

## Burrowing seabirds affect forest regeneration, Rangatira Island, Chatham Islands, New Zealand

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**Abstract:** The forests of Rangatira Island (218 ha) in the Chatham Islands are a critical breeding site for a number of rare and threatened forest bird species, but are also home to more than three million seabirds, which could significantly affect forest regeneration processes. We surveyed the forests of Rangatira Island by establishing 40 permanent forest plots, estimated seabird density through burrow counts, and analysed soil properties. To determine if seabirds were impacting on forest regeneration, we established exclosures (0.25 m<sup>2</sup>) in 30 of the forest plots, and examined the role of canopy gaps in forest regeneration. The tallest current forest (c. 15 m), dominated by *Plagianthus chathamicus*, has mostly regenerated since stock were removed in 1959. Mean burrow density was estimated to be 1.19 per square metre, all soils were highly acidic (pH 3.36–5.18), and burrow density was positively correlated with soil phosphorus. Seedling density of woody species in seabird exclosures measured after 9, 24 and 33 months was significantly higher than in the adjacent non-gap plots, and seedling density was positively associated with reduced canopy cover. Seedling densities were also significantly higher in canopy gaps than in adjacent non-gap plots, but seabird burrow density was significantly lower in gaps. These results suggest that canopy gaps allow forest regeneration despite the negative impacts of seabird burrowing. However, the gap makers, largely senescing *Olearia traversii*, are slowly disappearing from the forests. The cohort of *Plagianthus* that has regenerated following farm abandonment may progressively collapse, allowing regeneration to continue in small openings, but there is also the potential for a catastrophic blowdown. This might have serious implications for forest-dwelling birds, invertebrates, and plants.

**Keywords:** canopy gap; forest composition; forest structure; seabird trampling; seedling disturbance; soils; treefall

## Introduction

Rangatira (South East) Island in the Chatham group (44°20' S, 176°10' W) is a small island (218 ha) that ranks among the Southern Hemisphere's most important wildlife sanctuaries. Most of the island is forested and these forests support the largest or the only breeding populations of several rare and critically endangered bird species, namely, the black robin (*Petroica traversii*), and the other Chatham Island endemics the snipe (*Coenocorypha pusilla*), tūi (*Prothemadera novaeseelandiae chathamensis*), tomtit (*Petroica macrocephala chathamensis*), red-crowned parakeet (*Cyanoramphus novaeseelandiae chathamensis*), warbler (*Gerygone albofrontata*), and fantail (*Rhipidura fuliginosa penita*) (Nilsson et al. 1994). Several tree or shrub species in serious decline or nationally vulnerable also occur on Rangatira Island,

including the Chatham Island tree daisy (*Olearia chathamica*), Chatham Island ribbonwood (*Plagianthus chathamicus*) and the Chatham Island tree hebe (*Hebe barkeri*) (Walls et al. 2003).

Rangatira Island also supports a large population of burrow-breeding seabirds. Estimates from burrow counts put the population at around three million birds, which equates to approximately 14 000 birds per hectare, or 1.4 birds per square metre across the entire island (West & Nilsson 1994). At such high densities, these birds must have a major influence on the island's ecology, primarily by transferring nutrients from the marine ecosystem to land (Smith 1978; Siegfried 1981; Polis & Hurd 1996; Mizutani & Wada 1998; Wainright et al. 1998; Anderson & Polis 1999; Mulder & Keall 2001) and through disturbance associated with their burrowing and trampling activities (Gillham 1960; Campbell 1967; Johnson 1975; Warham 1996; Maesako

1999). Disturbance by seabirds has the potential to cause catastrophic vegetation collapse. Grassholm Island, off the coast of Wales, supported half a million puffins (*Fratercula arctica*) in 1890, but trampling and burrowing by birds led to almost complete vegetation loss and extensive erosion, to the point that the island could no longer support a large seabird population (Lockley 1953). A similar scenario was found among the islands off Western Australia, where burrowing seabirds so altered the vegetation of an island that it was no longer suitable for breeding, forcing a general exodus to another island in the group. When the original island's vegetation had sufficiently recovered the burrow-breeding seabirds returned (Gillham 1961). On Little Mangere Island, Chatham Islands, the collapse of the forest that supported the last remaining black robin population was attributed in part to the impact of burrowing by sooty shearwaters (*Puffinus griseus*) (Butler & Merton 1992). The forest habitat of Rangitira played a critical role at that time, and continues to do so, in saving the black robin from extinction (Butler & Merton 1992; Department of Conservation 2001).

As the only island in the Chathams group with a sizeable forest that is also free of introduced mammals, Rangitira Island's status as a wildlife sanctuary is critically dependent on maintaining its forest cover. However, studies on Rangitira Island show that interspecific and intraspecific competition for breeding burrows is intense (Was et al. 2000; Sullivan & Wilson 2001), perhaps indicating a lack of suitable habitat elsewhere in the Chatham Islands and/or an increase in seabird populations with implications for forest regeneration.

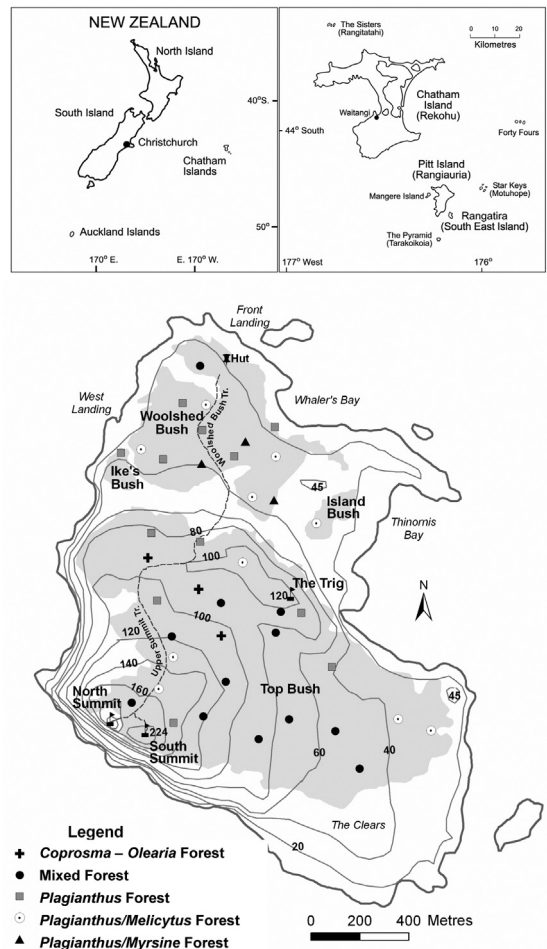
Despite this, we have little understanding of forest dynamics on the island, and particularly how seabirds might impact on regeneration processes and long-term forest replacement. This study had four aims: (1) to describe the current composition, size- and age-structure of forests on Rangitira Island and to infer from this past regeneration processes; (2) to quantify variation in seabird burrow density across the island; (3) to examine the impact of seabirds on seedling regeneration in the forest understorey; and (4) to assess the importance of canopy gaps as sites for tree regeneration.

