

## Restoring bird pollination of *Fuchsia excorticata* by mammalian predator control

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**Abstract:** Many restoration projects aim to increase populations of native fauna and flora, but benefits to the ecological interactions between species are unknown. The restoration of bird pollination services to *Fuchsia excorticata* (tree fuchsia) was examined at Maungatautari, in the Waikato Region, New Zealand. At Maungatautari, a pest-exclusion fence encloses ~3400 ha of native forest, within which most mammalian pests were eradicated between 2004 and 2007. In December 2010, 140 five-minute bird counts at Maungatautari and a non-treatment site, Pirongia Forest Park, indicated that tūi (*Prosthemadera novaeseelandiae*) and bellbirds (*Anthornis melanura*), key pollinating species, were significantly more abundant at Maungatautari than Pirongia. We then examined whether greater bird numbers at Maungatautari translate into enhanced bird services. A previous study correlated visual pollen scores on *F. excorticata* flowers to fruit set, allowing rapid assessment of pollination levels. Pollination service to *F. excorticata* was significantly greater at Maungatautari, with good pollen loads on the stigmas of both female and hermaphrodite flowers there, compared with inadequate pollination on both sexes at Pirongia. Observations of bird visitors to *F. excorticata* flowers found significantly higher visitation rates at Maungatautari than Pirongia, consistent with the better pollination levels. Pollination levels of *F. excorticata* were compared with data from 68 sites from around New Zealand with a range of mammalian predator control levels. Sites that were pest-fenced, islands, or mainland islands (and assumed to have lower densities of mammalian pests) had good pollen scores on female plants, whereas at unmanaged sites females had inadequate pollination. This study indicates that higher abundance of pollinating birds as a result of mammalian pest control restores the pollination service to *F. excorticata*.

**Keywords:** *Anthornis melanura*; conservation; five-minute bird counts; *Notiomystis cincta*; pollen loads; *Prosthemadera novaeseelandiae*; restoration; trophic cascade

### Introduction

Bird mutualists provide plants with a range of services, including pollination and seed dispersal, which contribute significantly to maintaining plant populations and community composition (Kearns et al. 1998; Şekercioğlu et al. 2004). However, large declines in range and density of bird species worldwide potentially place at risk the ecosystem services that birds provide (Şekercioğlu et al. 2004; Traveset & Richardson 2006). Failure of either pollination or dispersal mutualisms could increase the risk of plant extinction (Bond 1994). Extinction risk is influenced by three factors: the likelihood of pollinator or disperser failure, the extent to which reproduction depends on the mutualism (e.g. flowers require visits by pollinators or seeds require visits by dispersers), and the demographic importance of seeds (i.e. the population is seed-limited) (Bond 1994). New Zealand is particularly at risk of mutualism failure because the prehuman avifauna has been considerably altered (Şekercioğlu et al. 2004), and New Zealand has a high proportion of bird-pollinated and bird-dispersed trees compared with other temperate regions (Lord 1999; Kelly et al. 2010).

In New Zealand, tūi (*Prosthemadera novaeseelandiae*), bellbirds (*Anthornis melanura*) and silvereyes (*Zosterops lateralis*)<sup>1</sup> are the most important pollinators (Craig et al. 1981; Kelly et al. 2006). Hihi (stitchbird *Notiomystis cincta*) would also have been important pollinators in the North Island before becoming restricted to offshore islands and a few intensively

managed mainland sites to which they have been recently reintroduced (Craig et al. 1981; Kelly et al. 2006; Chauvenet et al. 2012). Although no pollinating birds are thought to have become extinct (Atkinson & Millener 1991), all extant pollinating bird species, with the exception of silvereyes, have restricted distributions and/or densities compared with in prehuman times (Higgins et al. 2001; Kelly et al. 2006, 2010). These reductions have largely resulted from predation by introduced predatory mammals, but are also related to habitat loss and, more speculatively, perhaps sometimes avian disease (Higgins et al. 2001; Innes et al. 2010).

