental

Table 4. Comparison of relative abundance of soil micro-invertebrates (mean  $\pm$  SE) on invaded and uninhabited islands presented as numbers per unit weight of soil, with significant differences in bold. F- and p-values (in parentheses) have been derived from one-way ANOVA. Degrees of freedom are 1 for treatment and 16 for residual.

Taxon	No. per 100 g soil		
	Invaded	Uninvaded	F- and p-value
Rotifera	2.09 $\pm$ 8.07	18.17 $\pm$ 0.66	5.41 ( <b>0.033</b> )
Enchytraeidae	1.70 $\pm$ 0.44	6.72 $\pm$ 1.23	16.71 ( <b>0.001</b> )
Nematoda	866.59 $\pm$ 273.59	3653.19 $\pm$ 903.23	14.39 ( <b>0.002</b> )

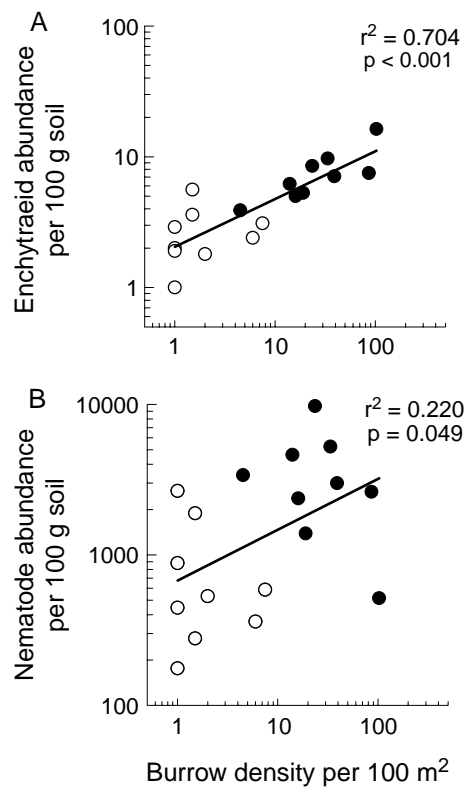


Figure 4. Relationship between burrow density ( $n+1$ ) for all 18 islands and (A) Enchytraeidae abundance and (B) Nematoda abundance. Uninvaded islands = filled symbols; invaded islands = empty symbols.

disturbance through suppression of seabirds (Mulder et al. 2008), we found no evidence for any invertebrate group responding positively to rat invasion. For example, minute land snails (almost all  $<5$  mm  $\phi$ ), which should benefit from long litter residence times and deep litter layers (Barker and Mayhill 1999), were less abundant on islands invaded by rats, at least per unit land area. We did find differences between invaded and uninvaded islands for land snail community structure (PCA results) but species richness of this group was unaffected by island invasion status. We suggest that the reduced abundance of land snails on invaded islands is an indirect effect of interrupted nutrient subsidy and reduced availability of food sources such as algae and fungi growing within the surface litter. A similar indirect effect probably operates for other minute invertebrates unlikely to be preyed on by rats. For example, Collembola were less abundant in samples from invaded islands than uninvaded islands on a per area basis (Fukami et al. 2006). Hymenoptera were also less abundant on invaded islands, and the majority of these (75%) were minute parasitic wasps ( $<5$  mm) that are likely to be sensitive to reductions in the availability of specific invertebrate hosts. Few of the Hymenoptera were ants, which are poorly represented in the New Zealand fauna. Further, we found fewer Psocoptera on invaded islands. These minute (1.5–2 mm long) insects congregate in freshly fallen foliage, which on uninvaded islands may be an indirect consequence of seabirds breaking through the canopy while landing.

