

Effects of invasive rats and burrowing seabirds on seeds and seedlings on New Zealand islands

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Abstract Rats (*Rattus rattus*, *Rattus norvegicus*, *Rattus exulans*) are important invaders on islands. They alter vegetation indirectly by preying on burrowing seabirds. These seabirds affect vegetation through nutrient inputs from sea to land and physical disturbance through trampling and burrowing. Rats also directly affect vegetation through consumption of seeds and seedlings. Seedling communities on northern New Zealand islands differ in composition and densities among islands which have never been invaded by rats, are currently invaded by rats, or from which rats have been eradicated. We conducted experimental investigations to determine the mechanisms driving these patterns. When the physical disturbance of seabirds was removed, in soils collected from islands and inside exclosures, seedling densities increased with seabird burrow density. For example, seedling densities inside exclosures were 10 times greater than those outside. Thus the negative effects of seabirds on seedlings, by trampling and

uprooting, overwhelm the potentially beneficial effects of high levels of seed germination, seedling emergence, and possibly seed production, which result from seed burial and nutrient additions. Potential seedling density was reduced on an island where rats were present, germination of seeds from soils of this island was approximately half that found on other islands, but on this island seedling density inside exclosures was 7 times the density outside. Although the total negative effects of seabirds and rats on seedling densities are similar (reduced seedling density), the differences in mechanisms and life stages affected result in very different filters on the plant community.

Keywords *Rattus rattus* · *Rattus norvegicus* · Seed · Seedling community · Filter effects

Introduction

Rats (*Rattus norvegicus*, *Rattus rattus*, *Rattus exulans*) have invaded more than 45 island groups worldwide (Atkinson 1985; Drake and Hunt 2009), where they have major impacts on plant populations, burrowing seabird populations, and thus entire island communities. When rats extirpate burrowing seabird colonies they curtail allochthonous inputs of nutrients and end the disturbance regime that burrowing seabirds impose.

Seabirds are abundant on many islands worldwide, where they are major drivers of ecosystem processes (Gillham 1956; Croll et al. 2005; Ellis 2005; Fukami et al. 2006). Seabirds transport nutrients from sea to land and their allochthonous inputs (guano, dead chicks, egg shells, and occasional dead adults) increase soil nitrogen, carbon, and phosphorus concentrations, but also soil acidity (Okazaki et al. 1993; Anderson and Polis 1999; Mulder and

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Keall 2001; Fukami et al. 2006; Roberts et al. 2007). Seabird inputs cascade through island systems affecting vegetation composition (Ellis 2005; Bancroft et al. 2005a) and productivity (Ellis 2005; Wait et al. 2005). Through trampling and burrowing, seabirds that nest in burrows (order Procellariiformes—prions, petrels, and shearwaters; order Charadriiformes—auks) cause physical disturbance to island ecosystems. These disturbances can bury seeds and litter, resulting in reduced litter aboveground (Fukami et al. 2006). Physical disturbance can also prevent seedling establishment (Maesako 1999; Roberts et al. 2007) and alter plant species composition (Ellis 2005). Burrowing seabirds can change soil physical properties, for example by increasing soil penetrability and the range of soil surface temperatures (Bancroft et al. 2005b). Seabird colonies can act as disturbed patches in the landscape, increasing species richness (Archer et al. 1987) and the probability of plant invasion (Mulder et al. 2009). However, at very high burrow densities some plants may not be able to survive the severe disturbance regime (Vidal et al. 2000).

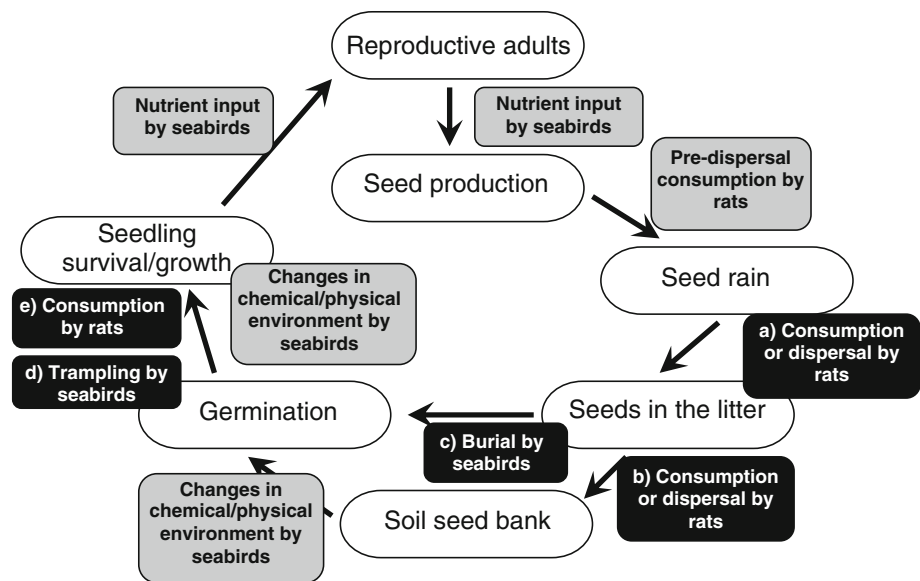
After rats have been eradicated from islands, seedling recruitment of some woody plants has increased (Allen et al. 1994; Campbell 2002; Clayton et al. 2008; Grant-Hoffman 2009), and depression of plant recruitment has been attributed to rat herbivory in enclosure studies and comparisons between areas with and without rats (Campbell and Atkinson 1999, 2002), but many of these studies focus on effects of Pacific rats (*R. exulans*), a smaller species than ship rats (*R. rattus*) or Norway rats (*R. norvegicus*). While all of these rat species are predators of seabirds (Drever and Harestad 1998; Major et al. 2007; see review by Jones et al. 2008), Pacific rats prey on smaller-bodied seabirds and do not reduce overall seabird burrow densities as much as ship and Norway rats (Worthy and Holdaway 2002). By using experiments we can better isolate the direct effects of invasive rats versus those driven by changes to seabird densities.