## Study site

Rangitira Island is the southern-most volcanic centre of the Chatham Islands (Fig. 1), and at about 3.8–4 million years old it is amongst the youngest of the Chatham Island volcanoes. It is composed entirely of a dipping sequence of coarse-grained volcanic sediments that have accumulated near a volcanic vent (Watters 1978). Volcanic breccias form the crags with softer basaltic lapilli tuffs near the coast (Hay et al. 1970; Campbell

et al. 1993). A notable geological feature of Rangitira Island is the well-preserved marine terraces, about 15 m and 80 m above sea level. It is thought these were formed when the sea level was higher during the warmer inter-glacial stages of the Pleistocene (Hay et al. 1970; Watters et al. 1987).

Temperatures are cool with a year-round average of about 11°C. Frosts are infrequent and light, although hail showers are common in the winter months. Annual rainfall varies from 715 to 1050 mm and dry summer spells are common, sometimes lasting more than a month, but skies are often overcast (averaging



**Figure 1.** Rangitira Island showing location and classification of forest survey plots ( $n = 40$ ). The shaded area is forest. Inset: Chatham Islands' location in relation to New Zealand, and Rangitira Island's position within the Chatham Islands archipelago.

74%). Summer humidity is high, often exceeding 80% (Thompson 1983; Campbell et al. 1993). The almost incessant wind is referred to as the 'Roaring Forties'. From Woolshed Bush in the north and The Clears in the south-east the island slopes gently upward to the highest point (224 m) where the south-facing rampart-like cliffs plunge vertically to the sea (Fig. 1).

## Land-use history

### Moriore period

There is no record of permanent pre-European settlement on Rangatira Island, but Moriore claims to the 1870 Land Court hearing confirm the island was significant to them. Moriore probably spent periods ashore harvesting food, but the virtual absence of the kopi tree (*Corynocarpus laevigatus*), believed to have been brought to the Chatham Islands from New Zealand by Moriore and cultivated for their fruits (King 2000), suggests Rangatira Island was not settled permanently. There are large kopi tree groves, for example, on adjacent Pitt Island (2.5 km away), where an estimated 300 Moriore were living in 1790 (Richards 1972, 1982; Wills-Johnson 1996; King 2000).

### European era

In the early 1800s a sealing station was established on Rangatira Island and pigs (*Sus scrofa*) and sheep (*Ovis aries*) were introduced (Richards 1982). Dogs (*Canis familiaris*), cats (*Felis catus*) and rats (*Rattus norvegicus*, *R. rattus*) never established on Rangatira Island, which probably accounts for the survival there, but not elsewhere, of the Chatham petrel (*Pterodroma axillaris*) and the New Zealand shore plover (*Thinornis novaeseelandiae*). On Chatham Island these predators have extirpated most of the original avifauna (Atkinson 1978; Veitch & Bell 1990; Tennyson & Millener 1994). Rangatira Island is also the main refuge for other terrestrial and oceanic bird species.

Whalers, accompanied by farm animals, including goats (*Capra hircus*), arrived around 1839 and systematic clearing of Rangatira Island's forests for pasture and potato cropping began shortly after (Ritchie 1970; Holmes 1984). Stock numbers fluctuated over the next 100 years. The last lessee (Nielsen), who farmed the island until it became a reserve in 1954, had over 1000 sheep and approximately 20 cattle (Bell 1953). Apart from a few strays shot in 1961, all the stock had been removed by 1959 (Ritchie 1970).

Little has been published on the early vegetation of the island or changes since stock were removed. While vegetation on Chatham and Pitt islands was described by early botanists (e.g. Cockayne 1902), they did not visit Rangatira Island. Fleming (1939), in an account of his 1937 visit, wrote 'bracken "clears" and pasture-land alternate with beautiful park like bushlands' but

gave no details of forest species. However, a photo (Wotherspoon collection, Auckland Museum) taken on this visit in the Woolshed Bush area (Fig. 1) shows scattered *Olearia traversii* trees set in pasture grass. As on Chatham Island (Rekohu), these *Olearia* appear to be the only surviving remnants of the original forest, which would have been opened up by fire and stock and then exposed to wind and salt damage. At the time Rangatira Island became a reserve in 1954, the forest was described as significantly reduced in area and quality (Bell 1953); only one-third of the island (Top Bush, Fig. 1) was forested, with a heavily browsed understorey and a sparse canopy vulnerable to damage by salt-laden winds.

Since grazing ceased the forest has regenerated on both the lower (Woolshed Bush) and upper (Top Bush) marine terraces. Forest remnants, such as Ike's Bush and Island Bush (Fig. 1), appear as 'forest islands' set in grassland in photographs taken by B.D. Bell in 1961. However, in 2002 while these forest islands were still visible, they were set in a sea of bracken (*Pteridium esculentum*) overrun with *Muehlenbeckia australis*, which also covers much of the forest margins (Roberts 2004). In the area called 'The Clears' (Fig. 1), which adjoins the seal colonies, stumps and logs are evidence of a forest that has been killed by the wind after the stunted, sheltering margin had been broken down by sheep and cattle (Bell 1953). On this eroding salt-marsh, forest regeneration is slow due to permanent soil loss in an area of extreme exposure to southerly storms. Taylor (1991) listed plant species and estimated their relative abundance, and West and Nilsson (1994) recorded plant species presence/absence in association with burrow habitat, but did not measure frequency. Nilsson et al. (1994), when recording bird life on the island, estimated the forest to cover 98 ha or 45% of the island area.

## Methods

### Forest sampling

To describe the present composition and structure of the forests we established 40 permanently marked plots (10 × 10 m) in April and May 2002. Plots were located using stratified random sampling. We gridded a map of the island into squares (100 × 100 m), and numbered all grid squares having at least two-thirds forest cover. Of these, we selected at random 10 grid squares in Woolshed Bush (five each on NW and SE sides of the main track), and 20 grid squares in Top Bush (10 on NW and 10 on SE sides of the island), and assigned a plot to each grid square (Fig. 1). It can be difficult to avoid damaging seabird burrows when walking across the island, and to confine impact, a network of walking tracks has been established, providing access to almost

all parts of the island. To minimise damage we used the intersection of two tracks in a grid square as the starting point to locate each plot, and due to the extreme fragility of the soil once off a track, and in many cases even on the track, 'petrel boards' (plywood squares attached to snowboard bindings) were worn. Plot location was chosen by heading a random distance (0–100 paces) along one of the randomly chosen tracks, and then a further random distance (0–20 paces) off the track into the forest. An additional 10 plots were subjectively placed in locations identified as having features not represented in the first 30 plots. This included smaller bush patches such as Ike's Bush and Island Bush, higher altitude locations, apparently older *Plagianthus* forest, and patches of very densely regenerating forest.

