

Direct and indirect effects of rats: does rat eradication restore ecosystem functioning of New Zealand seabird islands?

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Abstract Introduced rats (*Rattus* spp.) can affect island vegetation structure and ecosystem functioning, both directly and indirectly (through the reduction of seabird populations). The extent to which structure and function of islands where rats have been eradicated will converge on uninvaded islands remains unclear. We compared three groups of islands in New Zealand: islands never invaded by rats, islands with rats, and islands on which rats have been

controlled. Differences between island groups in soil and leaf chemistry and leaf production were largely explained by burrow densities. Community structure of woody seedlings differed by rat history and burrow density. Plots on islands with high seabird densities had the most non-native plant species. Since most impacts of rats were mediated through seabird density, the removal of rats without seabird recolonization is unlikely to result in a reversal of these processes. Even if seabirds return, a novel plant community may emerge.

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Introduction

Humans have introduced rats (*Rattus* spp.; Rodentia: Muridae) to islands across the globe, suppressing or eliminating populations of native seabirds (e.g. Atkinson 1985; Blackburn et al. 2004; Jones et al. 2008), reptiles (e.g. Whitaker 1973; Towns and Daugherty 1994; Cree et al. 1995), large invertebrates (e.g. Ramsey 1978; Bremner et al. 1984), and mammals (e.g. Burbidge and Manly 2002) as a result of predation by rats. In the past decade the rate at which three rat species (*R. rattus*, *R. norvegicus* and *R. exulans*) have been eradicated from islands has greatly accelerated. For example, a recent review reported 332 successful rodent eradications from 284

islands covering a total of 47,628 ha (Howald et al. 2007). Many eradication campaigns are followed by re-introductions of native species. For example, a New Zealand Department of Conservation database of translocations covering years through 1998 lists 415 events, including 43 bird species, three invertebrate species, and five lizard species (McHalick 1998). Populations of some elements of the native biota (primarily sea and land birds, but sometimes mammals, reptiles or invertebrates) are often carefully monitored following rat eradication (e.g. Gaze 2001; Graham and Veitch 2002; Pascal et al. 2005; Sinclair et al. 2005; Smith et al. 2006).

Our understanding of how the eradication of rats from islands affects island functioning, including vegetation dynamics and ecosystem processes, lags behind our knowledge of how to remove invasive rats. However, knowledge of these effects of rat removal may be particularly important for islands that host large colonies of nesting seabirds (e.g. Sphenisciformes, Procellariiformes, Pelecaniformes, and Charadriiformes). Species in these groups frequently act as important ecosystem drivers in the absence of rats. These birds feed at sea but nest on land, often at very high densities (Marchant and Higgins 1990; Furness 1991). Thus, seabirds “subsidize” terrestrial plant and animal communities (terrestrial birds, arthropods, reptiles, and marsupials) as well as surrounding intertidal communities with marine nutrients. As a result, there can be larger populations in the presence of seabirds than is possible in their absence (e.g. Polis and Hurd 1996; Anderson and Wait 2001; Markwell and Daugherty 2002; Wolfe et al. 2004). The introduction of rats has resulted in large reductions or elimination of seabird populations from hundreds of islands, but the subsequent eradication of rats from some of these islands has not necessarily resulted in the immediate return of seabird colonies (Gaze 2000; Miskelly and Taylor 2004). Yet native animals are sometimes reintroduced before seabird colonies reestablish. For example, the terrestrial reptile *Sphenodon punctatus*, which benefits from seabirds and their burrows (Newman 1987), was released onto islands with little or no seabird recovery (Gaze 2001). Although the removal of rats prevents further negative impacts of rats on native species, it is unclear whether other characteristics of seabird islands will be restored that may be critical to the

recovery of native populations, including reintroduced species. To understand which processes are restored following the eradication of rats from seabird islands (in the absence of return of seabird populations), we need to know the extent to which the impacts of rats on island functioning are direct and thus potentially reversible once rats are eliminated, and to what extent they are indirect (via seabird populations in this case) and require the return of seabird populations. There is much anecdotal evidence suggesting that rat impacts via seabirds on aspects of island functioning such as nutrient cycling or secondary productivity are substantial, but no studies have aimed to specifically answer this question.

We used data from 21 islands located off the coast of the North Island of New Zealand to evaluate impacts of rats on four sets of variables related to plant community structure and ecosystem processes. Previous publications on this system have addressed differences in vegetation structure and ecosystem properties between islands with and without seabird colonies (Fukami et al. 2006; Wardle et al. 2007), but they have not distinguished between those impacts of rats that are a function of changes in seabird density (referred to as “indirect impacts” in this paper) and those that are not (referred to as “direct effects”). We compared groups of islands with three different rat histories (Table 1): islands on which rats have never been present (UNINVADED islands), islands on which rats are currently present (INVADED islands) and islands on which rats have been eradicated or repeatedly controlled (MANAGED islands). Two alternative hypotheses were tested: (1) direct effects of rats are large and primarily responsible for differences between INVADED and UNINVADED islands in vegetation and ecosystem processes. This would result in a reversal of most invasion impacts once rats are removed; (2) indirect effects of rats via alterations in seabird populations are large and primarily responsible for differences between INVADED and UNINVADED islands. This would result in little change following the removal of rats unless seabird colonies recover.

To test these hypotheses we focused on four sets of variables that might show responses over the time periods for which rats have been eradicated on some of these islands (2–20 years):

Table 1 Location and characteristics of islands used in this study sorted by rat history and seabird density

Rat history	Seabird status	Seabird densities	Island	Lat (°S)	Long (°E)	Area (ha)	Temp/RH June	Temp/RH January	Canopy cover (%)	Rat species (date eradicated)
Uninvaded	Present	101 (101.5)	Green	36.64	175.85	2.5	13.8/93	19.5/94	69	None
Uninvaded	Present	85 (52)	Middle	36.60	175.84	13.5	NA	NA	88	None
Uninvaded	Present	38	Archway	35.49	174.74	6.3	13.8/89	17.3/NA	87	None
Uninvaded	Present	32.5 (16)	Tawhiti Rahi	35.45	174.71	158.2	12.9/98	17.2/98	88	None
Uninvaded	Present	22.5 (14.5)	Ruamāhuanui	36.95	176.09	32.4	12.9/87	18.7/85	86	None
Uninvaded	Present	18 (12.5)	Aorangi	35.48	174.72	107.1	13.5/95	17.6/64	91	None
Uninvaded	Present	15 (11)	Ruamāhuaiti	36.97	176.06	25.5	12.9/91	18.2/95	86	None
Uninvaded	Present	13 (19)	Aorangaia	35.48	174.71	5.6	13.6/80	18.7/71	90	None
Uninvaded	Present	3.5	Ohinauiti	36.71	175.88	5.9	NA	NA	86	None
Managed	Present	14 (15)	Whenuakura*	37.22	175.89	3	NA	NA	87	Rn (1985)
Managed	Present	8 (6.5)	Otata	36.41	174.58	15	13.0/96	17.9/96	82	Rn (1987, 1991, 2002)
Managed	Absent	0 (4.25)	Motuhoropapa	36.41	174.57	8.6	13.0/95	18.3/95	88	Rn (1987, 1991, 2002)
Managed	Absent	0 (0.25)	Te Haupa*	36.51	174.74	6	NA	NA	75	Rn (1989)
Managed	Absent	0	Motutapere	36.78	175.4	45.6	12.1/96	15.8/87	92	Rn (1996; reinv; M)
Invaded	Present	5 (3)	Motueka	36.82	175.80	6.2	13.0/91	18.2/70	90	Rn
Invaded	Absent	1 (0.33)	Aiguilles	36.03	175.39	72.7	12.9/96	17.5/78	86	Rr
Invaded	Absent	0.5 (1.25)	Hauturu	37.21	175.89	10.3	11.4/95	17.2/85	86	Rn
Invaded	Absent	0.5 (0.33)	Goat	36.26	174.80	13.4	12.9/94	17.7/91	83	Rr
Invaded	Absent	0 (0)	Motukaramarama	36.68	175.37	10.1	13.0/95	18.7/69	91	Rn
Invaded	Absent	0 (0)	Motuoruhi	36.73	175.4	58.0	12.7/96	18.3/93	91	Rr or Rn (M)
Invaded	Absent	0 (0)	Pakihi	36.54	175.10	110	11.8/95	17.11/NA	83	Rn

