

LETTER

Above- and below-ground impacts of introduced predators in seabird-dominated island ecosystems

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Abstract

Predators often exert multi-trophic cascading effects in terrestrial ecosystems. However, how such predation may indirectly impact interactions between above- and below-ground biota is poorly understood, despite the functional importance of these interactions. Comparison of rat-free and rat-invaded offshore islands in New Zealand revealed that predation of seabirds by introduced rats reduced forest soil fertility by disrupting sea-to-land nutrient transport by seabirds, and that fertility reduction in turn led to wide-ranging cascading effects on belowground organisms and the ecosystem processes they drive. Our data further suggest that some effects on the belowground food web were attributable to changes in aboveground plant nutrients and biomass, which were themselves related to reduced soil disturbance and fertility on invaded islands. These results demonstrate that, by disrupting across-ecosystem nutrient subsidies, predators can indirectly induce strong shifts in both above- and below-ground biota via multiple pathways, and in doing so, act as major ecosystem drivers.

Keywords

Allochthonous input, biological invasion, community structure, food web, nutrient enrichment, nutrient subsidies, spatial subsidies, trophic cascade.

Ecology Letters (2006) 9: 1299–1307

INTRODUCTION

The prevalence and strength of multi-trophic cascading effects of predators have long been debated, particularly in terrestrial ecosystems (Hairston *et al.* 1960; Spiller & Schoener 1990; Pace *et al.* 1999; Schmitz *et al.* 2000; Terborgh *et al.* 2001; Shurin *et al.* 2002). However, strong trophic cascades have been recently found to occur when one ecosystem is linked to another by across-ecosystem movement of top predators or their prey (Nakano & Murakami 2001; Croll *et al.* 2005; Knight *et al.* 2005; Maron *et al.* 2006). These studies have expanded our understanding

of trophic cascades by pointing to the previously overlooked role of across-ecosystem nutrient transports in influencing trophic interactions, and have yielded new insights into factors regulating the aboveground component of terrestrial communities. Yet, they inform little about the belowground component, which is not only functionally important for ecosystem processes, but is intricately linked to the aboveground component through a variety of interactions (Van der Putten *et al.* 2001; Wardle *et al.* 2004; Bardgett *et al.* 2006). Ecologists now recognize that a full understanding of the functioning of terrestrial ecosystems requires explicit consideration of both above- and below-ground biota

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(Van der Putten *et al.* 2001; Wardle *et al.* 2004; Bardgett *et al.* 2006). Despite this recognition, belowground responses to across-ecosystem trophic cascades remain largely unexplored. A few recent studies have investigated the belowground consequences of trophic cascades, but have used small-scale, within-ecosystem experiments in controlled environments, with some studies showing significant cascades (e.g. Wardle *et al.* 2005) and others finding none (e.g. Mikola & Setälä 1998). Such studies suggest plausible mechanisms, but cannot directly address large-scale, across-ecosystem dynamics of trophic cascades occurring in nature at the landscape scale.

In this regard, island ecosystems have the potential to serve as ideal model systems. This is because (i) different islands in an archipelago may contain different combinations of predators, particularly those introduced by humans; (ii) each island operates as a spatially discrete entity, which enables a level of true replication of independent ecosystems that can be achieved in no other way; and (iii) surrounded by water, islands can provide unambiguous examples of across-ecosystem linkages, between terrestrial and aquatic habitats. If non-native predators have been introduced to some islands and not others within an archipelago, then this difference provides a powerful tool for assessing large-scale impacts of predators, including those arising from their influence on across-ecosystem dynamics (Wardle 2002). However, few studies have used islands for such purposes (Spiller & Schoener 1990; Campbell & Atkinson 2002; Croll *et al.* 2005) and, to our knowledge, none has taken this approach to examine effects of predators on aboveground-belowground biotic interactions.

Here we use forested offshore islands (Fig. 1a) in warm temperate northern New Zealand as a model system for investigating how top predators, by affecting the across-ecosystem movement of their key prey, indirectly influence the structure and function of above- and below-ground communities. In the absence of introduced predators, seabirds, especially petrels and shearwaters, are highly abundant. These birds feed at sea, but nest in burrows from near sea level to the summit of the islands, often at high densities in forest (Fig. 1b). In doing so, they transport large amounts of nutrients from sea to land, in their guano, feathers, carcasses, eggs and food for their young (Mulder & Keall 2001). However, the rat species *Rattus rattus* and *R. norvegicus* have been accidentally introduced by humans to some of these islands (but not others) between 50 and 150 years ago (King 2005). Once introduced, rats consume seabird eggs and chicks and severely reduce seabird populations on the islands (Atkinson 1985; Blackburn *et al.* 2004). For this study, we selected nine rat-free and nine rat-invaded islands (see Table S1 in Supplementary Material). As we describe in detail below, the two groups of islands were comparable in size range, geology, climate, anthrop-