Sampling methods were based on Allen (1992, 1993). Each plot was gridded into four subplots ( $5 \times 5$  m). Within each of these, we measured the diameter at breast height (dbh; 1.35 m above ground) of all tree species with dbh > 3.0 cm, including dead standing trees. Trees with trunks growing horizontally were measured 1.35 m along the stem from where they were rooted, rather than at breast height. For multi-stemmed trees, we measured the dbh of the largest stem and recorded the number of stems > 3.0 cm dbh. Saplings, defined as stems > 1.35 m high but < 3.0 cm dbh, were counted in each subplot. We counted seedlings, defined as woody species < 1.35 m tall, in eight circular understorey plots, each with a radius of 0.49 m (area = 0.75 m<sup>2</sup>). Understorey plots were located at the subplot grid intersections.

### Compositional analysis of forest plots

We used cluster analysis to group the 40 forest plots on the basis of similarities in their composition and size structure in order to identify forest communities. To do this, we grouped trees into 3-cm-dbh size-class bins (e.g. 3–5.9 cm, 6–8.9 cm, and so on) up to 54 cm. Trees  $\geq 54$  cm dbh were put in a single bin. For each plot, we used the number of trees of each species in each size-class bin to calculate a similarity measure and perform a cluster analysis. Thus, plots that were grouped in the cluster analysis shared a similar tree species composition and size structure. We used the Bray–Curtis measure of similarity to construct a matrix of pairwise distances between plots, and an agglomerative clustering technique (unweighted pair-group method using arithmetic averages – UPGMA) to group plots on the basis of their pairwise similarities (Baker 1992). From the resulting dendrogram, we identified five main clusters of plots, which we recognised as forest communities. Combining the plots in each cluster, tree species in each size-class were totalled and converted into total stem density per hectare.

Bar graphs showing the size-class profile of forest canopy (Fig. 2a & 2b), subcanopy, and dead trees

(not shown) in each cluster were used to describe the chief characteristics of the forest communities (Table 1), which were named following Atkinson (1985). Figure 1 shows the distribution of forest communities across the island. In using only the largest stem in a multi-stemmed individual for analysis the resulting histogram of size classes can be biased towards smaller and thus apparently younger stems. However, here tree size was used as a coarse surrogate for tree age, in order to infer the type of regeneration processes in these forests, particularly to look for a lack of small individuals that might indicate a discontinuous pattern of regeneration, as in the case of *Plagianthus*. For this purpose, the largest stem of each individual is a sensible measure.

### Age structure

To determine the age structure of the forest we increment-cored the largest tree (with a minimum dbh of 8 cm) in each subplot ( $5 \times 5$  m) at 0.5 m above ground. Following standard dendrochronological procedures, increment cores were mounted in wooden blocks, sanded until tree rings were clearly visible (Stokes & Smiley 1968), and then growth rings were counted under a microscope. When cores missed the chronological centre but inner growth ring arcs were visible, we estimated the age of the missing portion using the geometric model in Duncan (1989). Where the centre of the tree was rotten, age was estimated using the partial core by assuming that the chronological centre was at the geometric centre (Norton et al. 1987). The age estimates reported in this study were not corrected for tree growth to coring height.

### Environmental variables and site features

To identify whether there was a relationship between environmental variables and forest structure and composition we recorded the following at each plot, using methodology adapted from Allen (1992): Slope (using a clinometer); aspect (using a compass to the nearest 1° at right angles to the general lie of the plot to calculate degrees from north); and altitude (m a.s.l.) (from NZ topographical map 1:50 000 (1998)).

In April 2004, using a corer ( $5 \times 10$  cm), soil was sampled from each forest plot (to the maximum depth possible without penetrating burrow chambers). Surface litter was first removed and four soil samples (approximately 600 ml) were taken within a 2-m radius of the plot centre. The four samples were mixed and approximately one-quarter was taken for analysis. In the laboratory soil samples were air-dried, sieved through a 2-mm mesh, and analysed for pH, N, C and P. Soil pH was determined in a suspension of soil (1 g) and distilled water (2.5 g), using a pH meter (Mettler Toledo). Total nitrogen and total carbon were determined by