Direct measurements of pollination services to plants show that mutualism failure is occurring for some bird-visited plant species on the New Zealand mainland, because of reductions in densities and species of pollinating birds (Robertson et al. 2008; Anderson et al. 2011). Work on the bird-pollinated plant *Rhabdothamnus solandri*<sup>2</sup>, comparing the New Zealand mainland where the sole pollinating birds are tūi, to island bird sanctuaries where all endemic bird pollinators are still abundant, showed fruit set was strongly pollen-limited on the mainland but not on the islands (Anderson et al. 2006, 2011). *Peraxilla* spp. mistletoes, *Sophora microphylla*, *Fuchsia perscandens* and *F. excorticata* are also frequently pollen-limited on the mainland (Robertson et al. 1999, 2008; Montgomery et al. 2001; Kelly et al. 2007, 2010).

Currently, mammalian predation is the main cause of declines and limitation of endemic forest birds in remaining

<sup>1</sup> Scientific names of birds follow New Zealand Birds Online: The digital encyclopaedia of New Zealand birds. <http://www.nzbirdsonline.org.nz>

<sup>2</sup> Plant names follow Nga Tipu Aotearoa – New Zealand plants. <http://nzflora.landcareresearch.co.nz/>

large native forest areas on the New Zealand mainland (Innes et al. 2010). Control of mammalian predators improves nesting success (e.g. kererū *Hemiphaga novaeseelandiae*, Clout et al. 1995; Innes et al. 2004; bellbirds, Kelly et al. 2005; bellbirds and grey warblers *Gerygone igata*, Starling-Windhof et al. 2011), and increases the abundance of particular species (e.g. kererū, Gillies et al. 2003; bellbirds, Kelly et al. 2005; tūī, O'Donnell & Hoare 2012). Mammalian pest control obviously benefits native bird species, and may also directly benefit native plant species by decreasing consumption of vegetative or reproductive parts (e.g. Cowan 1991; Sessions et al. 2001; Urlich & Brady 2005). The effects of mammalian pest control on bird–plant mutualisms remain less well known. In principle, pest control should restore pollination services (i.e. increase to levels existing in prehuman times, which are assumed to be similar to current levels on pest-free islands: Anderson et al. 2011) by increasing the abundance of bird mutualists. The only specific attempt to test this in New Zealand is that of Kelly et al. (2005), who attempted to restore the pollination service to the pollen-limited mistletoe *Peraxilla tetrapetala* by trapping stoats (*Mustela erminea*) to enhance bellbird numbers. They were unsuccessful; bellbird numbers increased, but pollination levels did not, for unknown reasons. More generally, it cannot be assumed that altering rates of pollination or dispersal will have an effect at the plant population level. For example, if plants are not seed-limited, then reduced fruit set from pollen limitation will have no effect, as enough seeds are still produced even at the lower pollination levels (Bond 1994).

Control of mammalian pests is becoming increasingly prevalent, often with the goal of restoring whole communities nearer to the prehuman state (Saunders & Norton 2001). The Department of Conservation (DOC), during 1995 and 1996, initiated the first 'mainland islands'. These are areas with species- and ecosystem-focused restoration goals, which have intensive sustained control of multiple pest species (Saunders & Norton 2001). Since 1999, sanctuaries, fenced to prevent ingress by mammalian predators, have been constructed on the mainland, allowing eradication or near-eradication of mammalian pests (Speedy et al. 2007; Burns et al. 2012; Innes et al. 2012) and subsequent reintroduction of some highly pest-sensitive native taxa such as hihi (Chauvenet et al. 2012).