Seabird density is the mean number of burrow entrances for two 100 m² plots per island; numbers in parentheses include values for additional plots established (where available). Temperature means are in °C and RH is relative humidity in %; values are for June 2004 and January 2005. Abbreviations for rat species: Rn, *Rattus norvegicus*; Rr, *Rattus rattus*. “M” indicates the presence of mustelids; ‘reinv’ indicates reinvaded. Islands with * were added in 2005

1. *Soil chemistry, soil moisture, and light environment*: The presence of burrow nesting seabirds can have large impacts on soil structure and chemistry (e.g. Blakemore and Gibbs 1968; Furness 1991; Bancroft et al. 2005a) including on islands in our study system (Fukami et al. 2006), where the dominant seabird species are burrow nesters. In turn, these variables are likely to affect plant productivity, seedling survival, and invertebrate populations.
2. *Tree foliar characteristics*: Plant foliar chemistry differs between islands with dense seabird populations and those without (e.g. Wainwright et al. 1998; Anderson and Polis 1999; Fukami et al. 2006), and we expected plant foliar characteristics to be strongly affected by seabird density. Variables such as leaf nutrient content and turnover rates are likely to reflect the levels of nutrients available to plants as well as food availability and quality for herbivores.
3. *Community structure of woody seedlings*: Changes in the density and diversity of the woody seedlings following rat eradication may foreshadow changes in the tree community. Vegetation in seabird colonies is often very different from that away from seabird colonies, likely as a result of trampling and nutrient deposition (e.g. Gillham 1956b; Wait et al. 2005; Bancroft et al. 2005b). Rats may have additional direct impacts on this community through seed predation and herbivory on seedlings (e.g. Allen et al. 1994; Delgado Garcia 2000; Campbell and Atkinson 2002; McConkey et al. 2003; Smith et al. 2006). Rats can also reduce populations of seed dispersers (Traveset and Riera 2005) and large herbivorous invertebrates (Ramsey 1978), potentially influencing recruitment and seedling growth of some species.
4. *Invasion by non-native plants*: If islands with different rat histories also differ in their susceptibility to invasion by non-native plants, this may result in diverging long-term successional trajectories. For example, islands on which rats have been eradicated could be more susceptible to invasion by non-native plants, as they lack both seabird-induced disturbances and omnivorous rats. Alternatively, high levels of disturbance by seabirds may favour ruderal species (Maesako 1991; Vidal et al. 2000), and many non-native species are ruderal (D'Antonio et al. 1999).

Results of this study will indicate how important the re-establishment of seabird populations is likely to be for the long-term restoration of vegetation composition and ecosystem processes on these islands.

Methods

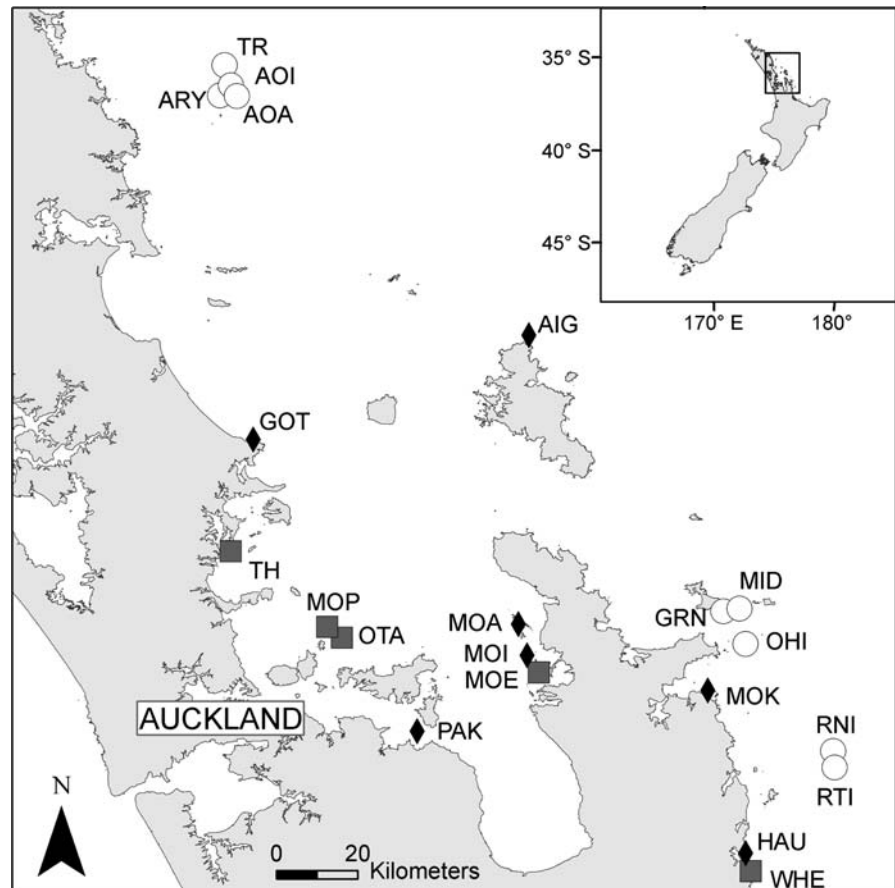
Study sites

Twenty-one islands located off the warm temperate North-East coast of the North Island of New Zealand (Table 1; Fig. 1) were selected based on rat history, size (similar ranges for each rat history), and the presence of well-developed multi-species secondary forest. For purposes of this paper, we define a *MANAGED* island as one on which active attempts at rat eradication have taken place (whether successful or not), although we note that in some cases other invasive predators (e.g. mustelids on Motuoruhi) may also have resulted in low rat numbers.

Generally, *UNINVADED* islands have substantial seabird populations while the other two groups of islands do not (Table 1), resulting in partial confounding of rat history and seabird density. However, although we lack invaded or managed islands with very high seabird densities, there is significant overlap in burrow densities between *UNINVADED* and *MANAGED* islands as well as between *MANAGED* and *INVADED* islands. The most abundant seabird species were *Pelecanoides urinatrix* (diving petrel, on Green and Middle), *Puffinus bulleri* (Buller's shearwater, on Archway, Aorangaia, Aorangi, and Tawhiti Rahi), *Pterodroma macroptera* (grey-faced petrel, on Ruamāhuaiti, Ruamāhuanui, Whenuakura, Otata, and Motueka), and *Pelagodroma marina* (white-faced storm petrel, on Ohinauiti).

Most islands have experienced some human habitation in the past but none are currently occupied. There were no significant differences in mean latitude, longitude, island size or distance to the mainland between islands with or without seabirds, or with different rat histories ($P > 0.3$ for all except latitude, where $P = 0.15$ for rat history and $P = 0.13$ for seabird presence). In the present study, all but two islands were visited between 10 February and 17 April 2004, and all islands were visited between 25 January and 19 April 2005 and between 15 February and 25

Fig. 1 Location of islands. *Black diamonds* represent *INVADED* islands, *grey squares* represent *MANAGED* islands, and *white circles* represent *UNINVADED* islands. Abbreviations are as follows: *AIG* Aiguilles; *AOA* Aorangia; *AOI* Aorangi; *ARY* Archway; *GRN* Green; *GOT* Goat; *HAU* Hauturu; *MID* Middle; *MOA* Motukaramarama; *MOE* Motutapare; *MOI* Motuoruhi; *MOP* Motuoropapa; *MOK* Motueka; *OHI* Ohinauiti; *OTA* Otata; *PAK* Pakihi; *RNI* Ruamāhuanui; *RTI* Ruamāhuaiti; *TH* Te Haupa; *TR* Tawhiti Rahi; *WHE* Whenuakura. Island details can be found in Table 1



March 2006. Quantitative Sorenson indices (Magurran 1988) for the three island categories based on mean stem densities for each woody species were as follows: *INVADED* and *MANAGED* = 0.618; *INVADED* and *UNINVADED* = 0.609; *MANAGED* and *UNINVADED* = 0.481. Thus *INVADED* islands were compositionally similar to both *MANAGED* and *UNINVADED* islands, but *MANAGED* islands were less compositionally similar to *UNINVADED* islands.