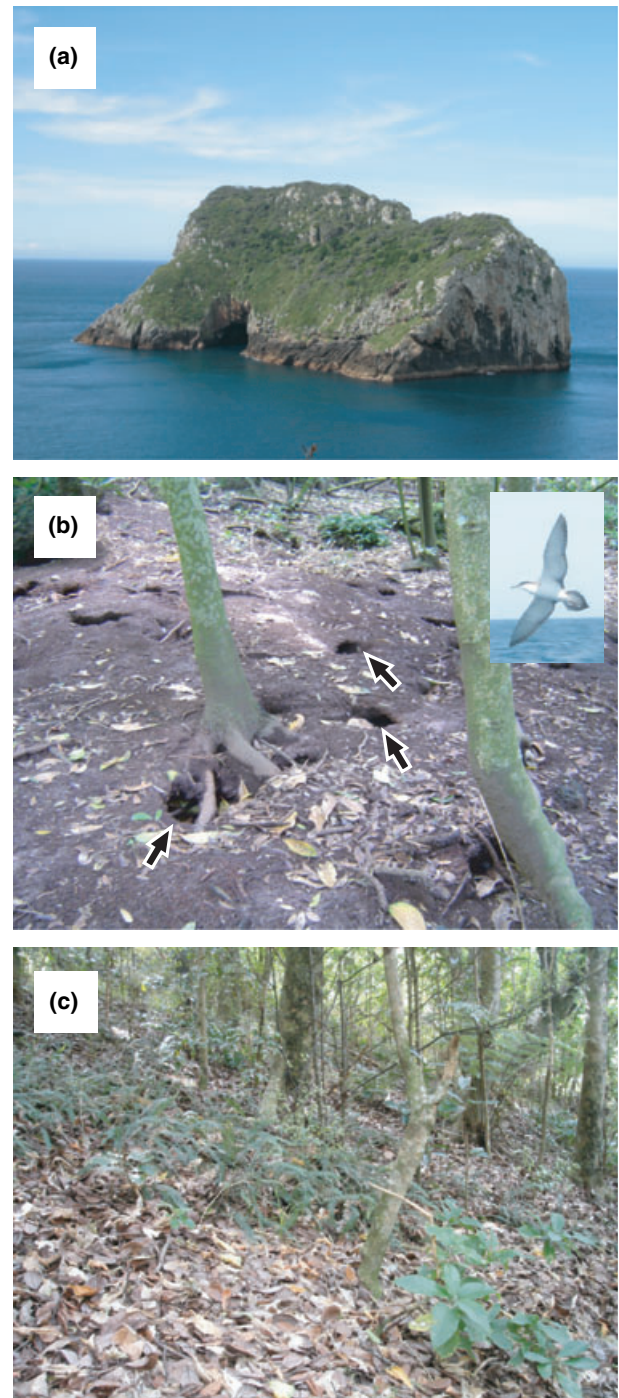


Figure 1 Study system. (a) Aorangaia (5.6 ha), a typical island used in this study. (b) Forest floor on Tawhiti Rahi, a rat-free island. (c) Forest floor on Aiguilles, a rat-invaded island. Rat-free islands are characterized by dense seabird burrows on forest floor (such as those of Buller's shearwater, *Puffinus bulleri*, shown in b). Burrow entrances are about 20–50 cm wide, some of which are indicated by arrows in (b). Rat-free islands are in sharp contrast to rat-invaded islands, where seabird burrows are virtually non-existent owing to rat predation of seabirds (c).

ogenic fire history and other environmental characteristics, and each of these islands served as an independent replicate ecosystem. Comparing them enabled us to directly examine large-scale, long-term effects of across-ecosystem trophic cascades. We studied both above- and below-ground responses, but with a particular focus on the latter.

MATERIALS AND METHODS

Study site

The islands are located in warm temperate northern New Zealand. We identified nine islands not invaded by any exotic mammals (except Aorangi, on which the pig *Sus scrofa* was eradicated in 1936; see King 2005), and compared them with the same number of islands that are within comparable size, climatic and geological ranges (Leathwick *et al.* 2003), but had been invaded by rats (see Table S1). Since portions of these islands were burned by humans from about 800 to 50 years ago, we restricted our sampling to well-developed multi-tree species secondary forest to maximize comparability across islands. In February to April 2004, we established two 10 × 10 m plots in the forested area on each island to make the following measurements.