The purpose of this study was to determine whether the control of mammalian pests indirectly restores the pollination service received by native plants. To examine this, Maungatautari Ecological Island was chosen as a focal fenced sanctuary and paired with a non-treatment site, Pirongia, which has a low level of mammalian pest control. We used *Fuchsia excorticata* to measure pollination service, as it is often pollen-limited on mainland sites, and pollination levels can be assessed visually (Robertson et al. 2008). Additionally, for comparison, data on pollination levels of *F. excorticata* were available from field surveys of sites around New Zealand with a range of predator-control levels. We have assumed: (1) that before human-induced reductions in native bird numbers over the mainland, *F. excorticata* would have received adequate pollen deposition on stigmas (i.e. would not have been pollen-limited); (2) that before pest control at Maungatautari, pollen deposition there would have been similar to that currently measured at Pirongia. The first assumption was supported by analogous data for *Rhabdothamnus solandri* (Anderson et al. 2011), where island bird sanctuaries allowed measurement of pollination under bird abundances that are probably representative of the prehuman situation; the second assumption was tested with data from other sites in New Zealand (objective 4 below).

This study had four objectives:

1. Determine the relative abundances of pollinating bird species at Maungatautari (treatment) and Pirongia (non-treatment).
2. Determine which bird species are visiting flowers of *F. excorticata* and compare their visitation rates at Maungatautari and Pirongia.
3. Compare pollination levels of *F. excorticata* at Maungatautari and Pirongia.
4. Compare pollination levels of *F. excorticata* at sites around New Zealand with and without intensive mammalian pest control.

## Methods

### Study sites

Maungatautari (38°01' S, 175°34' E), in the Waikato Basin, is the largest mammalian pest-fenced sanctuary in New Zealand (Innes et al. 2012). A 47-km-long pest-fence has been built around 3400 ha of forest, and the Maungatautari Ecological Island Trust (MEIT) works to eradicate mammalian pests and reintroduce endemic species (McQueen et al. 2004). Eradication of pest species began in two small trial areas (totalling 100 ha in September 2004) then was extended to the whole fenced area in November 2006, using aerially applied brodifacoum, with further applications in December 2006 and June–July 2007 (Speedy et al. 2007). The initial aerial poisoning operations would have killed the majority of mammals (Fitzgerald et al. 2009). At the time of this study, in November and December 2010, the only mammalian pests remaining on Maungatautari were low numbers of mice (*Mus musculus*), rabbits (*Oryctolagus cuniculus*) and hares (*Lepus europaeus*) (P. Quinn, MEIT, pers. comm.). By November 2010 six bird species, including hihi, had been reintroduced to Maungatautari (C. Smuts-Kennedy, MEIT, pers. comm.). Hence, Maungatautari had all four of the most important extant pollinators present (tūī, bellbirds, silvereyes, and hihi).

Pirongia Forest Park (37°59' S, 175°05' E), 35 km west of Maungatautari, is administered by DOC. The area used in this study, Pirongia mountain, covers 13 600 ha. Mammalian predators are present at Pirongia although intermittent aerial applications of sodium monofluoroacetate (1080) are used to control brushtail possums (*Trichosurus vulpecula*). Pirongia was most recently treated with 1080 in July 2007, resulting in a residual trap-catch rate of 0.42% (0.42 possums caught per 100 traps set) (M. Lewis, DOC, pers. comm.). Ship rats (*Rattus rattus*) and stoats, while most likely reduced in numbers by the poison operation, are expected to have recovered within a year (Murphy & Bradfield 1992; Innes et al. 1995; Murphy et al. 1999). The avifauna at Pirongia is representative of forest birds common to the Waikato region and similar to that at Maungatautari prior to pest eradication (Innes et al. 2003).

Both sites are volcanic in origin. Although Pirongia has a greater elevation range (90–959 m a.s.l.) than Maungatautari (280–797 m a.s.l.), the sites have similar vegetation at similar elevations. Vegetation changes altitudinally from lowland tawa (*Beilschmiedia tawa*) forests with emergent rimu (*Dacrydium cupressinum*), to upland forests composed predominantly of kāmahi (*Weinmannia racemosa*), tawari (*Ixerba brexioides*), and tawheowheo (*Quintinia serrata*) (Burns & Smale 2002; Clarkson 2002).