For all plots we obtained an index of seabird density by counting burrow entrances in 100 m² plots on each island (Table 1). Burrow densities on uninhabited islands averaged 29.8 burrow per m² (range = 3.5–101); given the high temporal and spatial variation in rat populations and severe logistical constraints inherent in visiting 21 islands, it was not possible to obtain a density estimate of rat populations. Our rat presence classifications are based on the knowledge of local conservation officers and our observance of signs of rat activity (e.g.

damaged seeds). On one *MANAGED* island (Te Haupa) and two *INVADED* islands (Hauturu and Pakihi) mice (*Mus musculus*) were also present.

Measurements

Forests on all islands in the study are undergoing secondary succession following past human disturbance, especially fire, most recently <50 years ago (Atkinson 2004). Most measurements were conducted in 10-m × 10-m plots located the most mature secondary forests that occurred on each island, avoiding successions dominated by *Metrosideros excelsa* (Fukami et al. 2006). In 2004, we established two haphazardly selected plots on islands without seabirds, and two plots on seabird colonies on islands with seabirds. In 2005, we added two additional plots in order to increase the range of seabird densities represented within each island: on seabird islands this resulted in the selection of two

areas with relatively low burrow densities (Table 1). On very small islands it was not always possible. On all islands we maximized variation in slope and aspect between plots where possible.

Soil samples (down to 30 cm) were collected from one 0.5-m × 0.5-m subplot within each plot (for islands with seabirds, only from the two plots on seabird colonies) and analyzed for %N, %P, %C, Olsen P, and pH. In each plot 21 1-m² plots were randomly located and all woody seedlings identified. From these data we calculated number of species at two scales (the 1-m² quadrat scale and the 100-m² plot scale) and evenness (H'_{\max}/H' , where H' is the Shannon–Weiner diversity index) at the 100 m² scale. Evenness values can range from zero to one (maximum evenness). In seven 1-m² quadrats per plot we measured soil temperature (at 5 cm depth), soil moisture (using a Delta-T thetprobe), canopy cover (using a spherical densiometer, Forest Densimeters, Bartlesville, OK) and litter weight (g dry weight from a 0.1 m² area). All plant species were identified in each of four vertical strata (0–0.3 m, 0.3–2 m, 2–5 m, 5–12 m, 12–25 m), and were classified as “native” or “non-native” based on the Flora of New Zealand (<http://nzflora.landcareresearch.co.nz/>). We report both the number of species per island and the number of records (sum of occurrences in all strata for two plots per island; non-native species occurred only in the lowest two strata).

We sampled six evergreen trees from these islands: *Coprosma macrocarpa* subsp. *minor* (Rubiaceae), *Corynocarpus laevigatus* (Corynocarpaceae), *Melicope ternata* (Rutaceae), *Macropiper excelsum* s.l. (Piperaceae), *Melicytus ramiflorus* (Violaceae), and *Planchonella costata* (Sapotaceae). These species were found on most (55–90%) of the islands. For each species we sampled up to ten individuals per island; where possible plants from within the 100 m² plots were used, but in most cases randomly selected individuals were added to obtain the desired sample size. From each tree the outermost three leaves (or, for *M. ternata*, leaflets) on each of three branches at a height of 1–2.5 m were collected (nine leaves or leaflets per plant). To examine changes in leaf morphology and chemistry we obtained dry mass, leaf area, %N and %C (by Leco, Laboratory Equipment Corporation), %P and %K (semi-micro-Kjeldahl method, Blakemore et al. 1987), condensed tannins (vanillin method, Broadhurst et al. 1978), and

total phenolics (Price and Butler 1977). To estimate rates of leaf turnover and productivity (as leaves produced per unit of stem diameter) in 2005 we selected four branches on up to ten randomly selected individuals per species. Stem diameter was measured and all leaves distal to that point on the branch were marked with fabric paint. In 2006 these plants were relocated, marked and unmarked leaves were counted, and stem diameter re-measured. Leaf annual turnover was calculated as the proportion of leaves that were lost between sampling dates (~1 year apart). Since number of days between sampling dates was not identical for all islands, we also calculated the proportion of leaves surviving on a per-day basis, but this did not change any of the results so they are not presented here. We calculated two additional variables we expected to be correlated (within a species) with productivity: the relative change in leaf numbers between years (number of leaves on the stem in 2006/number of leaves on the stem in 2005), and the change in the number of leaves per mm of stem diameter [(number of leaves in 2006 – number of leaves in 2005)/stem diameter].

Analyses

All analyses were performed in SAS (version 9.1; SAS Institute, Cary, NC, USA). Individual islands served as the units of replication; means per island were used for analyses unless indicated otherwise.

We used three different approaches to examine the relative importance of direct versus indirect impacts, and predict the likelihood that islands will return to a “pre-rat” state:

1. We compared the mean values of vegetation and soil variables for islands with the three different rat histories. If effects of rats are primarily direct, then we would expect the largest differences between *INVADED* and *UNINVADED* islands, with similar values for *MANAGED* and *UNINVADED* islands (for variables that respond quickly to rat removal) or values for *MANAGED* islands that are between those for *INVADED* and *UNINVADED* islands (for variables that change more slowly). If effects of rats are primarily indirect, then we would expect large differences between *UNINVADED* islands (which have high mean burrow densities) and the other two categories (which have low

mean burrow densities), but similar values for *UNINVADED* and *MANAGED* islands. Differences in means between the three rat histories were examined by ANOVA followed by contrasts between rat histories.

2. We examined the extent to which rat history could explain variation in vegetation and soil variables after seabird density effects had been accounted for. If rat effects are primarily indirect, we would expect any differences between rat histories to be explained primarily or entirely by differences in burrow densities. To determine the effects of rat history after accounting for seabird density we ran a hierarchical (Type I) ANCOVA including the log₁₀ of the seabird burrow density (number of burrow entrances in each 100 m² plot) and rat history. The burrow density was based on the plots in which the data were obtained, or for variables not directly associated with plots, on all data available.
3. For those variables for which we had data for all five *MANAGED* islands, we examined the extent to which time since eradication could explain vegetation and soil variables. If rat effects are primarily indirect, we would not expect time since eradication to correlate with the variables investigated. In contrast, if *MANAGED* islands follow a different successional trajectory than

either of the other two categories, we would expect time since eradication to correlate with the variables investigated, but no indication that long-term eradication will result in convergence with values for *UNINVADED* islands. Relationships between time since start of rat control (time between year in which control started and 2004) and response variables were examined by simple regression. We could not perform this analysis for soil chemistry data (we had values for only three *MANAGED* islands) or for tree data (no single tree species was present on all five *MANAGED* islands)

Results

Burrow densities

Burrow densities differed between rat histories (values based on all plots): *UNINVADED* islands had a mean of 29.7 ± 10.3 burrow per 100 m² plot, significantly more than *MANAGED* islands (5.2 ± 4.4 burrows/100 m², $F_{(1,18)} = 4.51, P = 0.048$) or *INVADED* islands (0.7 ± 0.4 burrow/100 m², $F_{(1,18)} = 7.74, P = 0.012$), although those latter two categories did not differ significantly from each other ($F_{(1,18)} = 0.14, P = 0.72$).