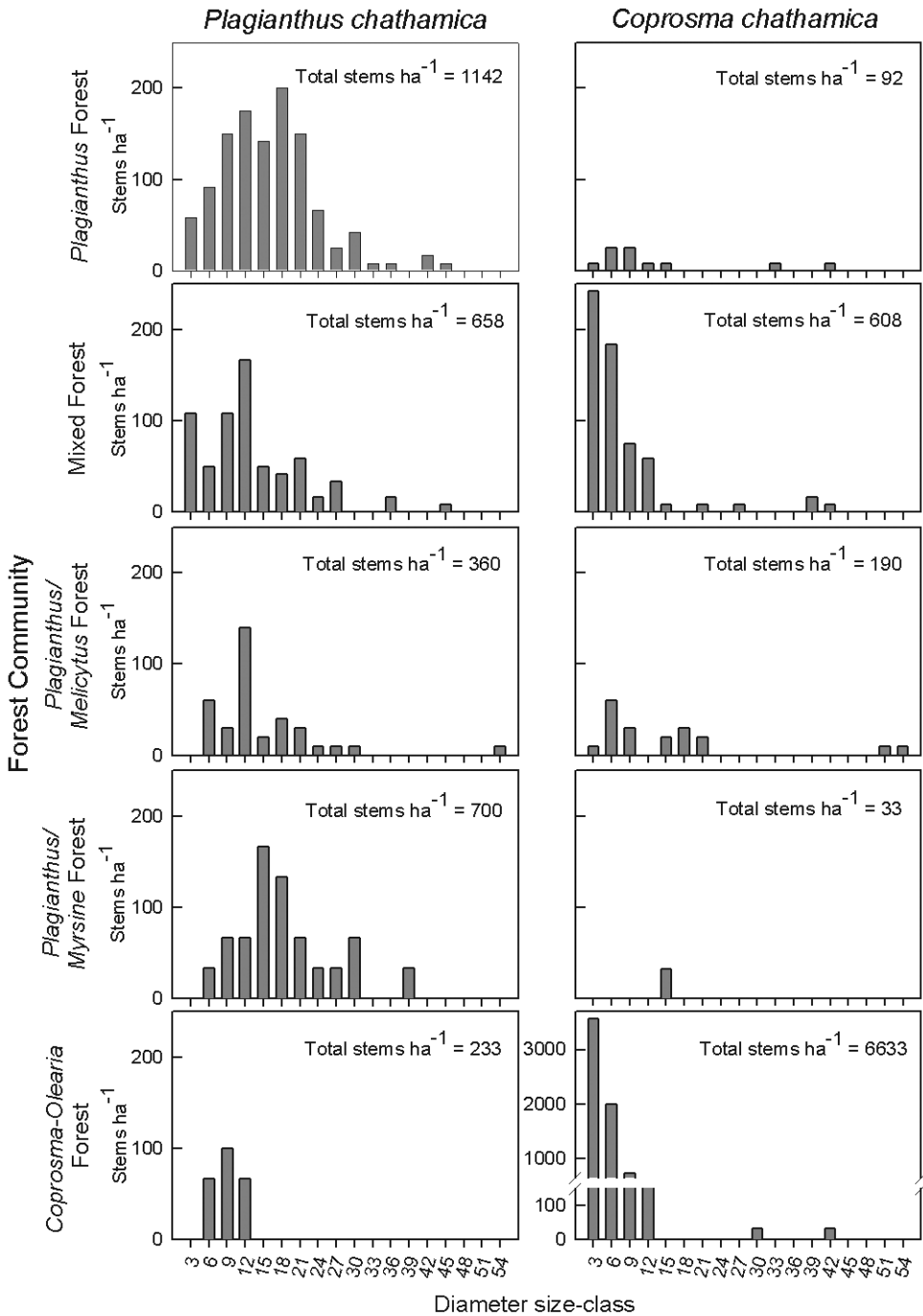
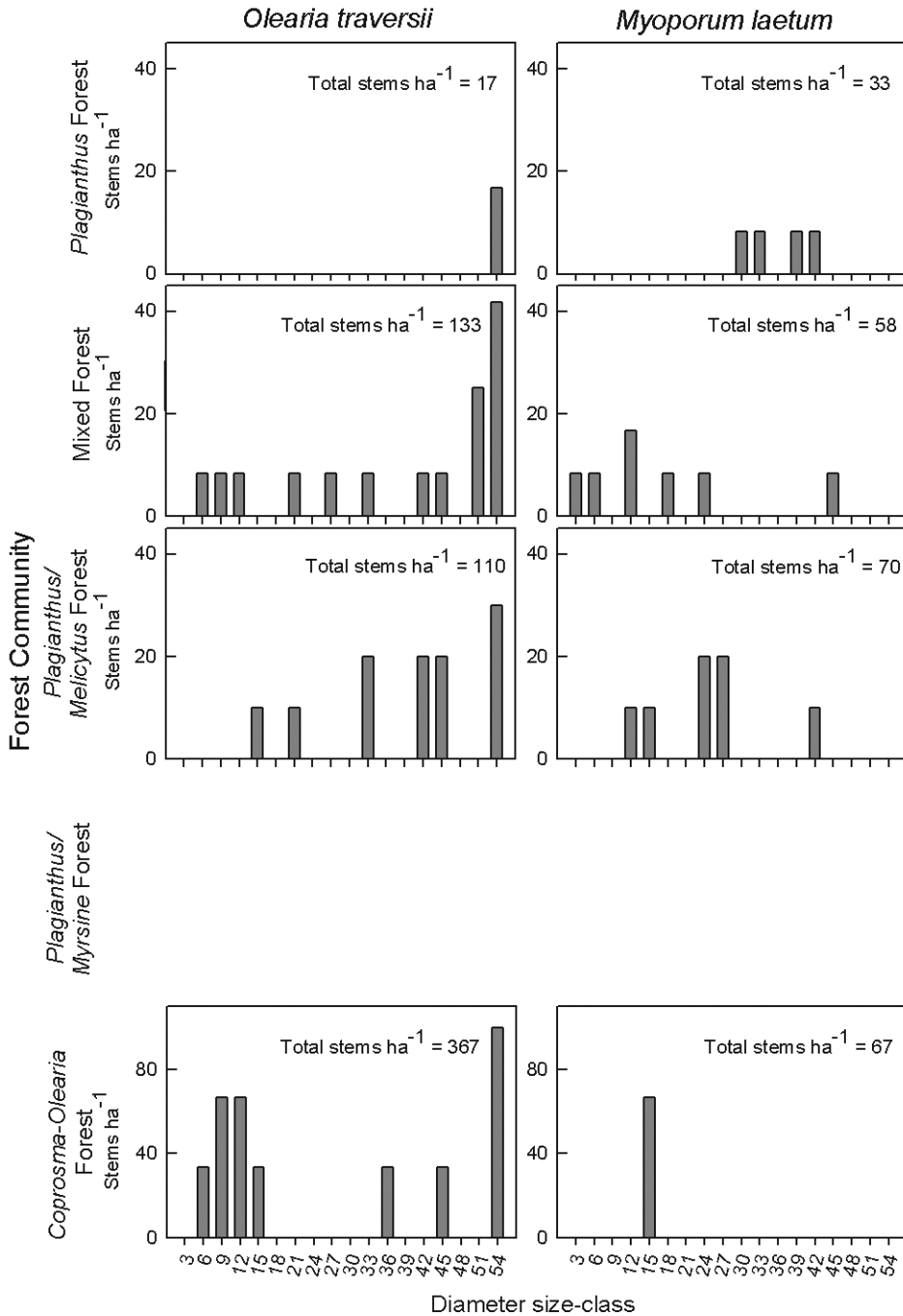


Figure 2a. Bar graphs showing density of stems in diameter size-class for two of four main canopy species found in five forest communities identified by cluster analysis on Rangatira Island.



**Figure 2b.** Bar graphs showing density of stems in diameter size-class for two of four main canopy species found in five forest communities identified by cluster analysis on Rangatira Island.

**Table 1.** Summary of the characteristic features of the five forest communities identified by a cluster analysis (see text) followed by a size-class profile, from 40 forest survey plots located on Rangatira Island. Nomenclature follows Atkinson (1985).

**Plagianthus Forest** (12 plots). Canopy of *Plagianthus chathamicus* (ribbonwood) and an understorey (of equal density) of *Melicytus chathamicus* (māhoe) and *Myrsine chathamica* (matipou); few other species present. The size-class profile shows few live or dead species in the larger dbh class, suggesting this forest is a young forest community; 30% of the forest is in this forest type, which is found in Woolshed Bush, Ikes Bush and Top Bush.

**Mixed Forest** (12 plots). All canopy species (*Plagianthus chathamicus*, *Olearia traversii* (akeake), *Coprosma chathamica* (karamū), and *Myoporum laetum* (ngaio)) and all understorey species, including *Macropiper excelsum*, present; 30% of the forest is in this forest type. A higher dbh size-class (including dead trees) was found in this forest, suggesting a more mature forest. This forest was predominantly found in Top Bush (11 out of 12 plots).

**Plagianthus/Melicytus Forest** (10 plots). Canopy of *chathamicus* and understorey dominated by *Melicytus chathamicus*; 25% of the forest is in this forest type, which is found in Woolshed Bush, Island Bush and Top Bush and favours forest edges.

**Plagianthus/Myrsine Forest** (3 plots). Canopy dominated by *Plagianthus chathamicus* and understorey by *Myrsine chathamica*. Both *Macropiper excelsum* and *Olearia traversii* are absent; 7.5% of the forest is in this forest type. This forest community is only found in Woolshed Bush.

**Coprosma–Olearia Forest** (3 plots). Canopy of *Coprosma chathamica* and *Olearia traversii*. These plots are generally characterised by young, densely regenerating *Coprosma chathamica* forest in the damper areas of Top Bush; 7.5% of the forest is in this forest type.

dry combustion, using a carbon and nitrogen analyser (Leco CNS-2000 Analyser). Available phosphorus was extracted with a solution of 0.03 M ammonium fluoride and 0.1 M HCl (Bray & Kurtz 1945) and was determined colorimetrically by the phosphomolybdate blue method. We used ANOVA and Tukey's HSD to identify variables that differed among forest communities.