Plot measurements

In each plot, we determined vegetation properties by calculating the total basal area of all trees present through diameter measurements (≥ 2.5 cm diameter at 1.35 m height), and seedling densities by counting all seedlings in at least 21 grid-based subplots of 1 × 1 m each. Seabird burrow entrances (Fig. 1b) were counted in each plot as a proxy for seabird abundance. A soil and litter sample was taken from a 0.5 × 0.5 m subplot within each plot. In each subplot, all the surface litter was collected and a soil sample was then taken for each of three depth layers: 0–10, 10–20, and 20–30 cm. All litter samples, and all soil samples within each depth layer, were bulked within each island since the islands represented the only true unit of replication for this study (Wardle *et al.* 1997; Wardle 2002). For each litter and soil depth sample, we measured active microbial biomass (substrate-induced respiration) (Wardle 1993) and basal respiration (Anderson & Domsch 1978), nematode abundances (extracted and assigned to main feeding groups) (Yeates *et al.* 1993), and resource base (%N, %C, %P, %Olsen P, %NO₃-N, %NH₄-N). We also collected a 2-L litter sample, which was then extracted and all invertebrates identified to order; although rats are omnivorous (Townes *et al.* 2006), in this study, we focus primarily on the orders below the size range preyed on by rats (< 10 mm) (Townes *et al.* 1997; Green 2002). In addition, litter mass was determined by bulking the litter collected from the two quadrats and drying at 60 °C.

Stable isotopes

Field-moist soil from each of the three depth layers was sieved to 2 mm, dried at 60 °C for at least 48 h, and ball-milled. The samples were then analysed for $\delta^{15}\text{N}$ on a PDZ Europa GSL Elemental Analyser attached to a PDZ Europa 20–20 CF-IRMS. Repeat analysis of the laboratory standard, referenced against IAEA N-1 to normalize measurements to atmospheric N, yielded precision of $\pm 0.2\text{‰}$. On each island, we also took the three outermost leaves of three randomly chosen branches from three randomly chosen individuals of *Melicytus ramiflorus* (Violaceae) and *Coprosma macrocarpa* (Rubiaceae), which were common on most of the islands. Leaves were dried at 60 °C for at least 48 h, and ball-milled. Portions of three leaves from a single tree that lacked obvious pathogens and animal-derived deposits were homogenized in approximately equal proportions by surface area. Leaf samples were analyzed for %N, and for $\delta^{15}\text{N}$ in the same manner as for the soil samples.

Plant nutrient supply

We conducted phytometer experiments (Bellingham *et al.* 2001) to investigate the supply of nutrients from the soil. We collected soil from each plot on each island at each of the three depth layers, bulked it within each island for each depth layer, and transported it to the glasshouse. Subsamples of each of the three resultant soil samples for each island were placed in three 1-L pots. Each pot was planted with a seedling of a different phytometer species: *Entelea arborescens* (Tiliaceae), *Corynocarpus laevigatus* (Corynocarpaceae), and *Strebilus banksii* (Moraceae). We maintained the plants in the glasshouse for a year, after which we destructively harvested the pots to measure total biomass and foliar %N and %P.

Litter decomposition

Twelve litterbags, each containing 5.0 g dry weight of *Corynocarpus laevigatus* litter, were placed on the soil surface within the plots on each island. These bags consisted of three bags of each of 4 mesh sizes (4.0, 1.0, 0.1 and 0.025 mm), which selectively excluded decomposer fauna on the basis of body size (Vossbrink *et al.* 1979; Setälä *et al.* 1996). The bags were collected after a year, bulked within each island, and analysed for dry weight remaining.

Statistical analysis

We used ANOVA to test for effects of island status, soil depth or litter-bag mesh size, and their interaction. We also used ANCOVA to test for effects of covariates relating to island geographical attributes. Data were transformed as necessary to satisfy assumptions of ANOVA and ANCOVA.