## Study species

*Fuchsia excorticata* (Onagraceae) is a long-lived endemic tree, reaching 13 m in height, that has several features that make it an ideal indicator species for pollination service. This species is found in lowland to subalpine forests throughout New Zealand, is bird-pollinated, and frequently pollen-limited on the New Zealand mainland (Robertson et al. 2008). The blue pollen of *F. excorticata* is conspicuous against the yellow stigma, permitting visual assessment of pollen presence. Visual scores of pollen loads on *F. excorticata* stigmas are well correlated with fruit set, allowing rapid assessment of pollination (Robertson et al. 2008). This species also appears to be seed-limited (Bell 2010), even though its seed is persistent in the seed bank (Moles et al. 2000), indicating that pollen-limitation has consequences at the population level. It is a partially seral species that is later overtopped by other trees (Robertson et al. 2008), and is typically found near riverbanks, along forest margins, and in disturbed habitats (Godley & Berry 1995). *Fuchsia excorticata* is a highly preferred food of possums, and heavy browsing by possums has caused dieback or local extinction throughout much of its range (Pekelharing et al. 1998; Sweetapple et al. 2004). Hence, reproduction by seed is important for the maintenance of this species, and seed production is sensitive to bird densities (Robertson et al. 2008).

*Fuchsia excorticata* is gynodioecious, and although high fruit set is possible for both female and hermaphrodites, fruit production in hermaphrodites and especially in females is frequently pollen-limited (Robertson et al. 2008). Hermaphrodites are self-compatible and able to autonomously self when pollinators are absent (Godley & Berry 1995; Robertson et al. 2008). However, selfed offspring have lower fitness and suffer from strong cumulative inbreeding depression (Robertson et al. 2011). While sex ratios are variable between locations, hermaphrodites always outnumber females (Robertson et al. 2008). Flowers of female plants are much smaller than those of hermaphrodites and produce less nectar (Delph & Lively 1985).

Elsewhere in New Zealand, the current key pollinators of *F. excorticata* are tūī and bellbirds (Delph & Lively 1985; Robertson et al. 2008), but hihi would probably once have been an important pollinator (Godley & Berry 1995; Kelly et al. 2006). Silvereyes are often observed feeding on *F. excorticata* flowers, and can pollinate female flowers effectively but are primarily nectar robbers of the larger hermaphrodite flowers (Delph & Lively 1985; Robertson et al. 2008).

## Five-minute bird counts

Five-minute bird counts (Dawson & Bull 1975) were used as an index of pollinating-bird abundance at Maungatautari (treatment) and Pirongia (non-treatment) in December 2010. All birds seen or heard within a 100-m radius of a stationary observer were recorded during a 5-min period. Following Innes et al. (2003), a total of 36 bird count stations at Maungatautari and 34 count stations at Pirongia were used, and each count station was counted twice on different days. One observer (JMI) made all counts, alternating daily between treatment and non-treatment sites. Pollinating birds were defined as tūī, bellbirds, silvereyes, and hihi. To determine if Maungatautari and Pirongia had different relative abundances of each pollinating bird species, Poisson generalised linear models (GLMs) were used in the statistical package R (version 2.14.1; R Development Core Team 2011). Each species was analysed separately, using the sum of the two counts for that species at each count station to allow for the nested data structure.