#### *Burrow density*

The total number of seabird burrow entrances in each plot (10 × 10 m) were counted as the best available measure of burrowing activity. We did not distinguish between burrow entrances of different size. For simplicity, and because the actual number of burrow chambers was not determined, our measure of burrow density is the number of entrances per square metre.

#### **Seabird exclusion experiment**

To examine the impact of seabird burrowing on woody seedling regeneration, we placed a seabird enclosure paired with a control plot in the centre of each of the 30 randomly located forest plots (10 × 10 m). The enclosures were constructed from wire mesh (25 × 20 mm) with dimensions of 0.5 × 0.5 m and 0.2 m high, open on the bottom, and held in place with aluminium pegs at each corner and at the midpoint along each side. The paired plots were located so that they did not cover burrow entrances but were no more than 1 m apart, and the enclosure or control treatment was randomly assigned. The plots were put in place in April 2002, at which time all woody seedlings in the enclosure and control plots were recorded. When the plots were remeasured in 2003, one enclosure was found to be impacted by burrowing so that pair was dropped from

the 2003 analysis and the enclosure repaired. However, this enclosure was included in the sampling after 24 months (April 2004) and 33 months (January 2005), as a change in seedling height over time was not used in the final analyses, as in most of the enclosures (with a few exceptions) the seedling cohort of one year was replaced with a new cohort the next.

In January 2003, canopy cover above the paired enclosures and controls was estimated by taking a digital photograph at each plot centre using a fisheye lens. The digital images were analysed using Adobe Photoshop Software (version 7). The Histogram function was used to calculate the number of sky pixels in the image. Following Sullivan's (2003) methods the colour selection was set to pure white and the fuzziness to 150, which was sufficient to distinguish white cloud and blue sky from foliage.

To explore the variation in seedling counts among enclosure plots, we examined the relationship between the number of seedlings counted in enclosure plots in 2005 and four explanatory variables: soil N and P, percent of the canopy that was open to the sky (from the fisheye photographs), and density of bird burrows. We modelled the relationships using a log link function assuming the errors follow a negative binomial distribution to allow for overdispersion in the counts. Parameters were estimated using maximum likelihood.

#### **Regeneration in forest canopy gaps**

To assess the importance of canopy gaps as sites for tree regeneration, we surveyed canopy gaps along 30 belt transects (100 × 20 m) located along walking tracks to minimise burrow damage; their start located

by stratified random sampling. Five transects were allocated to each of the eastern and western sides of Woolshed Bush, and 10 transects to each of the eastern and western sides of Top Bush. A transect start location was chosen by randomly choosing a track, a start point, and a direction. From the start location, we walked along the track in the selected direction and located all canopy gaps 10 m either side of the track. A canopy gap was defined as an area  $\geq 25 \text{ m}^2$  (equivalent to a square  $5 \times 5 \text{ m}$ ) created by a tree or limb fall, extending through all levels of forest and open to the sky. Each canopy gap was delimited by vertically projecting the opening in the canopy to the ground surface (Brokaw 1982). Canopy gap area,  $A$ , was calculated by measuring the length,  $L$ , (longest distance from gap edge to gap edge) and width,  $W$ , (longest distance at right angles to the length), and using the formula for an ellipse:  $A = \pi LW/4$  (Stewart et al. 1991).

Along the length of the gap, we located a series of circular understorey plots each with a radius of 49 cm (area =  $0.75 \text{ m}^2$ ). These were positioned by laying a measuring tape along the length of the gap and locating a plot every metre alternately to the left and right of the tape. The distance from the tape was randomly chosen. Because plots were located every metre, we measured more plots in larger gaps. In each plot, we counted the number of woody seedlings of each species. We also counted the number of seabird burrow entrances in the rectangular area defined by the length and width of the canopy gap.

To compare regeneration patterns in gap versus non-gap areas, we paired each gap with a non-gap site of equivalent dimensions and repeated the entire sampling procedure. Each non-gap site was located a random distance (between 5 and 10 m) in a random direction away from the gap edge. For comparison between gaps and non-gaps all data were converted into density per hectare.

## Results

### Composition and structure of the forests

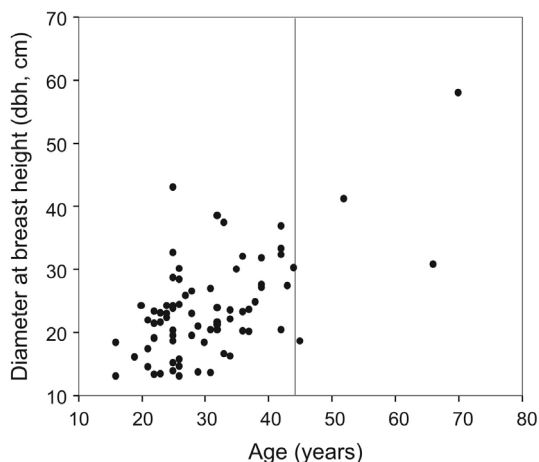
The forests of Rangatira Island comprise, in varying combinations, eight major tree species (four canopy and four subcanopy). The canopy species are *Plagianthus chathamicus*, *Olearia traversii*, *Coprosma chathamica* and *Myoporum laetum*. Over the forested part of the island, these form a continuous cover with a maximum canopy height varying between 10 and 15 m.

The four canopy species have different size-frequency distributions, and this combined with the relative density of canopy and subcanopy species distinguishes the forest communities (Fig. 2a & 2b). Overall stem density per hectare was significantly higher in the *Coprosma*–*Olearia* Forest than the

*Plagianthus* Forest ( $P < 0.05$  Tukey's HSD test), but not significantly different from the other forest communities. Both *Olearia* and *Myoporum* occur at low densities as scattered, often large trees, with very few stems in any size category (Fig. 2b). *Coprosma* (Fig. 2a) has a reverse-J-shaped size distribution in two of the five forest communities, with many small stems and progressively fewer in the larger size-classes, while *Plagianthus* (Fig. 2a) has a bell-shaped size distribution in all forest communities with most stems in the range 9–24 cm dbh. The four subcanopy tree species, *Melicytus chathamicus*, *Macropiper excelsum*, *Myrsine chathamica* and *Pseudopanax chathamicus*, all have a reverse-J-shaped size distribution (not shown). *Melicytus* dominated the 3–9 cm dbh classes but there were no trees larger than 15 cm dbh. *Myrsine* occurs at much lower density but was found in all size classes up to 30 cm dbh. Dead standing trees with dbh  $> 15$  cm were virtually absent from every forest community except the Mixed Forest.

The understorey subplots revealed very patchy seedling establishment. Of the canopy species, *Plagianthus* was the dominant woody seedling (c.  $4200 \text{ ha}^{-1}$ ), with no *Olearia* or *Coprosma* seedlings in the subplots and very few *Myoporum*. By sapling height, *Plagianthus* density had dropped to 28 saplings  $\text{ha}^{-1}$ . Of the subcanopy species *Melicytus*, *Myrsine* and *Macropiper* were all found at high seedling densities (c.  $3000 \text{ ha}^{-1}$ ), which dropped to c.  $1000 \text{ ha}^{-1}$  for *Melicytus* and *Myrsine* and c.  $855 \text{ ha}^{-1}$  for *Macropiper* by the sapling stage.