Table 1 Effect of rat invasion, soil depth and their interaction on soil nutrients and pH

	Island status			Soil depth	Island status × soil depth
	Rat-free	Rat-invaded	<i>F</i> and <i>P</i> -values	<i>F</i> and <i>P</i> -values	<i>F</i> and <i>P</i> -values
Total C (%)	9.88 ± 1.67	5.27 ± 0.69	28.47 (< 0.001)*	15.85 (< 0.001)*	0.94 (0.396)
Total N (%)	0.78 ± 0.10	0.43 ± 0.05	35.94 (< 0.001)*	17.87 (< 0.001)*	0.71 (0.496)
Total P (%)	0.30 ± 0.09	0.13 ± 0.04	6.77 (0.012)*	0.69 (0.507)	0.05 (0.954)
Mineral N/total N (%)	12.67 ± 3.50	5.88 ± 1.16	15.16 (< 0.001)*	1.11 (0.339)	0.29 (0.749)
Olsen P/total P (%)	6.92 ± 1.31	3.88 ± 0.90	13.40 (0.001)*	0.04 (0.964)	0.02 (0.982)
δ ¹⁵ N (‰)	14.13 ± 0.62	10.87 ± 0.97	20.85 (< 0.001)*	2.82 (0.070)	1.16 (0.321)
pH	4.85 ± 0.21	6.63 ± 0.15	45.72 (< 0.001)*	0.24 (0.791)	0.29 (0.749)

Mean values ± SEM are presented for rat-free and rat-invaded islands ($n = 9$ islands for each island status). The ratios of mineral N to total N and of Olsen P to total P provide measures of the ratio of labile forms of N and P relative to total N and P. *F* values (with *P*-values in parentheses) from two-way ANOVA are presented for effects of island status (rat-free or rat-invaded), soil depth (0–10, 10–20, or 20–30 cm), and two-way interaction. Analyses were done on log-transformed data, except for δ¹⁵N and pH. *Statistically significant values ($P < 0.05$).

RESULTS AND DISCUSSION

Effects of rat invasion on seabirds and soil nutrients

As expected, there was little evidence of seabird use of rat-invaded islands, whereas there was heavy seabird use of rat-free islands. On average, seabird burrows in the forests we studied (mean canopy height ± SEM: 8.0 ± 0.7 m) were 24 times more abundant on rat-free islands (mean ± SEM: 36.6 ± 11.3/100 m²) than on rat-invaded islands (mean ± SEM: 1.5 ± 0.8/100 m²) ($t = 6.45$, $P < 0.001$, log-transformed). We also found significant differences in the total concentrations (total C, N and P) and availability (ratios of mineral N to total N and of Olsen P to total P) of soil nutrients between rat-free and rat-invaded islands (Table 1). Furthermore, δ¹⁵N was significantly greater in soils from rat-free islands than in those from rat-invaded islands (Table 1). Soils and organisms that contain marine-derived N are known to have higher δ¹⁵N values than those that obtain N locally within islands (Dawson *et al.* 2002; Croll *et al.* 2005; Maron *et al.* 2006). Thus, our results confirm that seabirds are substantial transporters of nutrients from the ocean to the islands (Mulder & Keall 2001) and that these effects are significantly reversed on islands invaded by rats.

We used depthwise soil sampling to determine whether seabird burrowing reduced stratification in the soil profile to consequently affect the vertical distribution of soil nutrients. While soil depth affected total C and N (Table 1), we found no significant interactive effects of rat invasion and soil depth, indicating that soil mixing by seabirds did not affect vertical stratification of soil nutrients (Table 1).

Effects of rat invasion on community and ecosystem properties

Our data indicated that seabird predation by rats further resulted in wide-ranging cascading effects below ground.

Trophic groups negatively affected by rat invasion included herbivorous nematodes (Fig. 2a), enchytraeids (Fig. 2d), microbe-feeding nematodes (Fig. 2e), rotifers (Fig. 2f), minute land snails (Fig. 2c), and collembolans (Fig. 2g), while some other groups, such as microflora (Fig. 2b) and predatory nematodes (Fig. 2h), were not significantly affected. The fact that not all trophic groups responded negatively to rat invasion is consistent with the hypothesis that the relative importance of bottom-up and top-down regulations varies among different trophic levels in the soil food web (Wardle *et al.* 2005). For example, we suspect that the lack of a significant response of microflora, a group of primary consumers (Fig. 2b), was because the promotion of secondary consumers by seabirds (Fig. 2d–g) resulted in top-down forces that overrode bottom-up fertilization effects on microflora. Meanwhile, we suggest that other primary consumers (Fig. 2a, c) responded positively to soil fertilization by seabirds because predation pressure was weaker on them than on microflora (Fig. 2).