Seed and seedling communities represent the species pool from which future dominant plants will arise (Grime 1998), and invasive rats and burrowing seabirds may be placing very different filters on these potential plant communities. Reductions of seed and seedling densities may result from consumption of seeds and seedlings by rats, and from physical disturbance by seabirds; these mechanisms likely select for different plant characteristics. Although rats are broadly omnivorous (Innes 2005a, b), they prefer seeds to vegetative plant parts (e.g., seedlings), and they select plant species with certain characteristics, for example small seeds with relatively few physical or chemical defenses (see review by Grant-Hoffman and Barboza 2009). In contrast, impacts of physical processes, such as soil homogenization following burrowing or trampling, are likely to be more similar across plant species, although

different life stages may be more vulnerable. Seeds often benefit from burial (e.g., Maun 1998; Chauhan et al. 2006; Zhu et al. 2009): seeds on the soil surface are more likely to suffer from low moisture availability (Harper and Benton 1966; Chauhan et al. 2006), predation (e.g., Reichman 1979; Crawley and Long 1995; Maron and Simms 1997; Hulme and Borelli 1999; Andresen and Levey 2004; Orrock and Damschen 2007), or decay due to greater environmental fluctuations (Taylorson 1970). However, emergence tends to be negatively correlated with depth of burial as deeply buried seedlings fail to germinate or emerge (e.g., Maun 1998; Oldham and Ransom 2009; Zhu et al. 2009), and small seeds may not be able to emerge from greater depths (Baskin and Baskin 1998; Grundy et al. 2003; Zhu et al. 2009). The characteristics that confer resistance to rat herbivory are likely quite different from those that confer resistance to trampling by seabirds, resulting in very different selection pressures, even if overall impacts are similar. In tropical forests variation in seedling damage levels and subsequent mortality due to litter fall can be explained in part by rate of growth (faster growing seedlings are less likely to be damaged; Clark and Clark 1991), and more rapid growth may reduce mortality caused by trampling because larger seedlings are less susceptible to physical disturbance (Grant-Hoffman 2009). However, rapid growth rates may be negatively correlated with chemical defenses that protect seedlings from rat consumption (e.g., Coley 1987; Bazzaz et al. 1987; Fine et al. 2006). The repercussions of these different mechanisms may cause differences in future vegetation communities, and removal of invasive rats may cause unexpected results as food webs may have been irrevocably altered (Zavaleta et al. 2006). In this manner, rats may alter the vegetation on these islands such that post-eradication vegetation communities do not closely resemble pre-eradication communities and active management of the vegetation community may be needed. By understanding the mechanisms that drive the patterns seen in seed and seedling communities, scientists and managers can concentrate their efforts on species and processes most affected by rat invasions.

Islands in northern New Zealand with no history of rats and islands with current rat invasions had similar seedling densities and seedling species richness and diversity, whereas islands from which rats had been eradicated had higher seedling densities but lower seedling species richness and diversity and were dominated by a few woody seedling species (Grant-Hoffman 2009). In this study, we examined the mechanisms by which invasive rats and burrowing seabirds affect plant regeneration on some of the same islands. Seeds and seedlings are likely to influence different stages of tree regeneration (Fig. 1), so we test the following hypotheses:

Fig. 1 Diagram of woody plant reproductive cycle indicating potential effects of invasive rats and burrowing seabirds. Letters in boxes refer to mechanisms addressed. Boxes indicate mechanisms tested in this paper



1. Seabird burrowing will homogenize the seeds in the litter and soil layers (Fig. 1c), resulting in increased seed density in the soil and decreased seed density in the litter, and a more similar composition in the two layers.
2. Rats will selectively consume seeds in the litter layer (Fig. 1a, b), resulting in lower seed density and species richness of both seeds and seedlings. Predation of seabirds by rats will result in reduced seabird numbers, which in turn will reduce burial of seeds from the litter layer, and will result in seed communities which are dissimilar between the litter and the soil.
3. Deep burial of seeds by seabirds will reduce seedling emergence (Fig. 1c), reducing the similarity between the seed bank and the emerging seedling community.
4. Trampling and uprooting by seabirds will reduce seedling numbers (Fig. 1d), but have a smaller impact on seedling composition.
5. Selective consumption by rats will reduce seedling numbers and seedling species richness (Fig. 1e).

Materials and methods

Study area

The studies were carried out on warm temperate northern New Zealand islands from January to May 2005 and 2006. We collected litter samples from 21 islands (see Grant-Hoffman 2009 for details on these islands). These islands have a history of anthropogenic disturbance (fire and, on some, farming), are covered with secondary forest, and have current or have had past populations of burrowing seabirds (Procellariiformes; Holdaway 1999; Worthy and

Holdaway 2002). Additionally, we performed enclosure experiments on six of these islands (Middle Island, Ruamāhuanui, Whenuakura, Te Haupa, Hauturu, Motueka; Table 1). These six islands were chosen from the 21 based on ease of access (necessary for repeated visits), and their known rat status. All are of volcanic origin except Te Haupa (sedimentary origin), range in size from 3 to 45.6 ha, and are within 20 km of the mainland. Because the rodent status of Hauturu was uncertain, we excluded it from germination trials (Table 1). Additionally, we performed feeding trials on one island (Pakihi). This island was chosen because we could stay on the island for several days, which was necessary for feeding trial data collection.