Of 153 trees cored, only *Plagianthus* ( $n = 75$ )



**Figure 3.** Relationship between diameter at breast height (1.35 m) and age (years) for cored *Plagianthus* trees ( $n = 75$ ) in 40 plots on Rangatira Island, Chatham Islands. The vertical line indicates stock removal 43 years ago.



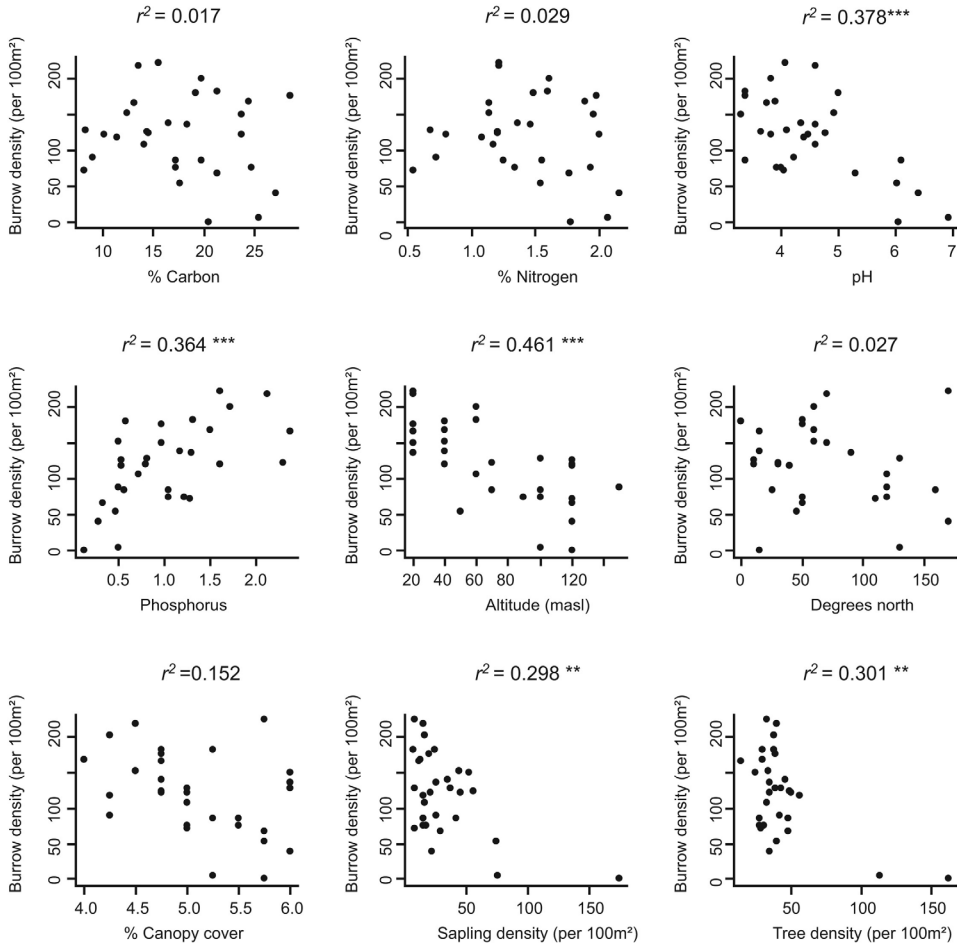
produced rings clear enough for accurate ageing. The majority of *Plagianthus* trees aged were less than 43 years old. Assuming that coring the largest tree on each plot provides an estimate of the age of the forest, we surmise that most of the present *Plagianthus* forest has regenerated since farming ceased in 1959 and most stock were removed (Fig. 3).

Of the environmental variables we measured, only soil pH differed among communities, with the pH significantly lower in both the *Plagianthus* ( $4.02 \pm 0.12$ ) and *Plagianthus/Myrsine* ( $3.36 \pm 0.02$ ) ( $P < 0.05$  Tukey's HSD test) compared with the other forest communities

(Mixed Forest  $5.18 \pm 0.31$ , *Plagianthus/Meliccytus*  $4.72 \pm 0.37$ , *Coprosma-Olearia*  $5.06 \pm 0.99$ ).

**Seabird burrow density and soil characteristics**

Within plots, seabird burrow counts ranged from 0 to 223 per 100 m<sup>2</sup>, with a mean burrow density of  $1.19 \pm 0.10$  m<sup>-2</sup>. The soil characteristics of all plots (mean  $\pm$  SE) were: total %C  $17.74 \pm 1.03$ , total %N  $1.43 \pm 0.08$ , and P mg/kg  $1024 \pm 110$ . All soils were highly acidic (pH  $4.52 \pm 0.18$ ), and burrow density was positively correlated with soil phosphorus and negatively with altitude, pH, sapling and tree density (Fig. 4).



**Figure 4.** Relationship of seabird burrow density to environmental variables, sapling and tree density (stems ha<sup>-1</sup>), and soil properties. Seabird burrow density is shown on the y-axis in all graphs for consistency but is not meant to imply that the variable on the x-axis causes variation in burrow density. In several cases, variation in burrow density is more likely the cause of variation in the x-axis variable (e.g. for soil nutrients). Altitude (masl = metres above sea level), Degrees North (degrees away from north).  $r^2$  values are the coefficient of determination: \* =  $P < 0.05$ , \*\* =  $P < 0.01$ , \*\*\* =  $P < 0.001$  (with the  $P$ -values corrected for multiple comparisons using the Bonferroni procedure).