Invaded islands further showed significant shifts in ecosystem processes driven by the belowground organisms. Specifically, soil basal respiration (i.e. microbial CO₂ production) in litter tended to be greater on rat-free islands than on rat-invaded islands ($t = 1.81$, $P < 0.089$, square root-transformed; Fig. 3a). On the other hand, litter decomposition rate was significantly higher on rat-invaded islands than on rat-free islands, particularly when larger soil animals (1–4 mm width) had access to litter (island status: $F_{1,60} = 19.30$, $P < 0.001$; mesh size: $F_{3,60} = 9.32$, $P < 0.001$; island status × mesh size: $F_{3,60} = 3.34$, $P < 0.025$; arcsine-transformed; Fig. 3b). These results (Fig. 3b) cannot be fully explained by the abundance of the larger-bodied animals, which were in fact more abundant on rat-free islands ($P < 0.05$ for litter shredders such as amphipods and lepidopteran larvae; see also Fig. 2g). We suspect that seabirds influenced the functional

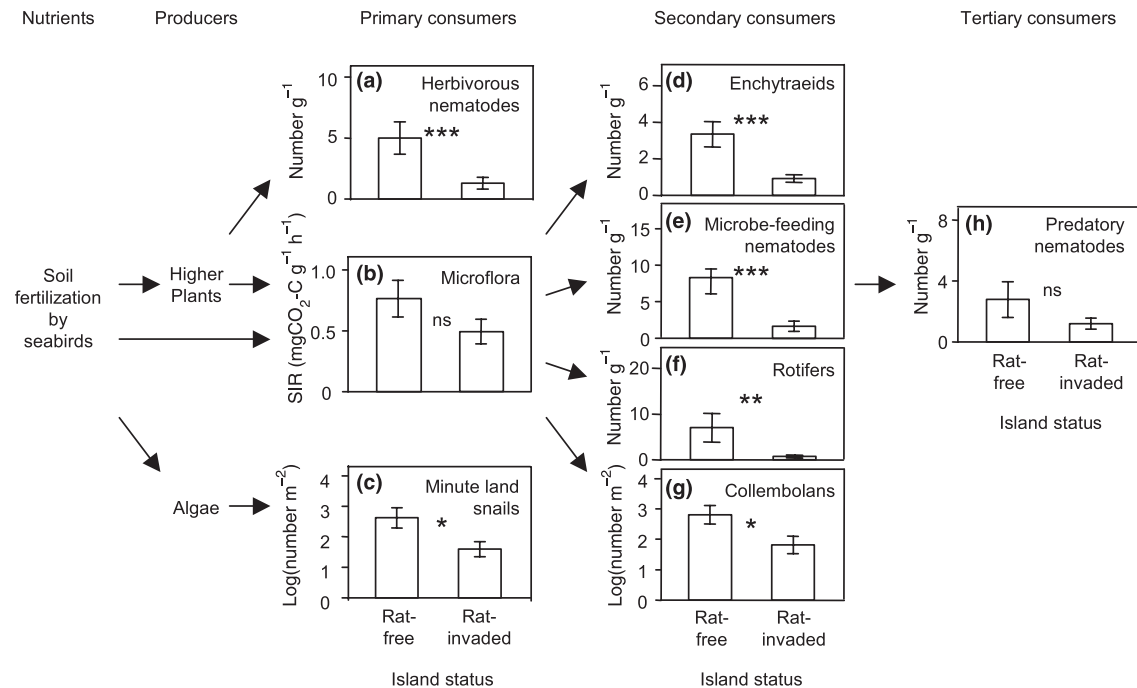


Figure 2 Response of belowground trophic groups to rat invasion of islands. Arrows indicate directions of nutrient flow (note that only a subset of the soil food web is shown). Results are shown as means \pm SEM ($n = 9$ rat-free and 9 rat-invaded islands). * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; ns, non-significant; SIR, substrate-induced respiration in litter and soil.

role of soil fauna through microhabitat modification: on rat-invaded islands, litter was more abundant (Fig. 4c) and contiguous (Fig. 1c) due to less disturbance by seabirds; this probably resulted in increased soil and litter moisture and allowed larger soil animals (1–4 mm width) to concentrate around the litterbags laid on the soil surface. Additionally, many litterbags had been buried deep into soil by the burrowing activity of seabirds on rat-free islands, thus likely limiting the large animals' access to them. As a consequence, larger animals contributed to litter decomposition to a greater extent on rat-invaded islands (Fig. 3b).