Table 2 Results of analyses for direct and indirect rat effects for soil and environmental variables

Variable	Rat history			<i>F</i>	<i>P</i>	Burrow density	<i>R</i> ²	<i>F</i>	<i>P</i>	Rat history after burrow density	<i>F</i>	<i>P</i>
	<i>U</i>	<i>M</i>	<i>I</i>									
Soil temperature (°C)	19.1 ^{ab}	22.6 ^a	16.8 ^b	2.64	0.099	–	0.06	1.06	NS	–	2.60	NS
Soil moisture (%)	10.6	11.9	14.0	1.28	NS	Negative	0.20	4.78	0.042	–	0.09	NS
Soil pH	5.1^a	6.9^b	6.7^b	8.08	0.004	Negative	0.66	30.12	<0.001	–	0.15	NS
Soil (%C)	11.1^a	5.3^{ab}	4.9^b	4.50	0.028	Positive	0.37	9.18	0.008	–	0.28	NS
Soil (%N)	0.92^a	0.45^b	0.40^b	5.53	0.015	Positive	0.41	10.89	0.005	–	0.43	NS
C:N ratio	12.0	11.7	12.43	0.71	NS	–	0.00	0.00	NS	–	1.05	NS
Soil total P (%)	0.46 ^a	0.18 ^b	0.11 ^b	2.79	0.093	Positive	0.26	5.47	0.034	–	0.18	NS
Soil Olsen P	237 ^a	57 ^{ab}	37 ^b	3.20	0.068	Positive	0.49	14.77	0.002	–	0.25	NS
Litter mass (g/m ²)	17.9	23.3	17.0	0.88	NS	–	0.02	0.40	NS	–	1.16	NS
Canopy cover (%)	19.2	16.1	12.3	1.20	NS	Negative	0.23	5.73	0.027	–	0.12	NS

Values are means per rat history (*U* *UNINVADED*; *I* *INVADED*; *M* *MANAGED*) based on mean values per island. Comparison of rat histories was by ANOVA followed by contrasts between rat histories; significant differences (bold text) at *P* = 0.05 are indicated by different letters. Effects of burrow density and rat history after burrow density were evaluated using an ANCOVA with burrow density entered prior to rat history. “NS” indicates a *P* value >0.1. *N* = 21 for soil temperature, moisture, litter weight and canopy cover, and *N* = 19 for soil chemistry variables

Soil and environmental variables

Soil chemistry

Soil pH, %C, %N, total P, and Olsen P, differed according to islands' rat history, but not soil C:N ratio (Table 2). All significant differences were between the UNINVADED islands and one or both of the other categories, which did not differ from each other. Furthermore, in all but one case, differences in rat history effects could be attributed entirely to differences in seabird burrow density (Fig. 2a–c); in no case did rat history explain any additional variation beyond this. Thus, seabird density can explain differences in soil chemical characteristics but there is no evidence for direct effects of rats.

Environmental variables

Only soil temperature showed marginally significant differences according to islands' rat history; soil moisture, litter weight and canopy cover showed no differences (Table 2). However, seabird density was negatively correlated with soil moisture, primarily because high values were limited to islands with no burrows (Fig. 2d). In addition, there appeared to be a relationship between canopy cover and burrow density (Fig. 2e), but this relationship was driven entirely by one outlier; when this was removed, there was no relationship ($F_{(1,18)} = 0.77$, $P = 0.45$). Furthermore, although there was no significant negative relationship between litter mass and burrow density, closer inspection of the data on a per-plot basis (Fig. 2f) suggests that this is because islands with few burrows can have either low or high litter mass, but islands with many burrows (>20) generally have low litter mass. When we examined the five MANAGED islands only, time since eradication did not explain any of the variation in physical variables ($P > 0.1$ for all).

Tree characteristics

Leaf morphology

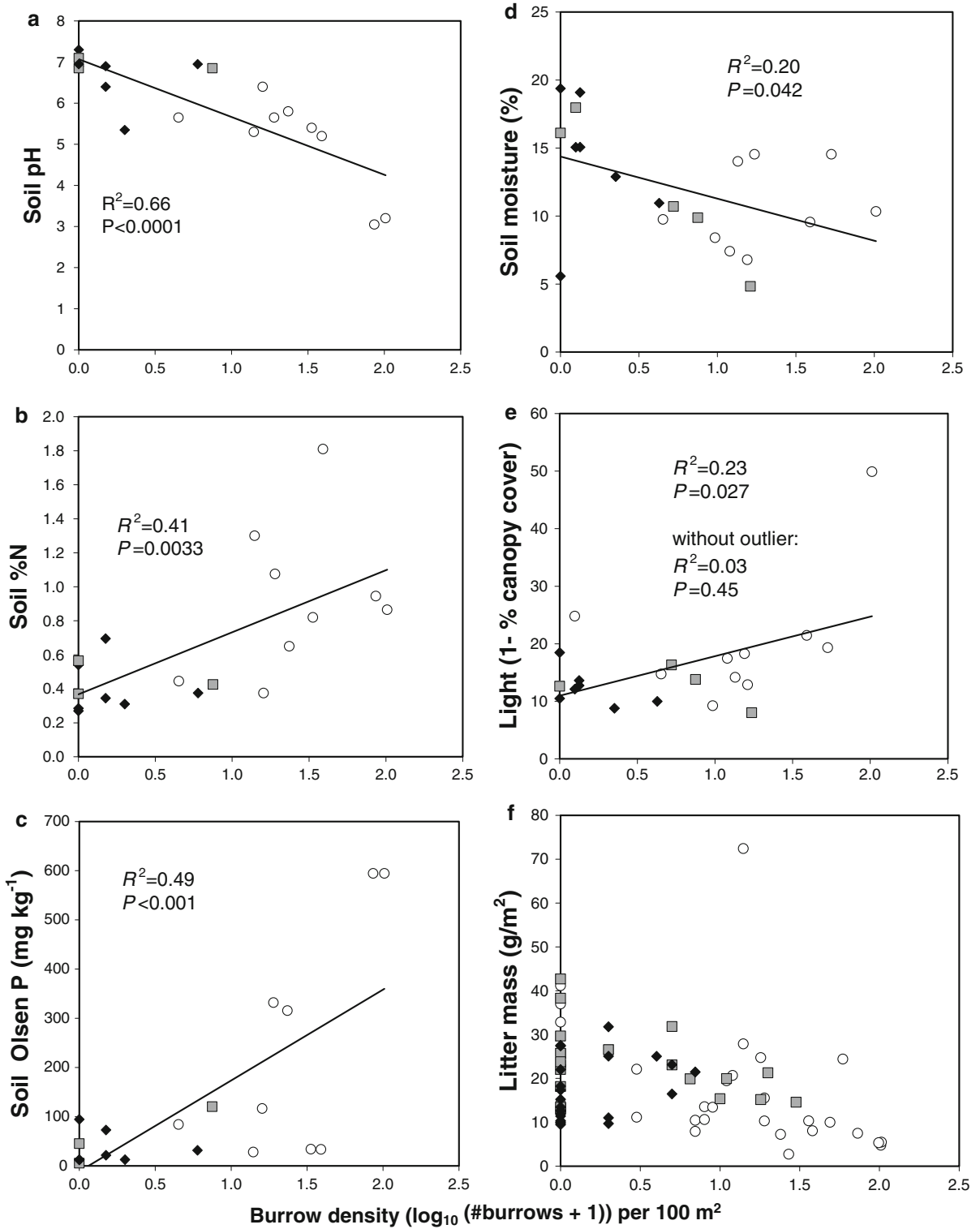
There were few differences between rat history categories in leaf morphological variables, and no evidence for intermediate values on MANAGED islands (Fig. 3; Table 3). There was no consistent pattern across species for leaf area (Fig. 3a). Leaf mass did

Fig. 2 Relationship between seabird burrow density and soil chemical or environmental characteristics. *Black diamonds* represent INVADED islands, *grey squares* represent MANAGED islands, and *white circles* represent UNINVADED islands. **a** Soil pH; **b** soil %N; **c** soil %; Olson P (mg kg^{-1}); **d** soil moisture (%); **e** canopy cover (%); **f** litter mass (g m^{-2} dry weight). All values are means per island across two plots (pH, %N, Olsen P) or four plots (canopy cover, soil moisture) except litter weight, which is presented on a means per-plot basis (see text for explanation). Because the number of plots per island used differed between the variables, mean burrow density for islands differs between panels

tend to be greater for plants on uninvaded islands than for the other two categories (significantly so for *C. macrocarpa* and *M. ramiflorus*; Fig. 3b), resulting in a general pattern of highest LMA on uninvaded islands (Fig. 3c). However, the LMA difference was significant for only one species (*M. ternata*, Table 3). Leaf morphology also did not show a consistent relationship with burrow density, and for the one significant relationship (a negative one for leaf mass in *M. ramiflorus*), rat history still explained variation after accounting for burrow density (Table 3). Thus, although there is evidence that rats directly affect leaf morphology for some species, there is little evidence that plants on MANAGED islands are more similar to rat-free islands than islands on which rats are still present.