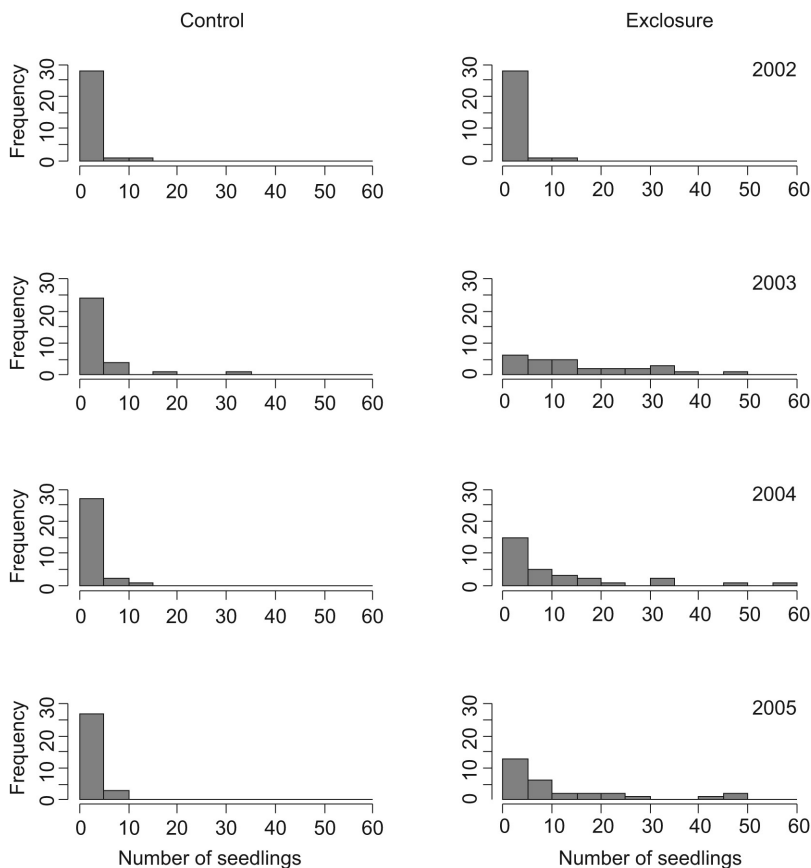
### Seabird exclusion experiment

There was no significant difference in woody seedling density between the 30 paired exclusion and control plots when the plots were established (paired Wilcoxon rank sum test,  $V = 6$ ,  $P = 0.17$ ). At all subsequent measurements, there were clear differences between treatments with, on average, more seedlings found in exclusion than control plots (Fig. 5). In 2005, the mean number of woody seedlings counted in control plots was  $1.1 \pm 0.50$  and in exclusion plots was  $13 \pm 2.9$ . There was nevertheless substantial variation in seedling counts among exclusion plots and seedling species composition from one count to the next. At the first count of seedlings in exclusion plots in 2003, *Plagianthus* (44%) and *Melicytus* (39%) were found to be the most common (total seedlings = 700). By 2005, however, *Plagianthus* (3%) were rarely found and *Macropiper* (55%) became the most abundant, with *Melicytus* (39%) remaining unchanged (total seedlings = 103). By comparison, in the control plots at the first count in 2003, *Plagianthus* represented only 19% of total

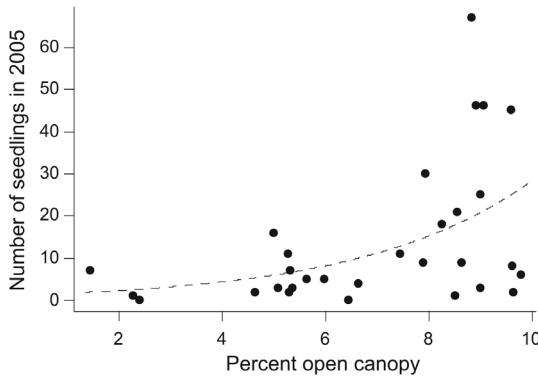
seedlings (390) whereas *Melicytus* represented 69%. By 2005 *Plagianthus* (3%) had virtually disappeared and *Macropiper* (39%) and *Melicytus* (54%) were the most common (total seedlings = 33). We found no significant differences in seedling density or seedling composition among forest communities, and no correlation between seedling density and environmental variables, with the exception that seedling counts were higher in more open- canopied plots (change in deviance relative to a null model of no relationship = 11.6, 1 d.f.,  $P < 0.001$ ), with a greater number seedlings under higher light conditions (Fig. 6).

### Regeneration in forest canopy gaps

We searched a total of 6 ha along transects and found 14 canopy gaps, six in Woolshed Bush and eight in Top Bush. Canopy gaps were small (mean area  $< 32 \text{ m}^2$ ), usually having been created by the fall of a single tree. The total area found in canopy gaps was  $438.6 \text{ m}^2$ , or 0.73% of the area surveyed.



**Figure 5.** Frequency distributions of the total number of seedlings found in all seabird exclusion and control plots ( $0.5 \times 0.5 \text{ m}$ ) during annual measurements from 2002 to 2005 (exclusion plots were established after measurement in 2002).  $n = 30$  exclusion and 30 control plots in all years except 2003, when  $n = 29$ . Not shown are three plots in 2003 and one plot in 2005 that each had  $>60$  seedlings.



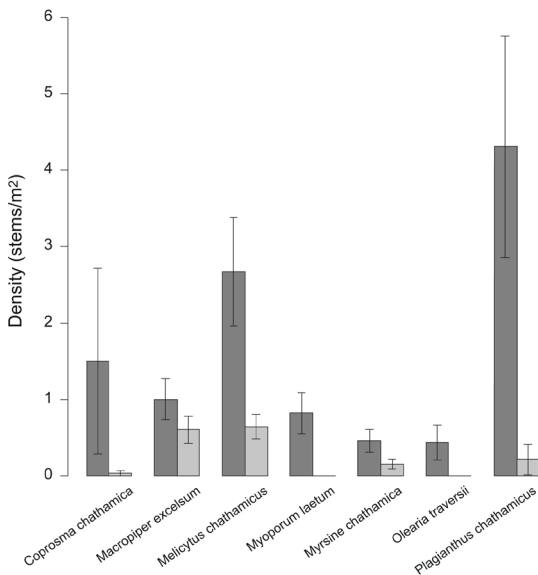
**Figure 6.** Relationship between number of seedlings counted in seabird exclosure plots ( $0.5 \times 0.5$  m) and percent canopy cover. The dotted line is the maximum likelihood regression line obtained using a log link function and assuming negative binomial distributed errors to allow for overdispersion in the counts.

**Table 2.** Paired t-tests comparing mean number of woody species ( $n = 7$ ) seedlings in 14 canopy gaps and 14 non-gap plots, and the mean density of burrows in canopy gaps compared with non-gap plots on Rangatira Island.

	n	Mean $\pm$ SE	t	P
Woody species <135 cm				
Gap	14	48.57 $\pm$ 5.71	6.689	0.001
Closed canopy	14	7.28 $\pm$ 1.90		
No. of burrows				
Gap	14	43.00 $\pm$ 8.23	-2.939	0.012
Closed canopy	14	66.64 $\pm$ 7.25		

Seventy-one percent of canopy gaps were created by the fall of *Olearia* trees and 21% by *Plagianthus*. The ratio of fallen *Olearia* to *Plagianthus* corresponds to the ratio of the larger size classes of these species (Fig. 2a & 2b). The dbh of gap makers ranged from 20 to 99 cm with a mean of 57 cm. Most fallen trees had been uprooted (71%) and the root system of all fallen trees had been heavily burrowed.

The seedling density of seven of the eight dominant canopy and subcanopy species was significantly higher in canopy gaps compared with non-gap plots (Table 2), with regeneration in canopy gaps dominated by *Plagianthus* and *Melicytus* (Fig. 7). There tended to be fewer seabird burrows in gaps than non-gap areas (Table 2).



**Figure 7.** Density (stems per hectare) of the main tree species (including seedlings) in 14 canopy gap plots compared with 14 control plots on Rangatira Island. Black shaded bars indicate canopy gap plots; grey shaded bars indicate control plots. Error bars are  $\pm 1$  SE.

## Discussion

### Forest structure and composition

The forests that have regenerated since farming ceased are relatively simple in structure and composition, and while it is possible to identify communities comprising different ratios of the species represented, these are not clearly differentiated by environmental factors. The post-farming forest remnant in Top Bush is presumed to be the nearest in composition to the original forest on the island, given that this was the largest surviving remnant. Our analysis identified this forest type as Mixed Forest with all canopy and subcanopy species present. Apart from one outlier (Fig. 1) this forest type was found only in Top Bush. If our presumption is correct, then the original canopy and subcanopy species mix has not regenerated across the island.