Like litter-inhabiting invertebrates, soil-inhabiting groups such as nematodes which are inaccessible to rats also showed clear negative responses to invasion by rats and seabird suppression. These effects were also reflected in the ordination analyses which showed differences in nematode community structure between invaded and uninvaded islands. Previous data from these islands points to greater soil nutrient availability and nutrient acquisition by plants on uninvaded islands (Fukami et al. 2006). Our study emphasizes that for soil organisms the most important effect of rat invasion involves interruption of nutrient transfer by seabirds from the ocean to the land. This is consistent with previous studies showing that predators of seabirds can greatly inhibit resource inputs to ecosystems (Croll et al. 2005, Maron et al. 2006, Wardle et al. 2007). It also highlights the strong bottom-up regulation of densities and community composition of organisms that has been frequently shown for mineral soil food webs, particularly those dominated by nematodes (Mikola and Setälä 1998, Wardle 2002). Our data point to profound changes as these food webs in seabird islands are transformed by invasion of rats from those that are nutrient-based and subjected to regular soil disturbance, to those that have high levels of consumption by invasive species with a lower resource input and significantly reduced disturbance.

Direct effects of invasive species such as rats are frequently reported since they are the most easily observed. For example, the reduced abundance or taxonomic richness that we found for selected groups of large invertebrates following predator invasions has also been found in other studies (Kuschel and Worthy 1996, Palmer and Pons 1996, McIntyre 2001, Pascal et al. 2004). However, indirect effects are rarely reported, even though they may be relatively common (White et al. 2006). Some recently documented examples include shifts in forest composition following suppression of the terrestrial crab *Gecarcoidea natalis* by the invasive yellow crazy ant *Anoploplepis gracilipes* (O'Dowd et al. 2003), changes in the composition of plant communities when introduced foxes suppress seabirds (Maron et al. 2006) and modification of marine intertidal communities by rats through suppression of oystercatchers and gulls (Kurle et al. 2008). Our results on seabird islands invaded by rats indicated that of 11 groups of invertebrates detrimentally affected, only Lepidoptera, Coleoptera and Chilopoda might suffer direct effects by virtue of their size and susceptibility to predation by rats. However, no direct relationship between these invertebrates and the presence of rats was found using path analysis, probably because we had no data on rat abundance by site. The predominance of indirect effects point to environmental chain reactions (sensu Atkinson 1989), in which multi-trophic consequences of seabirds on litter and soil biota are interrupted by invasions of rats. Not only were there significant changes to soil chemistry when seabirds were suppressed by rats, but there were also shifts in the composition of below-ground soil communities and above ground plant biomass (Fukami et al. 2006, Wardle et al. 2007).

Studies such as ours suffer limitations because they are based on circumstantial comparisons between islands. Such comparisons can not demonstrate causal relationships. However, they can provide guidance for developing