Burrowing seabird species differ in body mass, breeding times, and duration of nesting (Warham 1990). However, we did expect some overlap in the effects of different burrowing seabird species. We did not attempt to partition the effects of different species of seabirds and this is a limitation of our study. Since we are considering short-term effects, presence or absence of seabirds at the time of our field work may also have influenced results. Similarly, while the effects of ship rats and Norway rats are undoubtedly different, we did not partition these effects due to limited islands with histories of just one species of rat. These species of rats, while not interchangeable, do have considerable overlap in their effects (Townsend et al. 2006).

We placed two study plots in areas of higher burrow densities and two in lower burrow densities. High and low burrow density were relative values within each island (within-island comparisons) and required a minimum difference of five burrows per 100 m². Plots were placed in mature forest. We counted all burrow entrances within the 100-m² plot, but the ratio of entrances to actual burrows is probably not 1:1 (as there may be multiple burrow

Table 1 Information on islands used for experiments. All islands plus an additional 14 (see Grant-Hoffman 2009) were used for litter collection

Island	Latitude (°S)	Longitude (°E)	Area (ha)	Distance from mainland (km)	Rat history	Seabirds present	Seabird density (burrow entrances m ⁻²)		Data collected
							Mean	Range	
Ruamāhuanui (RNI)	36.95	176.09	32.4	19.9	Uninvaded	<i>Pterodroma macroptera</i>	0.14	0.02–0.35	Exclosure, germination
Middle Island (MID)	36.6	175.84	13.5	8.3	Uninvaded	<i>Pelacanoides urinatrix</i> , <i>Puffinus carneipes</i>	0.52	0.02–0.98	Exclosure, germination
Motueka (MID)	36.82	175.8	6.2	1.2	<i>Rattus rattus</i> or <i>Rattus norvegicus</i>	<i>P. macroptera</i>	0.03	0–0.06	Exclosure, germination
Te Haupa (TH)	36.51	174.74	6	10.5	<i>R. norvegicus</i> eradicated 1989, <i>Mus musculus</i>	None	0	0–0.01	Exclosure, germination
Hauturu (HAU)	37.21	175.89	10.3	0.5	<i>R. norvegicus</i> eradicated 1985(?), possible low population, <i>Mus musculus</i>	<i>P. macroptera</i>	0	–	Exclosure
Whenuakura (WHE)	37.22	175.89	3	0.9	<i>R. norvegicus</i> eradicated 1985	<i>P. macroptera</i>	0.15	0.04–0.29	Exclosure, germination
Pakihi (PAK)	36.54	175.1	110	1.4	<i>R. norvegicus</i>	None	0	–	Feeding trials

entrances or unused burrows) and may be different for different bird species (Warham 1990). Therefore, our burrow entrance counts are correlated with seabird burrow density, but the relationship with seabird density may be weaker.

Middle Island and Ruamāhuanui have no history of rodent invasion and have large populations of burrowing seabirds (Table 1). Whenuakura was invaded by *R. norvegicus* and these were eradicated in 1985. This island also has a population of grey-faced petrels (*Pterodroma macroptera*), which were never extirpated by the rats. Te Haupa and Hauturu both had invasions of *R. norvegicus* which were eradicated in 1989 and 1985, respectively. However, these islands also have current house mouse (*Mus musculus*) invasions which were previously masked by the presence of *R. norvegicus*. No seabirds were present on these islands during our study. Motueka had a current rat infestation (*R. rattus* or *R. norvegicus*) and some grey-faced petrels (*P. macroptera*). Pakihi has a current invasion of *R. norvegicus* (Table 1; WaxTags were used to confirm rodent presence, not to show absence or density), for a review of mammalian eradications on New Zealand islands see Clout and Russell 2006).

Changes to the seed community

Germination trials

We used germination trials to test for the impacts of seabird and rat activity on seed incorporation into the seed bank (Fig. 1b, c). One soil core (50-mm diameter) was collected from the approximate center of each plot (four plots each on Middle Island, Ruamāhuanui, Motueka, Te Haupa, and Whenuakura). We did not collect soil from Hauturu. Soil was separated into three depths (0–59 mm, 60–120 mm, and 130–200 mm) to determine if seabird activity had resulted in deep burial of seeds. Depths were chosen for ease of collection and to reflect depths that may be disturbed by seabird burrowing activity. From each soil depth we used the same volume (980 mm³) of soil for germination trials. Soils were placed in plastic bags, and kept cool until germination trials were started. Soils (3 depths per plot × 4 plots per island × 5 islands = 60 samples) were placed in pots in a greenhouse on 17 March 2006 and emerging plants were counted weekly and identified to species. The experiment was terminated on 1 December 2006 due to declining emergence rates and high liverwort and moss covering.

Reproductive material in litter collections

We evaluated post-dispersal seed availability by examining seeds and reproductive material in litter samples

(Fig. 1b, c). For this data set only we used 21 islands (Grant-Hoffman 2009). Seven litter samples were collected from each plot in a stratified random design. A sample consisted of all material on the surface of the soil within a 0.01-m² area. All reproductive material, including seeds, seed coats, fruits, and flowers, was removed from each sample and identified with help of a magnifying glass using Webb and Simpson (2001) as the primary reference. Both the reproductive material and remaining sample material were dried for 48 h at 60°C and weighed.