Leaf chemistry

In contrast to the leaf morphology results, there were large differences between rat histories in tree leaf chemistry, particularly for %N (five of six tree species had significant differences), but also for %P (two species) and %K (two species) (Table 3; Fig. 4). In every case, %N was lower for INVADED than for UNINVADED islands, while the reverse was true for %K. However, there was no consistent pattern for MANAGED islands, which sometimes had the highest %N and sometimes the lowest. In all cases where there were significant differences between rat histories, seabird burrow density was strongly and positively related to %N or %K, but in about half the cases significant differences between rat history categories continued to exist after this was taken into account. In contrast, seabird burrow density did not explain differences in the foliar %P of *C. laevigatus* and *P. costata*, which were different according to rat history. Including a second-order regression term for the burrow density



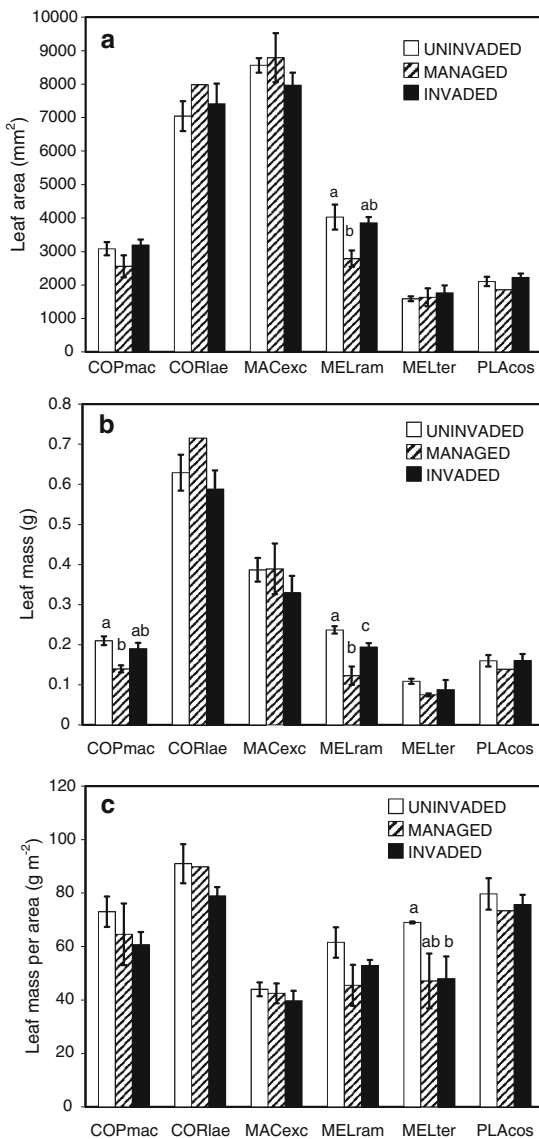


Fig. 3 Leaf morphology (mean \pm SEM) for six tree species by rat history. Values are based on means for individual leaves on each island. Abbreviations: COPmac *Coprosma macrocarpa*; CORlae *Corynocarpus laevigatus*; MACexc *Macropiper excelsum*; MELram *Melicactus ramiflorus*; MELter *Melicope ternata*; PLAcos *Planchonella costata*. For *C. laevigatus* and *P. costata*, the values for managed islands have no error bars because they are represented by only one island. **a** Leaf area (mm²); **b** leaf mass (g); **c** leaf mass per area (g m⁻²). Different letters indicate significant differences in means between rat histories ($P < 0.05$) in contrasts following ANOVA for the overall effect of rat history

(to account for non-linear relationships) sometimes improved the model but did not eliminate the significant rat history effects. Thus, although seabird density

explained much of the variation in leaf chemistry, it alone did not account for the rat history differences.

Leaf turnover and leaves per unit stem

No species showed significant differences in % annual turnover between rat histories ($P > 0.1$ for all). For *C. macrocarpa* and *M. ramiflorus* there were significant differences according to rat history for proportional change in leaf number between years (number of leaves in 2006 divided by number in 2005; Table 4). Both of these species plus *P. costata* also showed differences in number of leaves added per unit of stem diameter; in all cases, INVADED islands had the lowest values (Table 4). There was a positive relationship between proportional change in leaf number and burrow density for *C. macrocarpa*, but after this was included in the model, rat histories continued to differ. There was also a significant positive relationship between change in leaf number per unit of stem diameter for *C. macrocarpa* and *P. costata*, and in both cases this accounted for the significant differences between rat histories (Table 4). Thus we have some evidence for both direct and indirect impacts of rats on leaf production for some species.

Woody plant community structure

MANAGED islands had the highest seedling densities, but lower numbers of species than did the INVADED islands. MANAGED islands had much lower evenness than the other two groups of islands (Fig. 5, Table 5). Seedling species density (# species at the 1-m² and 100 m² scales) and evenness, but not seedling density (1-m² scale), were explained by seabird burrow density. However, significant differences remained after accounting for burrow density, with the largest differences between MANAGED and UNINVADED islands. Thus for seedling structure we have evidence for both direct and indirect effects of rats.

Plant species density (# species at the 100-m² scale) was negatively related to time since first eradication ($F_{(1,4)} = 28.5$, $P = 0.013$), and the pattern suggests that values for this variable on MANAGED islands are becoming more similar to that of UNINVADED islands over time (Fig. 6). However, seedling density and evenness were not related to time since eradication ($P > 0.1$).

Table 3 Results of analyses for direct and indirect rat effects for leaf characteristics and of six common tree species