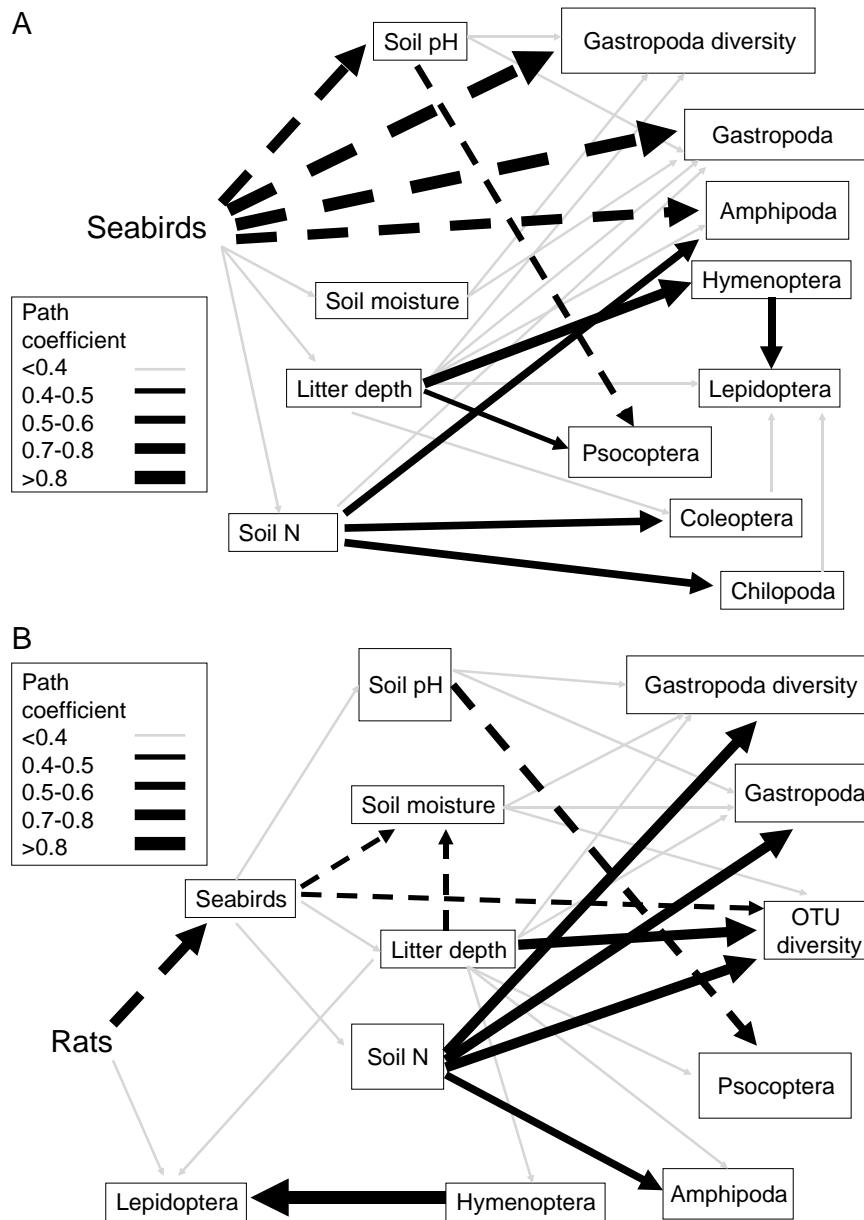


Figure 5. Path diagram for effects of seabirds measured for selected soil variables and invertebrate abundance (unless stated as diversity) on (a) uninhabited islands and (b) on islands invaded by rats. Approximate values for path coefficients are indicated by thickness of arrows, with black arrows for coefficients  $\geq 0.4$  and negative relationships indicated by broken lines. Grey arrows identify additional tested relationships (path coefficients  $< 0.4$ ). Invertebrate groups excluded to simplify figures and with all path coefficients  $< 0.4$  include (a) Collembola and OTU diversity and (b) Chilopoda, Coleoptera and Collembola.

hypotheses to be confirmed by testing (Caughley and Gunn 1996). One way to test our hypotheses would be for similar studies that include islands from which rats have been eradicated (Townsend and Broome 2003, Howald et al. 2007). Given that we recorded lower invertebrate abundances rather than lower species richness on invaded islands, if rats are removed below-ground invertebrates could eventually recover to develop communities little different from those on uninhabited islands. The spiders were a rare example of reduced diversity on invaded islands, but they should also be capable of recovery because many species disperse over water by ballooning. However, there are many complicating effects, including a legacy of the presence of rats. Species

that are affected directly by rat predation, and have the capacity to recolonise, should respond relatively rapidly when rats are removed. By comparison, groups affected indirectly, such as soil nematodes, are dependent on recolonisation by seabirds and associated changes to the soil environment to facilitate recovery. This can be a very slow process, may not proceed without direct intervention to encourage seabird recolonisation, and could produce unpredictable interactions over this period (Mulder et al. 2008). Of course, in the event of total extirpations, the changes that we report are likely to be irreversible without direct intervention. This could further complicate experimental design. However, we found no consistent evidence

of extirpation among below-ground macro- and micro-invertebrates due to rat invasion. Extirpations driven by invasion of rats on islands appear to be far more prevalent amongst above-ground mega-invertebrates such as tenebrionid beetles in the Mediterranean (Palmer and Pons 1996), giant stick insects in the Pacific (Pridell et al. 2003) and flightless crickets in New Zealand (McIntyre 2001). Debate about the effects of invasive species such as rats has focused mainly on these extirpations and their potential contribution to global extinctions (Gurevitch and Padilla 2004), but our study has demonstrated that there may be complex and subtle indirect effects on community and ecosystem properties that should not be overlooked (Simberloff 2006). The challenge for conservation biologists will now be to remove invasive species that affect community and ecosystem processes, test hypotheses about the effects of invaders on ecosystem drivers, assess whether the changes induced by the invasions can be reversed (Sinclair and Byrom 2006) and predict the time scales involved.

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