Feeding trials

We evaluated rat preferences for seeds of seven woody plant species (Fig. 1a, b). We placed similar biomass (based on seed size) of each seed into covered trays. The covers were designed to deter avian consumption. Ten trays were placed in areas around the island of Pakihi (Table 1) on 18 February 2006, to allow the animals to get accustomed to them. Feeding trials began on 10 March 2006. We used seeds, seed capsules, or fruits depending on what would be available to the rats in the wild. We chose species that we could easily collect, represented a variety of sizes, and represented species that we expected to be eaten as well as species we expected to be avoided (see review by Grant-Hoffman and Barboza 2009). Species and number of fruits used were: *Coprosma macrocarpa* (50 fruits), *Pittosporum crassifolium* (five seed capsules), *Pseudopanax lessonii* or *Pseudopanax chathamicus* (75 seed capsules), *Hedycarya arborea* (25 fruits), *Streblus banksii* (85 fruits), *Melicope ternata* (30 seeds), and *Dysoxylum spectabile* (five seed capsules). Each station housed four plant species and (due to limited availability of some species) each species was used in at least three stations. Due to abundant seeds, *C. macrocarpa* and *P. crassifolium* were used in all stations. All seeds were left out for 5 nights. Each morning we observed and recorded any remaining seeds. We also noted any signs of rats (chewed seeds, rat droppings, footprints). After 5 nights we recorded any remaining material and collected traps and remaining plant material.

Changes to the seedling community

Exclosure experiment

We used exclosures to test for the impact of seabird and rat activity on short-term seedling survival (six islands; Middle Island, Ruamāhuanui, Motueka, Te Haupa, Hauturu, and Whenuakura; Fig. 1d, e). Exclosures were constructed of wire mesh (20 mm) and plastic piping and were approximately 0.32 m² in area. Exclosures were designed to exclude both seabirds (*Pterodroma macroptera*,

Pelacanoides urinatrix, *Puffinus carneipes*) and adult rats (*R. norvegicus*, *R. rattus*), but the mesh was not sufficiently small to exclude mice or juvenile rats. On three of the islands (Middle Island, Ruamāhuanui, and Whenuakura) only seabirds were excluded. On two islands (Te Haupa and Hauturu) seabirds were excluded, but seabird burrow density was low (see Table 1), and the presence of mice may have reduced the ability to detect impacts. On one island (Motueka) rats and few seabirds were excluded.

We randomly placed two exclosures along with one cage control (to account for unintended effects of exclosure structures), and one unmodified control plot marked with flagging tape (4 plots × 6 islands = 48 exclosures and 48 control areas) within each 100-m² plot. Exclosures were placed on islands in February and March 2005 and left in place for 1 year. We placed a WaxTag (which shows teeth marks when investigated by rodents) within each exclosure to determine if rats were present in the exclosures. Seedlings were counted and identified to species once when the structures were set out in February and March 2005 and once approximately 1 year later in February and March 2006, initial counts were subtracted from total counts. All exclosures were removed from islands in February and March 2006.

Statistical analyses

All analyses were performed in SAS version 9.1 (SAS 2002).

Germination trials

We ran analyses of covariance (ANCOVAs) for the two islands with the same rat history (uninvaded, Middle Island and Ruamāhuanui). In this analysis, we blocked by island to consider idiosyncrasies of each island. We then ran separate ANCOVAs for the three remaining islands (Whenuakura, rat eradicated; Te Haupa, rat eradicated but with mice present; and Motueka, rat invasion at the time of our study). Plots were the unit of analysis, burrow density was included as a continuous variable (log₁₀ scale), depth was included as a categorical treatment, and a burrow density by depth interaction was also included in the model. Response variables were total number of seedlings, species richness, and the proportion of individuals that were non-native.

Reproductive material in litter collections

We examined the relationship between the species richness of the seed community and amount of reproductive material (total weight and weight as a percentage of the total), and rat status and burrow density (log₁₀ scale). Since the

presence of rats was always associated with low seabird density, these two variables were partially confounded. We therefore performed analyses at two scales: within islands and among islands. At the within-island scale plots were the unit of analysis and we were testing mainly for seabird effects. Response variables were averaged per plot (seven samples per plot) and we included island as a blocking variable. At the among-island scale islands were the unit of analysis and we were testing mainly for rat effects. At this scale response variables were averaged per island and we included island size and distance to mainland as covariates to account for variation due to the size of the island (MacArthur and Wilson 1967). We also analyzed adult woody plant species richness as a response variable (for which we had data for 18 of the 21 islands; Cameron et al. 2007; Bellingham et al. 2010; P. J. Bellingham unpublished data) to account for variation due to seed rain.

Feeding trials

We calculated the percent of plant material of each species removed from the six stations that were visited by rats using totals for the entire 5-night period. We attributed seed removal to rats based on signs such as chewed seeds, feces, or footprints.

Exclosure experiment

The original design included four plots per island, each containing four subplots with a total of three treatments (two exclosures, a control, and a cage control; $n = 16$ per island). However, since we found no significant differences between controls and cage controls ($P > 0.1$ for tests including island and plot nested in island), these two treatments were combined, resulting in two treatments (exclosed and control) and two replicates per treatment in each plot.

We ran separate ANOVAs for the two uninhabited islands (Middle Island and Ruamāhuanui), the rat-eradicated island (Whenuakura), the two islands (Te Haupa and Hauturu) with low seabird burrow densities (excluded) and mice (not excluded), and the one island (Motueka) on which rats were still present. For these analyses plots within islands were the experimental units: we used means per plot for each treatment and ran an ANOVA that included plot nested in island in the model (equivalent to a paired t -test). We considered the effects of the exclosure treatment (two levels, exclosure or control) on seedling density, species richness, and percent of individual seedlings that were non-native species. To test whether seabird density could explain the seedling response to exclosure treatments we took the difference between exclosed and control treatments in each plot and tested for a relationship with seabird burrow density.