In contrast to the generally negative effects of rats below ground, rats had consistently positive effects on above-ground plant biomass (Fig. 4a–c). Seabirds have been shown to promote greater temporal fluctuations in soil moisture by burrowing (Gillham 1956; Bancroft *et al.* 2005; see Fig. 1b), to cause physical disturbance by trampling (Gillham 1956; Bancroft *et al.* 2005) thus reducing opportunities for tree seedling regeneration (Maesako 1999), and to lower soil pH (Table 1) by depositing guano (Mulder & Keall 2001). Burrowing by seabirds may also cause forests to be more vulnerable to natural disturbance, such as windstorms (Cameron 1990). In our study system (Fig. 1), it is apparent that rats alleviated these adverse effects of seabirds on plants (Fig. 4a–c). It is also possible that rats benefited plants by preying on herbivorous insects, although the relative importance of this potential effect remains

unclear. The contrasting responses above vs. below ground suggest that the positive effects of seabirds on belowground biota (Fig. 2) through elevating soil fertility (Table 1) were substantial enough to outweigh any negative indirect effects via decreased plant-derived resource input to the soil. However, our data also indicate some indirect seabird effects on belowground biota through fertilization effects on plants. For example, foliar N and $\delta^{15}\text{N}$ in common tree species were greater on rat-free than on rat-invaded islands (Fig. 4d, e). This seabird-induced increase in plant foliar nutrient concentrations would in turn likely increase the quality of plant litter entering the soil, thereby enhancing abundances of belowground fauna (Fig. 2) and respiration rates in litter (Fig. 3a). This scenario is consistent with the results of the phytometer experiments that we performed, in which plants attained greater total biomass and sometimes greater foliar nutrient concentrations when they were grown on the soil from rat-free islands than from rat-invaded islands (Fig. 4f, g).

We found no significant interactive effects of rat invasion and soil depth on any of the community or ecosystem properties examined above or below ground, indicating the lack of strong effects of soil mixing by seabirds (see Tables S2 and S3). These results closely match those for soil nutrients (Table 1), reinforcing the hypothesis that seabirds affected the community and ecosystem properties primarily by nutrient input rather than by soil mixing.

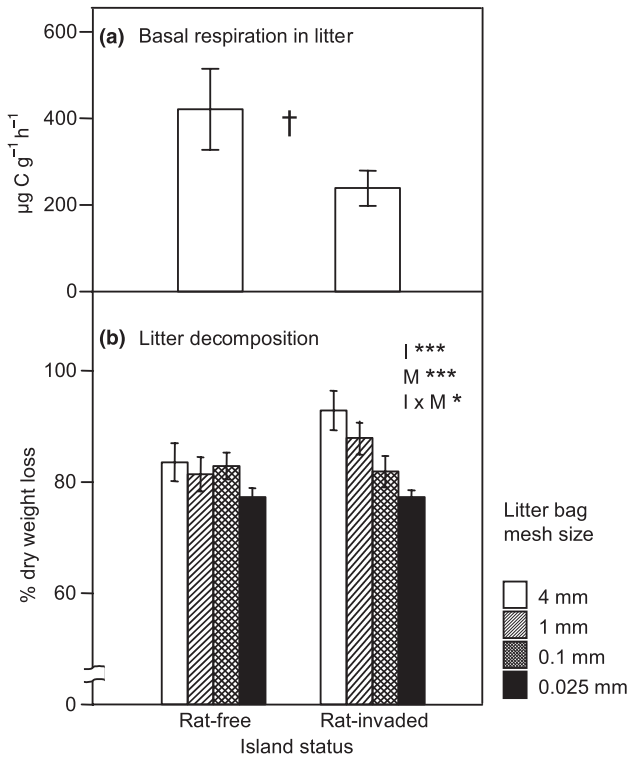


Figure 3 Changes in ecosystem processes driven by belowground organisms in response to rat invasion of islands. Results are shown as means \pm SEM ($n = 9$ rat-free and 9 rat-invaded islands). † $P < 0.10$; * $P < 0.05$; *** $P < 0.001$. I, effect of island status; M, effect of litterbag mesh size; I \times M, effect of island status \times litterbag mesh size interaction.