## Bird visitors to *Fuchsia excorticata* flowers

To identify bird visitors to *F. excorticata* flowers at Maungatautari and Pirongia, observations were conducted during November 2010. At each site, 10 observation stations were selected from which several flowering *F. excorticata* could be clearly viewed. A total of 75 min was spent in five 15-min blocks at each station. Each station was only visited once per day. During an observation period, for each avian flower visitor, the bird species and visit duration in seconds were recorded, using 8×42 binoculars at a distance of 5–10 m. Additionally, the number of receptive flowers (those with a green corolla) visible at the station was estimated to provide a mean number of flowers present at that station across all observations. To spread observation efforts evenly across both sites during the flowering period and minimise the effect of large-scale weather patterns on bird activity, Maungatautari and Pirongia were visited on alternate days. Visitation rates were expressed as the number of seconds of bird activity per 100 flowers per hour for each bird species at an observation station, following Robertson et al. (2008). Non-parametric Wilcoxon rank sum tests in R were used to analyse visitation rates for each species, using observation stations as replicates. As silvereyes rob hermaphrodite flowers but pollinate the smaller female flowers (Delph & Lively 1985; Robertson et al. 2008), only visits to female flowers were included in analysis of this bird species.

## Pollen loads at Maungatautari and Pirongia

To assess the level of pollination received by *F. excorticata*, the quantity of pollen deposited on stigmas was scored visually. The amount of pollen received by stigmas is correlated with fruit-set for both female and hermaphrodite plants, providing an indication of how well the pollination mutualism is working (Robertson et al. 2008).

At Maungatautari and Pirongia, in November 2010, the percentage of the yellow stigma covered with blue pollen was visually scored on a five-point scale: (0) 0%; (1) 1–5%; (2) 6–20%; (3) 21–40%; and (4) 41–100%, using standardised methodology developed by the University of Canterbury and Landcare Research for the National Pollination Survey ([http://www.biol.canterbury.ac.nz/pollination\\_survey/](http://www.biol.canterbury.ac.nz/pollination_survey/), accessed 12 September 2011). Plants were selected on the basis of having 10 or more accessible flowers in the early to mid-stage of flowering (as indicated by a green corolla). On each plant, 10 receptive flowers were selected haphazardly across multiple branches. Stigmas were inspected using a 10× magnification hand lens. Flowers that had been damaged by silvereye robbing or other means were not scored. Plants were scored for pollen loads on two dates 2 weeks apart. As open flowers last for approximately 11 days and are only receptive for about the first five days (Delph & Lively 1985, 1989), the two visits scored separate groups of flowers.

Females were less common than hermaphrodites, which limited the number of female plants scored for pollen loads. The same plants were scored on both visits, except those with too few flowers at the second visit and one that had died. In total, the first visit scored 21 hermaphrodites and 15 females at Maungatautari, and 19 hermaphrodites and 6 females at Pirongia. The second visit scored 18 hermaphrodites and 11 females at Maungatautari, and 18 hermaphrodites and 5 females at Pirongia.

Robertson et al. (2008) first used this method to quantify pollination levels at seven sites across New Zealand. However,

in their work a four-point scale was used. Pollen loads were classed as (0) none, (1) few, (2) some, or (3) abundant (Robertson et al. 2008). Robertson et al. (2008) determined that a pollen score index of 1.5 indicated good pollination service on the basis of the relationship between pollen load and fruit set (Robertson et al. 2008). To examine whether having an extra pollen load class (0 to 4) would affect comparisons drawn between the two experiments, the classes of '3' and '4' in the data from this study were combined, as any scores of '4' were likely to have been scores of '3' in Robertson et al. (2008). The analysis was then rerun using the four-point scale. This made no difference to the conclusions compared with the original analysis. Thus, all analyses presented use the full five-point scale to match the National Pollination Survey.

To allow for the nested nature of the data (replicate flowers on replicate plants), analysis was performed using mean pollen scores per plant per visit. Mean pollen scores were analysed using analysis of variance in R. 'Plant' (a unique code for each plant examined) was fitted as an error term, to account for repeated measurements of the same plant at the two visits. Predictors fitted were site, visit, plant sex, and first-order interactions. All predictors are factors with two levels. Due to the non-orthogonal nature of the data, where unequal numbers of observations exist for each combination of factor levels, each term was placed last in the model to test for its significance (Type III adjusted sum of squares, Quinn & Keough 2002).