Comparisons between experiments

For each plot on each island we identified the species present in litter samples (see litter collections described earlier), the soil seed bank (based on the germination experiment), the seedling community in the absence of seabirds or rats (based on the exclosed plots in the exclosure experiment), and the seedling community in the presence of seabirds and/or rats (based on control plots in the exclosure experiment). We then calculated Jaccard's index of similarity for three pairs of seed samples: litter versus seed bank, seed bank versus protected seedling community, and protected versus unprotected seedling community. This index is calculated by dividing the number of species shared by both groups by the total number of species and ranges from 0 (no overlap) to 1 (complete overlap). For three of the islands (Middle, Ruamāhuanui, Motueka) we calculated Jaccard's indices for a fourth pair of communities: species found on the whole island ("whole-island flora"; Cameron et al. 2007; Bellingham et al. 2010) and species found in unprotected (control) plots. Floras for the remaining three islands (Whenuakura, Hauturu, Te Haupa) were not complete enough to perform that analysis.

We tested whether islands differed in similarity of communities by ANOVA followed by Tukey–Kramer contrasts where there were significant differences. We evaluated whether seabird density could explain community similarity by regressing Jaccard's indices for plots against plot burrow density (\log_{10} transformed).

Results

Changes to the seed community

Germination trials

More seedlings germinated from shallow soil layers, with often 2–3 times more seedlings in shallow layers compared to deep layers of soil from the same sample. There were also more seedlings in areas with high burrow densities, ranging from a 20–300% increase in seedlings from plots with lower burrow counts to plots with higher burrow counts. Similarly, on Middle Island and Ruamāhuanui (where no rats were present and seabird density was high), seedling density increased marginally with increasing burrow density ($F_{1,17} = 4.36$, $P = 0.052$, parameter estimate = 3.57). More seedlings germinated from the shallowest depth (depth 1) than from the deepest depth (depth 3; $F_{1,17} = 5.15$, $P = 0.018$; contrasts, $P = 0.01$; Fig. 2a). The middle depth was not statistically different from either the shallowest or deepest depths (contrasts, $P > 0.2$; Fig. 2a).

There was no interaction between burrow density and soil depth ($F_{1,17} = 0.08$, $P = 0.93$). Seedling density also increased with increasing burrow density on the invaded island (Motueka, which also had some seabirds present; $F_{1,6} = 17.22$, $P = 0.006$, parameter estimate = 1.06). As on uninvaded islands, on this island more seedlings germinated from the shallowest depth than from the deepest depth ($F_{2,17} = 9.67$, $P = 0.01$; contrasts, $P = 0.01$; Fig. 2a). There were no significant differences in seedling density between depths on the eradicated island (Whenuakura) or the rat-eradicated islands with mice (Te Haupa and Hauturu,

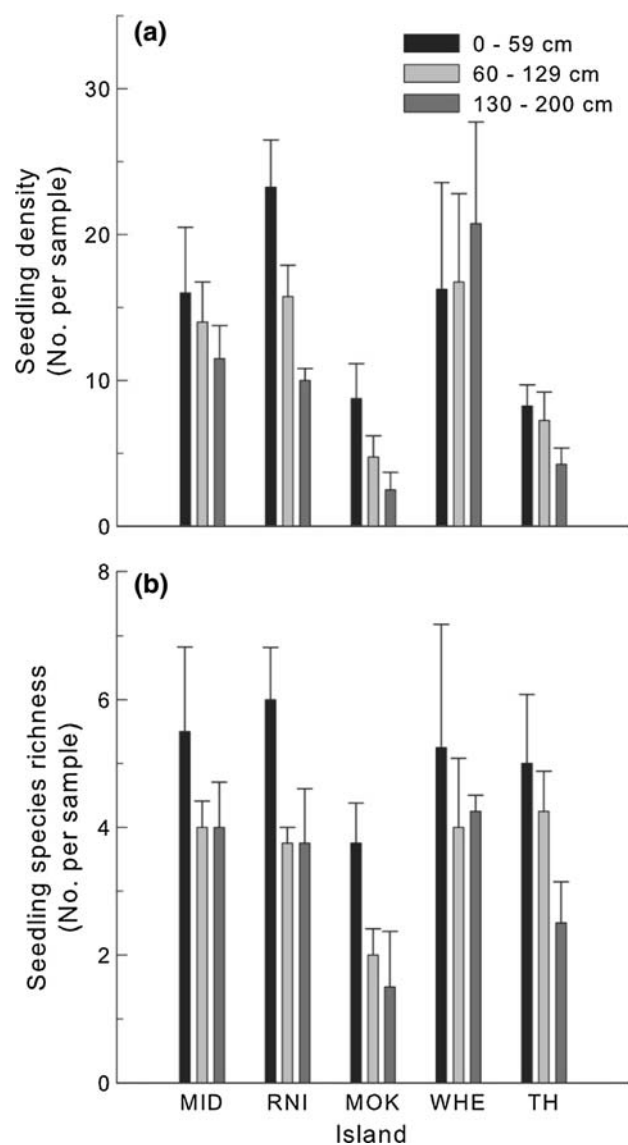


Fig. 2 Estimates of the soil seed banks from five islands at three soil depths, evaluated as **a** seedling density per sample and **b** species richness of seedlings germinated from soil samples across five island. Bars are mean \pm SE from four sample sites per island across a range of seabird burrow densities. For site abbreviations, see Table 1

$P > 0.1$; Fig. 2a), nor were there any relationships with burrow density ($P > 0.1$).