Variable	Species	Rat history	F	P	Burrow density	R ²	F	P	Rat history after burrow density	F	P
Leaf area	<i>M. ramiflorus</i>	U = I > M	3.22	0.07	-	0.01	0.12	NS	U > I ≥ M	3.18	0.07
Leaf mass	<i>C. macrocarpa</i>	U = I > M	5.36	0.019	Positive	0.19	3.54	0.082	U = I ≥ M	3.55	0.059
	<i>C. laevigatus</i>	-	0.51	NS	-	0.04	0.55	NS	U = M ≥ I	5.37	0.046
LMA	<i>M. ramiflorus</i>	U > I > M	17.08	<0.001	Negative	0.12	5.68	0.033	U > I > M	14.83	0.004
	<i>C. laevigatus</i>	-	0.30	NS	-	0.03	0.24	NS	U = M ≥ I	4.31	0.069
%N	<i>M. ternata</i>	U > I = M	3.85	0.062	Positive	0.32	4.89	0.06	-	-	NS
	<i>C. macrocarpa</i>	U > I = M	5.75	0.015	Positive	0.36	8.97	0.010	-	1.41	NS
%K	<i>C. laevigatus</i>	-	1.14	NS	Positive	0.42	10.9	0.016	I = M ≥ U	4.59	0.062
	<i>M. excelsum</i>	U = M ≥ I	2.97	0.098	Positive	0.70	10.89	0.009	-	0.26	NS
%P	<i>M. ramiflorus</i>	U = M > I	8.67	0.003	Positive	0.31	10.1	0.007	M = U ≥ I	4.23	0.039
	<i>M. ternata</i>	U > M = I	5.03	0.034	-	0.04	0.72	NS	M > I = U	5.81	0.028
%K	<i>P. costata</i>	U > M = I	5.06	0.067	Positive	0.36	6.54	0.031	-	1.29	NS
	<i>C. laevigatus</i>	I = U > M	4.20	0.063	-	0.14	2.99	NS	I ≥ U = M	5.68	0.041
%K	<i>P. costata</i>	U = I ≥ M	3.59	0.067	-	0.01	0.13	NS	U = I ≥ M	3.37	0.081
	<i>C. laevigatus</i>	I = M ≥ U	4.14	0.065	Positive	0.36	5.10	0.065	-	1.53	NS
Tannins	<i>M. excelsum</i>	M = I > M	10.89	0.003	Positive	0.36	10.39	0.010	I = M ≥ U	4.68	0.040
	<i>M. ramiflorus</i>	U = I ≥ M	2.78	0.096	-	0.30	1.75	NS	-	1.88	NS
Phenolics	<i>C. laevigatus</i>	-	0.70	NS	Positive	0.40	5.70	0.054	-	1.36	NS
	<i>M. ternata</i>	U = I ≥ M	6.56	0.031	Positive	0.28	4.23	0.073	-	1.30	NS

Values are means per rat history based on mean values per island for individual leaves or (for *M. ternata*) leaflets. Text in bold indicates significant differences or relationships at $P < 0.05$; NS indicates a P value > 0.1 . Data are given only for species with $P < 0.1$ for at least one test. Comparison of rat histories (U UNINVADED; I INVADED; M MANAGED) was by ANOVA followed by contrasts between rat histories. A “=” indicates no significant difference between adjacent values; a “>” indicates significant differences between adjacent values as well as between the highest and lowest values; “≥” indicates that the adjacent values do not differ but the highest and lowest ones do. Effects of burrow density (F , P and partial R^2 values) and rat history after burrow density (F , P) were evaluated using an ANCOVA with burrow density entered prior to rat history. N (number of islands) are as follows: *Coprosma macrocarpa* = 18; *Corynocarpus laevigatus* = 11; *Melicope ternata* = 14; *Melicopus ramiflorus* = 12; *Macropiper excelsum* = 14; *Planchonella costata* = 13. Note that for *C. laevigatus* and *P. costata* the MANAGED rat history was represented by only one island

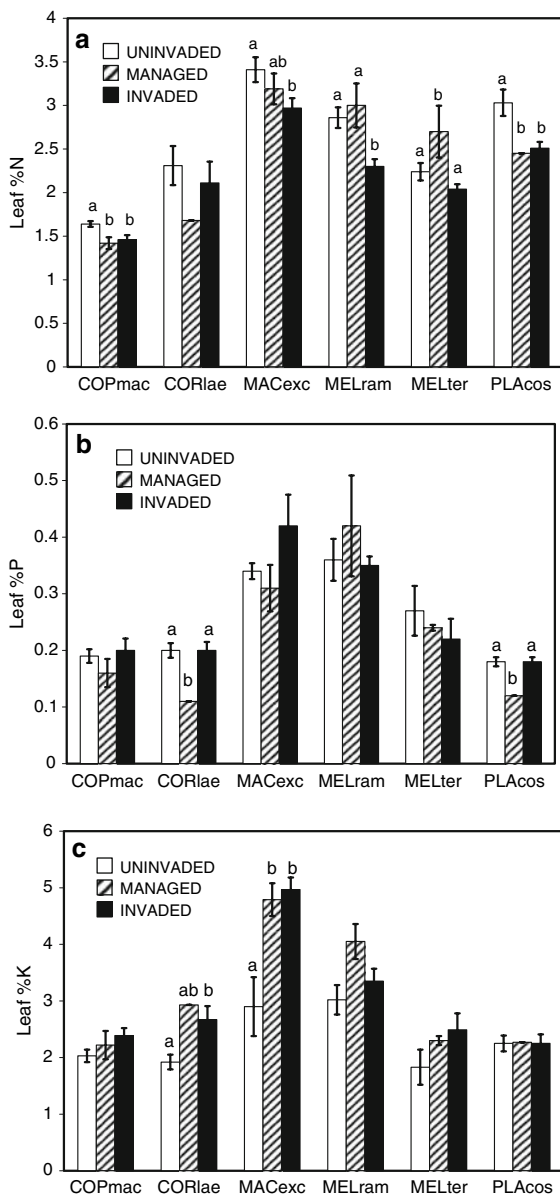


Fig. 4 Leaf macronutrient concentrations (mean \pm SEM) for six tree species by rat history. Abbreviations: COPmac = *Coprosma macrocarpa*; CORlae = *Corynocarpus laevigatus*; MACexc = *Macropiper excelsum*; MELram = *Melicytus ramiflorus*; MELter = *Melicope ternata*; PLAcos = *Planchonella costata*. For *C. laevigatus* and *P. costata*, the values for managed islands have no error bars because they are represented by only one island. **a** %N; **b** %P; **c** %K. Different letters indicate significant differences in means between rat histories ($P < 0.05$) in contrasts following ANOVA for the overall effect of rat history

($P > 0.3$ for both). There was no relationship between time since eradication and either variable for the MANAGED islands ($P > 0.3$ for both). Thus, differences between islands in terms of rat histories can be explained by seabird burrow densities.

Discussion

The well-known negative impacts of rats on seabird populations were reflected in the burrow densities for our three rat history groups: on average, burrow densities on INVADED islands were only 2% of those on UNINVADED islands. Although burrow densities on MANAGED islands were higher than those on INVADED islands, they were still only 17% of those on UNINVADED islands. For UNINVADED islands, the values for burrow densities used here are likely to be higher than means for whole islands because two plots per island were placed on seabird colonies; nevertheless, it is clear that most UNINVADED islands contain substantial seabird populations, while most MANAGED or INVADED islands do not. Other studies have shown that recolonization by seabirds following extirpation may happen slowly, if at all (Gaze 2000; Miskelly and Taylor 2004; Parker et al. 2007). Our results support the notion that seabirds may not rapidly recolonize islands without active management: of our five MANAGED islands, four had some seabird nests located in the sampling plots, but only one (Whenuakura) had a colony of similar size to those on most UNINVADED islands, and that island supported a colony of grey-faced petrel (*Pterodroma macroptera gouldi*), a large seabird that may not have ever been entirely eradicated by rats (Imber et al. 2000).