The deciduous *Plagianthus chathamicus* currently dominates four of the five forest communities (Fig. 2a), occurring in varying associations with the other main canopy species *Olearia traversii*, *Coprosma chathamica* and *Myoporum laetum*. *Olearia* occurs almost exclusively as large trees scattered throughout

the forest, and the present large *Olearia* trees appear to have colonised during, or persisted through, the farming era indicative perhaps of their resilience to disturbance compared with other forest species. While *Olearia* is abundant on the forest edges, we found no *Olearia* seedlings in the exclosures and few in the understorey plots or canopy gaps. Many of the large *Olearia* trees are now senescing, with *Olearia* being the dominant cause of canopy gaps, suggesting this species is declining and may disappear from within the forest as the remaining large trees die.

Most large *Plagianthus* trees that were cored had a date post-farm-abandonment (Fig. 3), and this together with their bell-shaped size distribution found in all forest types implies a pulse of regeneration post-farming, followed by a slowing of regeneration due to canopy closure. Of the other two canopy species, there were no *Coprosma* seedlings in either the exclosures or understorey subplots and it was rare in canopy gaps (Fig. 7). However, *Coprosma* was found in high densities as saplings and young trees in regenerating areas on the damper north-western side of Top Bush (Fig. 1). *Coprosma* is not regenerating elsewhere, suggesting a trend away from the original Mixed Forest community to a more homogenous forest dominated by *Plagianthus*, with *Coprosma* restricted to the western side of the island.

### Bird impacts, canopy gaps and forest regeneration

We recorded a mean seabird burrow density of  $1.19 \text{ m}^{-2}$ , similar to the burrow density of  $1.39 \text{ m}^{-2}$  recorded by West and Nilsson (1994) in 1989/90. This is high compared with other seabird colonies in New Zealand. Mulder and Keal (2001) recorded a density of  $0.84 \text{ m}^{-2}$  on Stephens Island, Cook Strait, Waugh et al. (2003) found a burrow density of  $0.24 \text{ m}^{-2}$  for Westland petrel (*Procellaria westlandica*), Fukami et al. (2006) recorded a density of  $0.36 \pm \text{SEM } 0.11 \text{ m}^{-2}$  across nine seabird islands in northern New Zealand, although Warham and Wilson (1982) estimated sooty shearwater burrow density to be  $1.16 \text{ m}^{-2}$  in *Olearia lyallii* forest on the Snares Islands. In a colony of *Puffinus tenuirostris* on Cape Queen Elizabeth, Tasmania, burrow density varied between  $0.04$  and  $0.74 \text{ m}^{-2}$  (Walsh et al. 1997).

Seabird burrow density varied across the island, with fewer burrows at higher altitude ( $>65 \text{ m}$ ) and in areas with a high density of saplings and trees (Fig. 4). This most likely reflects a preference by birds for more open-canopied forest because of the difficulty of burrowing in heavily rooted areas. Areas with higher densities of seabird burrows also had lower soil pH, consistent with findings in other seabird colonies (Ellis 2005), and higher available phosphorus levels. This was most likely the result of seabird guano lowering soil pH through nitrification from ammonium to nitrate after

mineralisation of organic nitrogen, and from greater inputs of P through nutrient transfer in areas more heavily used by seabirds (Smith 1978; Okazaki et al. 1993; Anderson & Polis 1999).

Exclusion of seabirds resulted in a marked increase in woody seedling numbers in the understorey exclosure plots (Fig. 5), implying that seabirds inhibit regeneration through their trampling and burrowing activities (Gillham 1956, 1960; Maesako 1985, 1999; Warham 1996; Mulder & Keall 2001). Nevertheless, there was no relationship between seabird burrow density (which we assume is a surrogate for bird activity) and the numbers of woody seedlings in the exclosures. Instead, the number of woody seedlings regenerating in seabird exclosures was positively related to the amount of open canopy directly above the exclosures, suggesting that in addition to seabirds, seedling regeneration is strongly limited by light availability. This finding is reinforced by the canopy-gap survey, which revealed high densities of seedlings regenerating in gaps. Hence, although there is an inhibitory effect of seabirds on seedling establishment and survival, this does not appear to be a barrier to successful regeneration under the higher light conditions found in canopy gaps. We further observed a lower density of burrows in gaps than in adjacent non-gap plots (Table 2), consistent with our finding that seabird burrow density was lower in plots with high densities of saplings and trees (Fig. 4). Birds may be forced to abandon burrows in areas of densely regenerating forest (such as in canopy gaps) due to difficulties in physically accessing the sites.

Gaps are central to forest dynamics (Runkle 1982; Brokaw 1987; Schnitzer & Carson 2001). However, little work has been done on canopy gaps on seabird islands with which to compare the findings of this study, though Johnson (1982) noted that in the low-canopy (6–8 m tall) *Olearia lyallii* and *O. augustifolia* forest on Putauhina Island (South-West Muttonbird Islands), windthrow usually involved more than one tree and clearings of 10–20 m across were the rule.

The treefall gaps on Rangatira Island covered 0.73% of the 6 ha surveyed and were generally small, with 12 of the 14 gaps having an area less than  $31 \text{ m}^2$ . While there are a number of factors that can lead to uprooting – windiness, growth form, rigidity and the height of trees above the surrounding forest (Peterson 2000; Martin & Ogden 2006) – an additional factor on Rangatira Island is the burrowing around tree roots, which loosens the soil, dries out the roots, and weakens the trees.

### Future of the forest

Rangatira Island is an important wildlife sanctuary dependent on the maintenance of forest cover to provide habitat for its many rare and endangered species. Our results show that most of the present forest is

young, resulting from regeneration following farm abandonment, and that the forest across the island comprises various mixtures of four dominant canopy and four dominant understorey species. Seabirds burrow at very high densities in the forest, and seabird activity has a significant inhibitory effect on seedling regeneration under closed canopies. Although several of the understorey species, including *Myrsine* and *Macropiper*, can regenerate from root suckers and form thickets, the dominant canopy species, *Plagianthus*, does not resprout and relies on regeneration from seed. Our results show that canopy gaps are critical for successful canopy tree regeneration, and that regeneration is dominated by *Plagianthus*, suggesting it will remain the major canopy species on the island. The large senescing *Olearia* that create most of the current canopy gaps are gradually disappearing from the forest. This will most likely cause a decline in the number of potential gap-makers until the post-farming cohort of *Plagianthus* senesces, or becomes unstable due to seabird burrowing. The future of the forest at this stage is unclear. If the *Plagianthus* canopy suffers a progressive collapse over a reasonably long time period, the forest could remain largely intact with tree replacement occurring in small gaps, as appears to be happening at present. There is also the possibility, given the density of burrowing seabirds, that the relatively even-age *Plagianthus* trees could simultaneously become susceptible to windfall, and the forest could become prone to a more catastrophic blowdown.

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