Similar to seedling density, species richness was generally high in areas with high burrow density and in shallow soil layers (Fig. 2b). Seedling richness increased with increasing burrow density on uninvaded islands ($F_{1,17} = 4.36$, $P = 0.05$, parameter estimate = 3.57) but not on the islands with rats present or eradicated ($P > 0.1$). Also, there were more species found at the shallowest depth than at either of the deeper soil depths on the uninvaded islands ($F_{2,17} = 4.82$, $P = 0.022$; contrasts, $P = 0.04$ for both; Fig. 2b). However, the lower two depths were not different ($P > 0.9$). Species richness of seedlings was not related to burrow density or depth of sample on the rat-eradicated island or the islands with mice ($P > 0.1$).

There was only a marginal increase in the percent of seedlings that were non-native with increasing burrow density on uninvaded islands ($F_{1,17} = 3.34$, $P = 0.085$). No other islands showed significant differences with burrow density, and total number of non-native seedlings was not affected by burrow density or soil depth ($P > 0.1$ for all).

There were no significant differences in seedling density or species richness between Middle Island and Ruamāhuanui. There were more non-native species on Middle Island than on Ruamāhuanui ($F_{1,23} = 35.0$, $P = 0.0004$). The numbers of non-native seedlings in our sample areas were low on both islands (no non-native species on Ruamāhuanui and 0.01 per sample area on Middle Island; $F_{1,23} = 11.70$, $P = 0.0033$).

Reproductive material in the litter

Unlike seedling density and species richness, reproductive material in the litter was generally low at high burrow density, when comparing plots within islands. Both the total weight of reproductive material and the percentage of the litter that was reproductive material declined with increasing burrow density when comparing plots within islands (total weight $F_{1,28} = 9.94$, $P = 0.004$; percentage weight $F_{1,28} = 7.81$, $P = 0.01$). However, for both total weight of reproductive material and percentage of the litter that was reproductive material, relationships were driven by plots on Middle Island, which had the highest burrow densities and relatively high amounts of reproductive material. For example, on Middle Island there was a 22-fold increase from the highest burrow density plot to the lowest burrow density plot in weight of reproductive material, the next largest increase, on another island, was sixfold. Middle Island also had 50% more reproductive material (by weight) than the next closest measurement from an island. When Middle Island was excluded from

analyses the relationship was no longer significant (Middle Island—total weight $F_{1,1} = 14,907$, $P = 0.005$; percent reproductive material $F_{1,1} = 688$, $P = 0.02$; all other islands—total weight $F_{1,25} = 1.39$, $P = 0.2$; percent reproductive material $F_{1,25} = 0.12$, $P = 0.73$). When comparing means per island the total weight of reproductive material and percentage of the total litter weight that was reproductive material were not related to either burrow density or rat status ($P > 0.1$).

While there were no trends in species richness of reproductive material in the litter when comparing plots within islands ($P = 0.5$), at the whole-island scale, uninvaded islands with high burrow densities had higher species richness of adult plants than invaded islands with lower burrow densities ($F_{2,14} = 5.27$, $P = 0.030$; contrasts $P = 0.03$).

Feeding trials

Rats visited six of ten feeding stations over a 5-night trial on Pahihi, as inferred from fruit damage, footprints, and feces, and reported results are from these six stations. Fruits of three species were frequently eaten and showed substantial removal of fruits (*P. crassifolium* 86.6%, *C. macrocarpa* 23.4%, and *S. banksii* 45.3%). Fruits of *P. crassifolium* and *C. macrocarpa* showed clear signs (teeth marks) of rat consumption. Fruits of *S. banksii* were consumed by an unidentified invertebrate within 48 h, at which point none of the stations that housed this species had been visited by rats. Fruits of *Hedycarya arborea*, *Pseudopanax* spp., *Dysoxylum spectabile*, and *Melicope ternata* were not eaten.

Changes to the seedling community

Exclosure experiment

Generally, both seedling density and species richness increased when either rats or burrowing seabirds were excluded (Fig. 3). When seabirds were excluded seedling species richness increased at least fourfold (Middle Island and Ruamāhuanui, $F_{1,7} = 35.15$, $P = 0.0006$; Whenuakura, $F_{1,3} = 169.00$, $P = 0.001$). Seedling density also increased marginally when seabirds were excluded on uninvaded islands (Middle Island and Ruamāhuanui; $F_{1,7} = 5.07$, $P = 0.06$), but not on Whenuakura ($P = 0.20$).

When both rats and seabirds were excluded, on Motueka, seedling species richness and seedling density increased (richness, $F_{1,3} = 14.29$, $P = 0.03$; density, $F_{1,3} = 15.21$, $P = 0.03$). On islands with few seabirds but with mice present, Hauturu and Te Haupa, seedling densities inside exclosures were greater than in control plots ($F_{1,7} = 6.71$, $P = 0.04$), but these differences were not as great as on other islands (Fig. 3a). On these islands