Our results demonstrate that these changes in seabird densities associated with rat invasion are likely to result in strong indirect impacts of rats on vegetation dynamics and soil: for every type of

Non-native plants

Plots in forests on UNINVADED islands had a significantly greater number of non-native plant species and non-native species records (species per plot and tier height) than on INVADED or MANAGED islands (Fig. 7a). Both the number of species and the number of records increased with burrow density ($F_{(1,17)} = 4.95$, $P = 0.040$ and $F_{(1,17)} = 10.41$, $P = 0.005$ respectively; Fig. 7b), and rat history did not explain any variation after seabird burrow density was accounted for

Table 4 Results of analyses for direct and indirect rat effects on leaf production

Variable	Rat history			F	P	Burrow density	R ²	F	P	Rat history after burrow density	F	P
	U	M	I									
Leaves 2006:2005	1.56^a	1.82^a	0.96^b	5.96	0.02	Positive	0.39	8.48	0.017	M > U ≥ I	5.56	0.03
Δ leaf # mm ⁻¹	1.71 ^a	1.30 ^a	1.09 ^b	2.92	0.09	-	0.07	1.62	NS	U > M = I	5.33	0.02
	0.103^{ab}	0.190^a	-0.060^b	4.54	0.01	Positive	0.36	7.31	0.027	-	2.57	NS
	0.124 ^a	0.135 ^{ab}	0.002 ^b	2.95	0.06	-	0.06	1.95	NS	-	1.95	NS
	0.138^a	-0.016^b	-0.037^b	6.26	0.003	Positive	0.070	10.41	0.03	-	0.18	NS

U UNINVADED; I INVADED; M MANAGED. Text in bold indicates significant differences or relationships at $P < 0.05$. Values for rat histories are means for (1) the ratio of leaves in 2006–2005, and (2) the difference in leaf number (# in 2006 minus # in 2005) divided by the stem diameter in mm. Comparison of rat histories was by ANOVA followed by contrasts between rat histories. Effects of burrow density (F, P and partial R² values) and rat history after burrow density (F, P) were evaluated using an ANCOVA with burrow density entered prior to rat history; are reported. Data are given only for species with $P < 0.1$ for at least one test; “NS” indicates a P value > 0.1 . N (number of islands) are as follows: *Coprosma macrocarpa* = 18; *Melicetyis ramiflorus* = 12; *P. costata* = 13

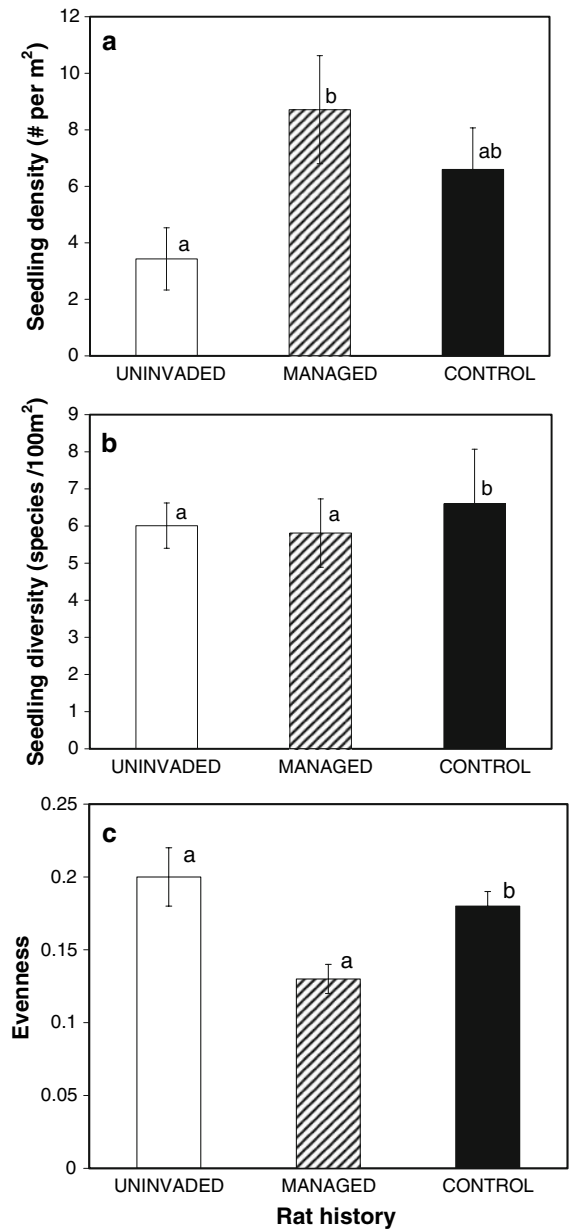


Fig. 5 Woody seedlings community characteristics (mean ± SEM) by rat history. **a** Density (# plants per 1-m² quadrat); **b** species richness (# species per 100 m²); **c** evenness. Different letters indicate significant differences in means between rat histories ($P < 0.05$)

variable examined there were at least some significant relationships with seabird burrow densities. The impacts of seabirds on soils are consistent with earlier studies that have demonstrated that seabird burrow density strongly affects soil pH and nutrient content, particularly %N, through transportation of nutrients

Table 5 Results of analyses for direct and indirect rat effects for seedling community variables

Variable	Rat history	<i>F</i>	<i>P</i>	Burrow density	<i>R</i> ²	<i>F</i>	<i>P</i>	Rat history after burrow density	<i>F</i>	<i>P</i>
Density(# ind. per m ²)	M = I > U	3.49	0.052	–	0.08	–	NS	–	2.36	NS
# Species (per 100 m ²)	I > M = U	5.14	0.017	Negative	0.39	14.37	0.002	–	2.53	NS
# Species (per m ²)	I > U = M	4.38	0.028	Negative	0.12	3.08	0.097	–	2.63	NS
Evenness	U = I > M	5.96	0.010	Positive	0.16	4.65	0.046	U > I > M	4.08	0.036

Text in bold indicates significant differences or relationships at $P < 0.05$; NS indicates a P -value > 0.1 . $N = 21$. U UNINVADED, I INVADED, M MANAGED. Comparison of rat histories was by ANOVA followed by contrasts between rat histories. A “=” indicates no significant difference between adjacent values; a “>” indicates significant differences between adjacent values as well as between the highest and lowest values. Effects of burrow density (F , P and partial R^2 values) and rat history after burrow density (F , P) were evaluated using an ANCOVA with burrow density entered prior to rat history. See Fig. 5 for mean values

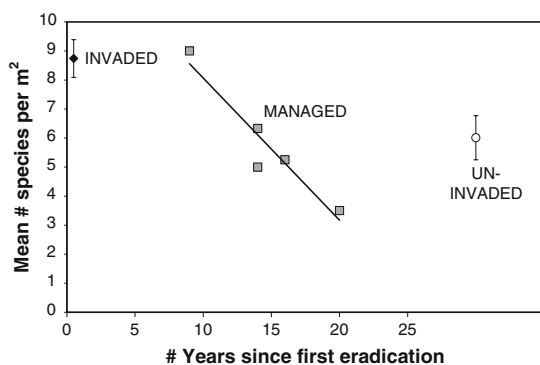


Fig. 6 Species richness of the woody seedling plotted against years since first eradication for managed plots. The additional values (black diamond and white circle) indicate the mean \pm SEM for the two other groups (INVADED and UNINVADED islands). Significant differences between means per category are provided in Table 4

from the ocean to the land (e.g. Ward 1961; Blakemore and Gibbs 1968; Furness 1991; Okazaki et al. 1993; Mulder and Keall 2001; Roberts et al. 2007). Effects of seabird density on leaf chemistry are also consistent with previous studies that point to evidence of increased rates of plant nutrient supply from the soil resulting from fertilization effects of seabirds (Wainwright et al. 1998; Anderson and Polis 1999).

In contrast to the strong and consistent effects of seabirds, only a few variables showed responses that could be attributed to direct effects of rats (i.e. differences between rat histories that could not be explained by effects of seabird density). The best evidence for direct impacts was for seedling community structure: MANAGED islands had particularly low evenness (dominance by only a few species) compared

with the other two island categories, and this could not be explained by seabird burrow density. Previous studies have established that rats selectively consume seeds and possibly seedlings (Delgado Garcia 2000; Campbell and Atkinson 1999, 2002; Meyer and Butaud 2008 this volume), and it seems likely that the species dominating the seedling community had particularly low rates of consumption by rats, possibly coupled with high longevity in the seed bank. However, it is unclear at this stage whether such differences in the seedling community will persist as this new cohort ages. Seedling species density (# species per 100 m²) was the only variable that could be explained by time since rat control was initiated, and this variable did appear to show convergence with values from UNINVADED islands so it is possible that the communities will become more similar over time. However, if these differences do persist, then the removal of rats may result in different (and simpler) tree communities than those found on either INVADED or UNINVADED islands. Finally, there may be direct impacts of rats on the seedling community that this community-level analysis could not identify. For example, *Streblus banksii* (Moraceae), a tree species known to be vulnerable to rats (Campbell and Atkinson 1999) was present on most UNINVADED islands but only one of the INVADED and none of the MANAGED islands (pers. obs). In the absence of a local seed source, regeneration of this species (and any others extirpated by rats) is likely to be a very slow process.