Accounting for potential effects of island geography

This study takes a comparative approach, with the islands treated as replicate ecosystems. As in any such studies, our results may be confounded by variables that co-vary with the factor of primary focus (Fukami & Wardle 2005), which in this case is rat invasion. In particular, the geographical features of islands can significantly influence community and ecosystem properties (Wardle *et al.* 1997, 2003). If the occurrence of rats co-varies with island geography, it may affect the interpretation of our data. For this reason, we used islands that are as comparable as possible in their geographical features: in fact, rat-free and rat-invaded islands did not differ significantly in longitude ($t = 0.30$, $P < 0.769$), latitude ($t = 1.78$, $P < 0.102$), area ($t = 0.18$, $P < 0.860$, log-transformed), elevation ($t = 1.15$, $P < 0.269$), distance to mainland ($t = 1.13$, $P < 0.281$), distance to nearest larger island ($t = 1.14$, $P < 0.277$, log-transformed), or distance from plots to shore within islands ($t = 0.35$, $P < 0.731$) (see Table S1).

We conducted ANCOVAs to further tease apart effects of rat invasion from those of island size and degree of isolation

on all of the community and ecosystem variables considered in this study. Island status (rat-free or rat-invaded) (and soil depth or litterbag mesh size where appropriate) was treated as a discrete factor (or factors), and island area (log-transformed), distance to mainland (log-transformed), distance to nearest larger island (log-transformed), or distance from plots to shore within islands, as a covariate. All but three of the significant effects of island status identified remained significant in the ANCOVAs, indicating that most of our results are not confounded by island size or degree of isolation. In one of the three exceptions, the effect of island status on collembolan abundance was not significant when distance to mainland was used as a covariate. In another, the same was true with minute land snail abundance. Lastly, the effect of rat invasion on soil $\delta^{15}\text{N}$ was not significant ($F_{1,47} = 1.86$, $P < 0.179$) when we considered distance to mainland, which had a significant effect ($F_{1,47} = 15.81$, $P < 0.05$). However, this result was driven mostly by two islands, Otata and Motuhoropapa, which had high $\delta^{15}\text{N}$ despite having been invaded by rats. Unlike the majority of our other islands, which have been inhabited by rats since > 100 years ago (King 2005), these islands have been periodically invaded by rats only since ca. 1956 (Moors 1985), and they have been exterminated repeatedly (see Table S1), with some subsequent return of seabirds in between. Seabirds can have long-term legacy in soil $\delta^{15}\text{N}$ (Mizutani *et al.* 1991), and the returning seabirds are also likely to have contributed to the increased soil $\delta^{15}\text{N}$. When Otata and Motuhoropapa are excluded from the ANCOVA, a significant effect on soil $\delta^{15}\text{N}$ is detected of island status (rat-free vs. rat-invaded) ($F_{1,41} = 20.61$, $P < 0.001$), but not of distance to mainland ($F_{1,41} = 3.52$, $P < 0.068$).

CONCLUSIONS

Overall, our results show that disruption of across-ecosystem resource movements by predators can exert a wide range of effects that cascade through multiple pathways both above and below ground. We believe these results help to bridge the gap between two recent concepts of ecosystem dynamics. One concept holds that many patterns observed within ecosystems can be understood only by considering lateral interactions across ecosystem boundaries in landscapes (Polis & Hurd 1996; Nakano & Murakami 2001; Jefferies *et al.* 2004; Polis *et al.* 2004; Croll *et al.* 2005; Knight *et al.* 2005; Maron *et al.* 2006), whereas the other stresses the role of vertical interactions between above- and below-ground communities in controlling ecosystem processes (Van der Putten *et al.* 2001; Wardle *et al.* 2004; Bardgett *et al.* 2006). Both concepts have proven useful, but have been developed independently of each other. Here we have empirically integrated them by explicitly incorporating the belowground subsystem into