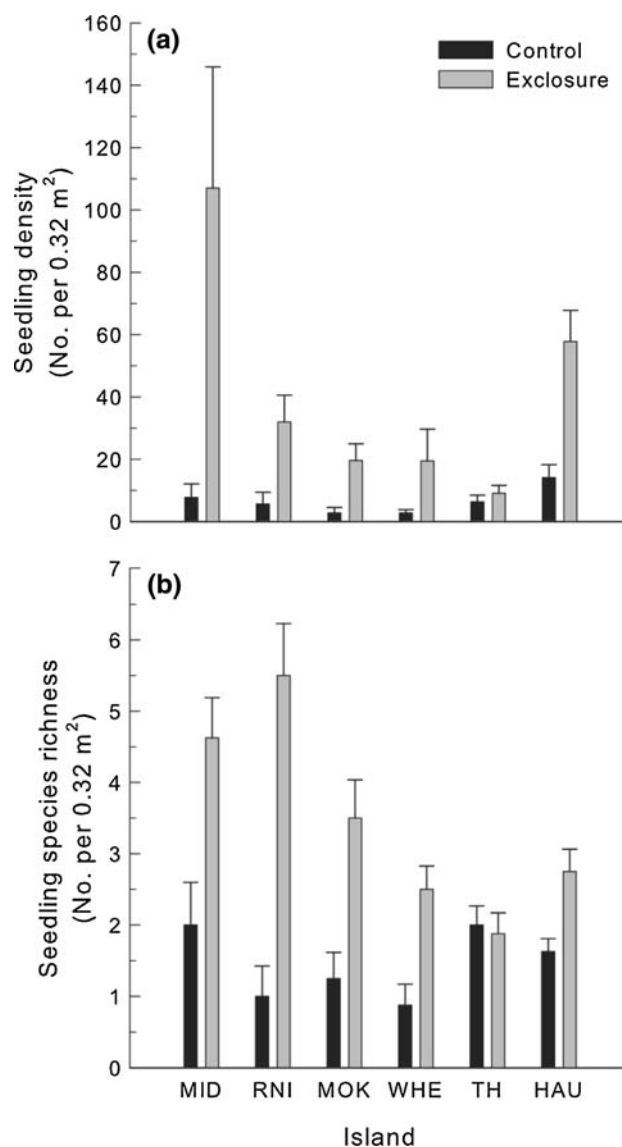


Fig. 3 a Seedling density and b seedling species richness inside exclosures and in adjacent control plots across islands. Bars are mean \pm SE, across all eight exclosures and controls per island from a range of seabird burrow densities. For site abbreviations, see Table 1

seedling species richness inside exclosures was only marginally greater than in controls ($F_{1,7} = 3.50$, $P = 0.10$; Fig. 3b). The difference between exclosed and control plots was similar for the islands with large seabird populations (91% of all seedlings were found in exclosures on Middle Island and Ruamāhuanui combined), and the island with rat populations (88% of seedlings in exclosures on Motueka), and lower on islands with no rats and few seabirds (76% of seedlings in exclosures on Hauturu and Te Haupa). Seedling density, seedling species richness, and the percentage of non-native plant species in exclosures or controls were not significantly related to burrow densities on any of the islands ($P > 0.1$).

Table 2 Analysis of similarity in seed and seedling composition across treatments and islands

Comparison	Burrow density ^A (<i>F</i> , <i>PE</i>)	Island ^B (<i>F</i>)	MID	RNI	MOK	WHE	HAU	TH
Litter vs. seed bank	6.44*, 0.12	3.40*	0.263 ± 0.11a	0.140 ± 0.03ab	0.175 ± 0.06ab	0.025 ± 0.025b	NA	0 ± 0b
Seed bank vs. protected seedlings	5.00*, 0.11	2.03	0.293 ± 0.09	0.213 ± 0.05	0.075 ± 0.05	0.103 ± 0.04	NA	0.093 ± 0.09
Protected vs. unprotected seedlings	0.72, 0.08	1.26	0.348 ± 0.14	0.21 ± 0.09	0.458 ± 0.19	0.395 ± 0.16	0.5 ± 0.07	0.65 ± 0.12
Whole-island flora vs. unprotected seedlings	11.73**, 0.07	0.56	0.095 ± 0.09	0.073 ± 0.07	0.045 ± 0.05	NA	NA	NA

Jaccard indices for sites (mean ± SE)

Difference letters indicate significant differences among sites ($P < 0.05$). NA Data unavailable to make this comparison; for site abbreviations, see Table 1
* $P < 0.05$, ** $P < 0.01$

^A *F* values and parameter estimates (*PE*) for the regression of Jaccard index values against burrow density (\log_{10} transformed)

^B *F* values for a test of differences between islands

Non-native plant species only occurred in sampling areas on the uninvaded islands (Middle Island and Ruamāhuanui), where the percentage of non-native seedlings found was not significantly affected by the enclosure treatment ($F_{1,7} = 0.91$, $P = 0.37$).

Comparisons between experiments

Burrow density explained overlap between communities (as measured by Jaccard's index of similarity) for three comparisons (Table 2): similarity increased with burrow density for litter versus seed bank, seed bank versus protected seedling community, and whole-island flora versus protected seedling community. In contrast, overlap between protected and unprotected seedling communities did not change with seabird density, although mean values were lower for the three islands with substantial seabird populations than for the three without.

Rat history explained variation in community similarity for only one comparison: litter versus seed bank (Table 2). Islands which never had rats had the greatest overlap in species presence between litter and soil bank, the island with rats was intermediate, and the islands where rats had been eradicated had the lowest values.

Discussion

Physical effects of seabirds on the seed community

Our study shows that the negative effects of seabirds on seedlings, by trampling and uprooting, overwhelm the

potentially beneficial effects of high levels of seed germination, seedling emergence, and possibly seed production, which result from seed burial and nutrient additions. Our experiments provide evidence that seabird burrowing results in increased seed density in the soil and decreased seed density in the litter, and a more similar composition in the two layers. There was no evidence that seed burial, by burrowing, reduced potential seedling density: soils from areas with high burrow density yielded greater seedling germination in the greenhouse and in enclosed plots. Higher seedling densities could be due to higher seed production, greater nutrient availability to plants as a result of seabird inputs, or to higher emergence rates (hypotheses we did not test). Studies from other systems have found high numbers of seedling emerging from areas with high seabird densities; seed germination from soils in wedge-tailed shearwater (*Puffinus pacificus*) colonies in Western Australia was 45 times greater than from soils in a nearby heath (Bancroft et al. 2005a), and on a densely seabird-burrowed island in southern New Zealand, exclusion of seabirds for 3 years increased tree seedling densities 13-fold (Roberts et al. 2007). Two mechanisms which could potentially increase germination and emergence on seabird colonies are conditions in burrows, which are often moister, with less variability in soil temperature than on the soil surface (Bancroft et al. 2005a), and higher nutrient content of soils, which could increase growth rates of germinants and enhance probability of emergence. Seedlings of three tree species grown in soils from uninvaded islands with active seabird colonies had greater biomass than those grown in soils from invaded islands with few seabirds (Fukami et al. 2006). Regardless of the

mechanisms involved, seabirds increase the total density of germinants.