Although we did not expect to find direct effects of rat history on leaf morphology and chemistry of trees as opposed to indirect effects related to seabird burrow density, we found six instances where such effects were highly significant (and another five which were marginally significant; by chance we would expect

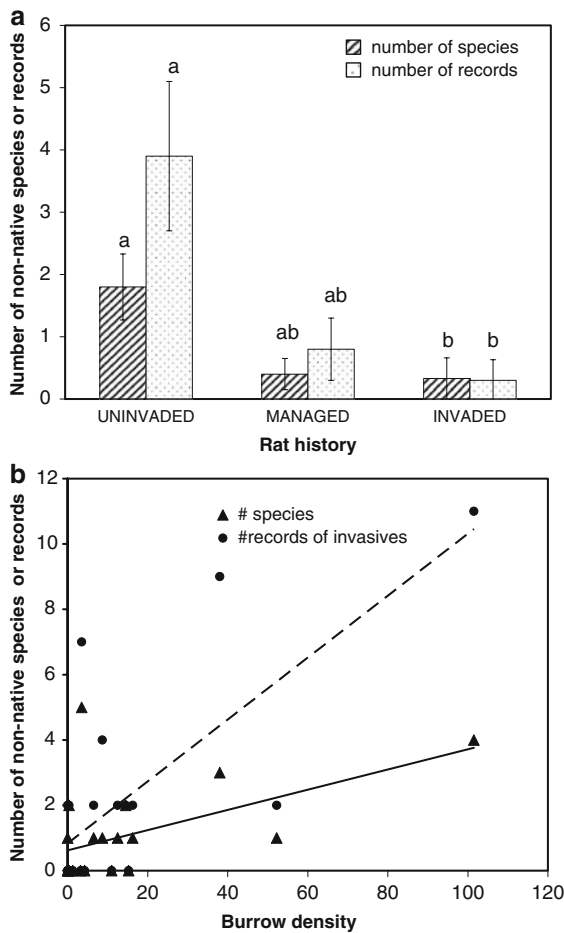


Fig. 7 Non-native plants by rat history and burrow density. **a** Mean (\pm SEM) cumulative number of species or records (sum of occurrences of non-native species in different strata) for two 100-m² plots. Different letters indicate significant differences in means between rat histories ($P < 0.05$); **b** number of species (solid line) or records (dashed line) plotted against seabird burrow density

approx. two at $\alpha = 0.05$ and four at $\alpha = 0.1$) These effects primarily involved rats directly influencing mean leaf mass and %N. The differences were not limited to one or two tree species, making it less likely that a small number of extreme species are driving the results. Similarly, there were differences between rat histories in leaf production (number of leaves in 2006 compared to the previous year) for two tree species that could not be explained entirely by burrow density but for which we do not have an explanation.

There is the potential for large and rapid changes in the plant communities on the UNINVADED islands: forests on islands which have never been invaded

by rats had the highest number of non-native plant species. This is particularly surprising because UNINVADED islands generally have severely restricted access and are visited by people less frequently than islands in the other two categories; those who do visit are required to take precautions designed to further reduce the accidental introduction of seeds. It should be kept in mind that only small total areas of islands were sampled; we do not know if the entire island flora differs among the three island categories in numbers or proportions of non-native plant species. The relationship between seabird density and numbers of non-native plant species also supports the contention that the presence of seabirds creates conditions that are particularly favourable for non-native ruderal plants (Ellis 2005). Numerous studies have found that invasive non-native plant species do best under high light and high nutrient regimes (factors generally associated with human disturbance, D'Antonio et al. 1999), and in our study high seabird burrow densities were correlated with both high nutrient levels and low canopy cover (high light availability). On Mediterranean islands, high densities of yellow-legged gulls (*Larus michahellis*) were shown to favour establishment by ruderal, wind-dispersed species with small seeds, characteristics typical of many invasive plant species (Vidal et al. 2000). In New Zealand, a thin litter layer may favour invasive plants over native plants (McAlpine and Drake 2003), and seabird islands generally had little litter. In addition, seabirds may actively transport seeds within or between islands (Gillham 1956a; Nogales et al. 2001; Burger 2005). Although these results need to be confirmed by larger-scale studies specifically aimed at relating seabird densities (and possibly seabird species) to susceptibility to invasion by non-native plants, these preliminary results do suggest that these islands with dense seabird populations are particularly vulnerable to invasion by non-native plants, and that over the long-term this may result in very different plant communities from the current ones or from those on MANAGED or INVADED islands.

It is apparent that the reversal of the main human impact responsible for degradation of our islands (the introduction of rats) is by itself unlikely to result in restoration to an uninvaded state: although there are some direct effects of rats on vegetation structure, most of the impacts of rats are mediated through reduced seabird densities, and densities on MANAGED

islands are considerably lower, on average, than on UNINVADED islands. There is also little evidence that MANAGED islands as a group are becoming more similar to UNINVADED islands over time: with the exception of some soil chemistry variables, MANAGED islands were not usually intermediate between INVADED and UNINVADED islands, and the only response variable that showed a relationship with time since eradication was species richness.

Whether the return of seabirds in densities similar to those prior to invasion will result in restoration to a pre-invasion state is less clear. On the one hand, variables related to ecosystem processes such as soil physical and chemical properties (moisture, pH, %C, %N, %P, and Olsen P), leaf chemical characteristics (%N and %K), and, to a lesser extent, leaf productivity, do show strong positive relationships with seabird density. On the other hand, there are several indications that plant community composition on MANAGED islands may not converge to that of UNINVADED islands. First, the low plant diversity (dominance by a few plant species) of MANAGED islands may alter competitive interactions and, coupled with the extirpation of some tree species, result in long-lasting changes in vegetation composition. Second, the disturbance regimes imposed by seabird colonies may increase the vulnerability of MANAGED islands to invasion by or rapid expansion of populations of non-native plant species, an example of a “surprise effect” following eradication of an invasive alien species (Caut et al. 2008 this volume). If this occurs early on in the recovery process, when the vegetation is still quite different from that of UNINVADED islands, it may lead to different impacts than on UNINVADED islands. These situations could lead to successional trajectories of UNINVADED and MANAGED islands that do not converge. In this sense, UNINVADED and MANAGED islands may represent two alternative stable states (Scheffer and Carpenter 2003; Suding et al. 2004). In other words, MANAGED islands may remain different in community composition from UNINVADED islands even after rat eradication and seabird reintroduction. If so, restoration of MANAGED islands to the original uninvaded state may require additional management such as active introduction and removal of plant species. To further complicate matters, many seabird dominated islands are undergoing secondary succession following many years of human disturbance, including past fire and in some cases cultivation (Atkinson 2004). Hence

restoration of these islands is especially challenging: an original ecosystem state is difficult to define and the restoration goal is often a fuzzy and moving target, making it difficult to assess the success of restoration (Simberloff 1990).

Our results provide evidence that upon removal of rats from islands, seabird colonies need to be re-established if vegetation processes and ecosystem functioning are to be restored. Methods exist that increase the rate at which seabird colonies are established, such as translocation of nestlings and acoustic attraction (e.g. Kress 1983; Miskelly and Taylor 2004; Priddel et al. 2006), but they are not widely used. However, although seabird colony reestablishment may result in the restoration of many aspects of ecosystem functioning, differences in species composition compared to uninvaded islands may persist. Furthermore, the re-establishment of seabird colonies may make the islands more susceptible to invasions by non-native plants, thus making invasive plant monitoring programs particularly important. Without active management beyond rat eradication and encouragement of establishment of seabird populations, plant community composition on islands previously populated by rats may require a much longer time to converge, or in some cases may never converge, with that of islands that have never been invaded.

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