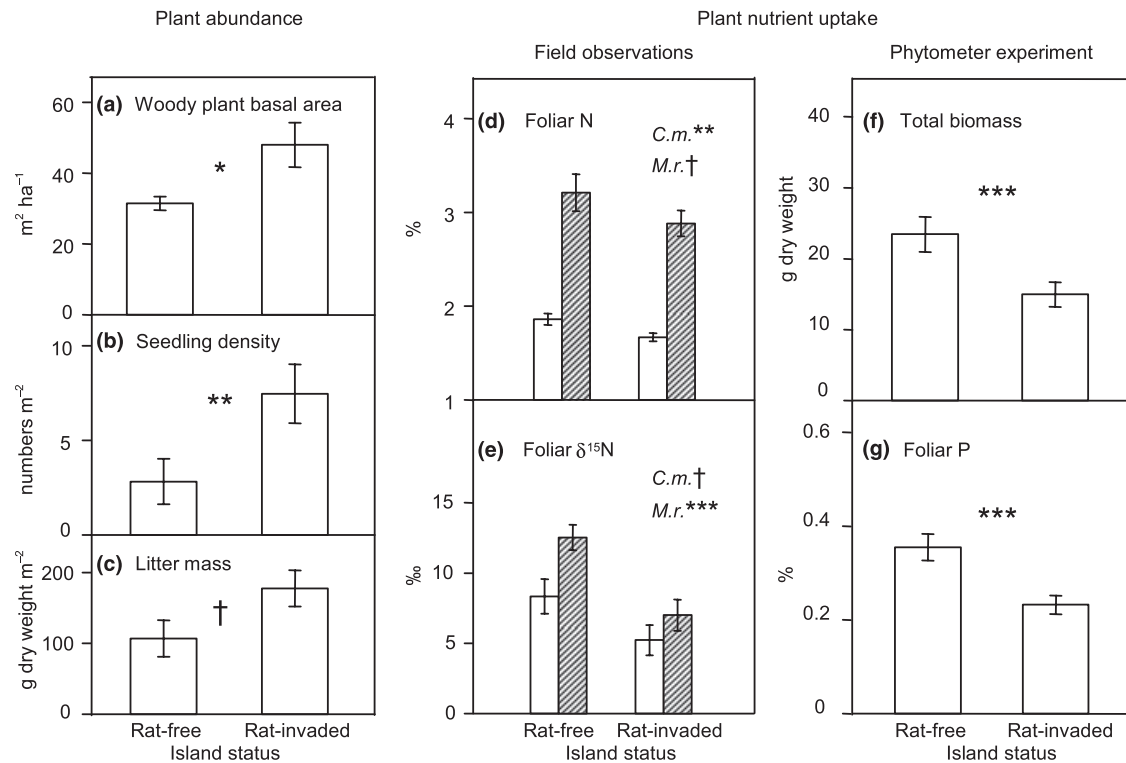


Figure 4 Response of plants to rat invasion of islands. Results are shown as means \pm SEM ($n = 9$ (7 for d and e) rat-free and nine rat-invaded islands). † $P < 0.10$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. *C.m.*, *Coprosma macrocarpa* (white bars). *M.r.*, *Meliclytus ramiflorus* (grey bars). Results for *Entelea arborescens* are presented in f and g (see Table S3 for other species).

the ecological landscape. What made this integration possible was the use of large-scale island-specific biological invasions (Fukami & Wardle 2005). Through this integration, we have provided evidence that across-ecosystem trophic cascades can greatly affect aboveground-belowground interactions and, in doing so, serve as major ecosystem drivers. Local extinctions of island-nesting seabirds due to introduced rats and other exotic mammals are well-documented worldwide (Steadman 1995; Blackburn *et al.* 2004). Our results indicate that these human-caused introductions of predators have not only reduced seabird populations, but that their effects may have indirectly influenced a variety of other organisms both above and below ground, ultimately resulting in wholesale changes in the functioning of the island ecosystems.

ACKNOWLEDGEMENTS

For permission to work on the islands they own, we thank the following iwi: Ngāti Hako, Ngāti Hei, Ngāti Manuhiri, Ngāti Paoa, Ngāti Puu, Ngāti Rehua, and Ngātiwai, as well as the Aldermen Islands Trust, John McCallum, Bryce Rope, and the Neureuter family. We thank the New Zealand Department of Conservation for facilitating our visits to the

islands they administer. We also thank Larry Burrows, Ewen Cameron, Laura Fagan, Steve Ferriss, Aaron Hoffman, Holly Jones, Brian Karl, Rau Kirikiri, Nora Leipner, Phil Lyver, Richard Parrish, Gaye Rattray, James Russell and Dan Uliassi for assistance, and Tom DeLuca, Lin Jiang, Micael Jonsson, Tadashi Miyashita, Duane Peltzer, Dan Simberloff, Wim van der Putten and three anonymous reviewers for comments. This study was supported by the Marsden Fund of the Royal Society of New Zealand, the US National Science Foundation (DEB-0317196), the New Zealand Department of Conservation, and the Japan Society for the Promotion of Science.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

Table S1 Islands used in this study.

Table S2 Effect of rat invasion, soil depth, and their interaction on belowground trophic groups.

Table S3 Results of phytometer experiments.

This material is available as part of the online article from: <http://www.blackwell-synergy.com/doi/full/10.1111/j.1461-0248.2006.00983.x>

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Editor, Michael Hochberg

Manuscript received 7 August 2006

First decision made 4 September 2006

Manuscript accepted 14 September 2006