Effects of rats on the seed community

Islands with different histories of rats have different seedling species compositions (Grant-Hoffman 2009), and our experiments demonstrate that this is likely due at least in part to selective consumption of seeds by rats. Consumption rates by rats in our feeding trials ranged from 0 to 89% over the course of 5 days and it is likely that consumption of seeds by rats contributed to lower densities and species richness of seeds in the litter and seed banks of the island invaded by rats. Overall, seedling densities and species richness of seedlings germinating from soils of an island where rats were present (Motueka) were about half those of islands from which rats were absent. However, we did not see a large drop in species richness on this island compared to other study islands. Similarly, overlap in seedling composition between exclosure and control plots on Motueka was intermediate in range (Table 2). However, similarity between exclosure and control plots may reflect past herbivory by rats, as species that are particularly vulnerable may already have been removed from the species pool. For example, absence or decreased populations of *Strebilus banksii*, a species preferred by rats, has been attributed to rat herbivory (Campbell and Atkinson 2002). Rats may also disperse some plant species. Seedlings of *Pittosporum crassifolium* can represent a significant portion of the seedling community on islands where rats have been removed (Grant-Hoffman 2009). Seeds of this species can pass through *Rattus norvegicus* digestion with no apparent harm to the seedcoat (Grant-Hoffman 2009), suggesting that consumption by rats may not always be detrimental.

Physical effects of seabirds on the seedling community

Trampling and uprooting of seedlings by seabirds on seedlings overwhelm the positive effects of seabirds on seedling germination, resulting in low seedling density observed on seabird colonies. However, on islands with substantial seabird colonies, seedling densities were almost 10 times greater inside exclosures than outside. This is consistent with our earlier findings from an observational study, where even low seabird burrow densities are associated with low seedling densities (Grant-Hoffman 2009). In addition, other studies have also found low seedling densities associated with seabird activity (Gillham 1956; Maesako 1999; Ellis 2005; Roberts et al. 2007). Experimental data from this study clearly show that these low seedling densities are a result of impacts to seedlings rather than seeds. Seabirds also had impacts on community

composition: excluding seabirds increased species richness at least fourfold, and seabird islands had the lowest overlap in community composition between exclosed and unexclosed plots for any of the islands. Reduced seedling species richness on seabird colonies may be the result of reduced seedling density (reducing the probability that any particular species will be found), or there may be selection for seedlings that are more tolerant of trampling or uprooting on seabird colonies.

Consumption of seedlings by rats

In addition to consuming seeds, rats also consume seedlings; seedling density was 7 times greater inside exclosures than outside on the rat-invaded island (Motueka). Some of this may be due to seed consumption; however, seedling consumption may also play a role. Several other studies have documented rats eating seedlings (see review Grant-Hoffman and Barboza 2009), and herbivory at the very early seedling stage has been found to have strong impacts on plant species in other systems (Clark and Clark 1985). Based on the highly selective consumption of seeds by rats, it is likely that seedlings of different species are not affected equally.

Seabirds and rats as filters on the plant community

Both rats and seabirds act as strong filters on the plant community, with similar total impacts on seedling density. However, characteristics that reduce vulnerability to rats are likely to be very different from those that reduce vulnerability to seabirds. Rats are highly selective in their consumption of seeds and possibly seedlings, and defense against rats is likely to involve characteristics such as secondary compounds in the seeds and tough seed coats (Grant-Hoffman and Barboza 2009). In addition, rats may be able to effectively search for preferred species and escape from predation in space may not be very likely (Price and Jenkins 1986). The negative impacts of seabirds occur primarily at the seedling stage, and characteristics that reduce vulnerability are likely to include rapid growth rates (to escape trampling) and root systems that resist uprooting. Thus making escape in space as well as in time possible. The seabirds on these islands, like many others, are colonial nesters, and this behavior results in variation in nesting densities across islands. This would give an advantage to species with dormancy, as they may be buried while seabirds are present, but emerge during a time of year when seabirds are not in residence. In the field, the number of seedlings <0.75 cm tall declined with increasing seabird burrow density whereas the number of larger seedlings, >0.75 cm, was unrelated to seabird burrow density. This suggests that seabirds are acting as a filter for small but not

large seedlings, and that species that attain a height >75 cm may be less vulnerable to the physical impacts of seabirds. This may be the result of escape in space, in time, or both. If the characteristics that provide protection against damage by seabirds are very different from those that provide escape from herbivory by rats, then one might expect a community that has experienced strong selection by seabirds followed by invasion of rats to be particularly impoverished. This matches observational data for islands where rats have been eradicated (Grant-Hoffman 2009). However, these hypotheses remain to be tested in the field.

In order for managers to manage plant populations where rats have invaded or where rats have been eradicated, they must address the legacy of rat consumption as well as the impacts that restoring burrowing seabirds and the ecosystem processes that these birds drive will have (Mulder et al. 2009). By understanding the mechanisms through which these animals affect plants at different life stages, managers can better understand and predict short-term changes. However, the ability to predict longer term changes requires the ability to link plant characteristics to the selection pressures that they face.

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