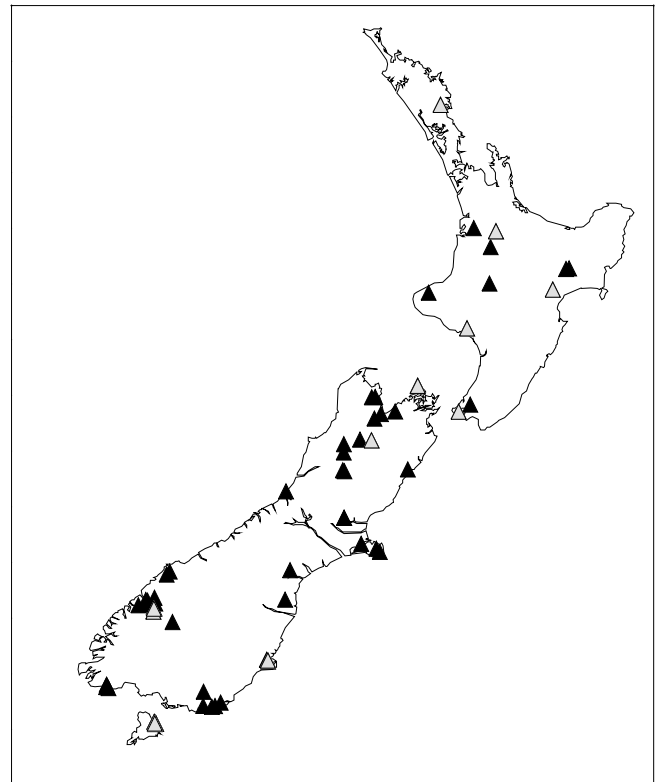
### National Pollination Survey

The National Pollination Survey was established in 2007 to assess the status of bird–plant mutualisms in New Zealand, using volunteers to measure the pollination service received by *F. excorticata*, as an indicator species for mutualisms generally. The data presented here are from surveys conducted in spring/summer 2007, 2008, 2009, 2010, and 2011, at 68 sites around New Zealand from Whangarei to Stewart Island (Fig. 1). At each site (or visit to a site), observers attempted to visually score 10 flowers on each of 10 hermaphrodite and 5 female plants using the five-point pollen load scale outlined above. Some sites had lower numbers of plants or fewer than 10 suitable flowers on a plant, in which case all plants present and up to 10 flowers per plant were examined. Data from Maungatautari and Pirongia in 2010 were included in the analysis, but more than 10 hermaphrodite and 5 female plants were examined per visit (see above). Sites had an average of 9.7 hermaphrodite trees (range 1–21) scored per visit and 4.4 female trees (range 0–15).

We used then-current DOC conservancy areas (<http://gis.doc.govt.nz/docgis>, accessed 27 October 2011) to divide National Pollination Survey sites into three regions, similar to the four regions used by Murphy and Kelly (2001), but combining northern and southern North Island categories due to a low number of records from the North Island. The three regions were North Island (all North Island DOC conservancies), Western South Island (Nelson-Marlborough, West Coast, Southland conservancies), and Eastern South Island (Otago, Canterbury). Eastern South Island is drier and has less forest and lower bellbird densities than Western South Island (Murphy & Kelly 2001). A separate 'low-predator' category was used for low-predator sites (islands without some important mammalian predators, and mainland sites with mammal-excluding pest-fences or intensive pest control), regardless of their geographic region. The low-predator category was used to examine whether *F. excorticata* at sites that have intensive

mammalian pest management and/or an absence of mammalian predators, and hence probably higher native bird densities, receive better pollination service. There were 7 North Island sites (including Pirongia in 2010), 28 Western South Island, 15 Eastern South Island, and 18 low-predator sites. The 18 low-predator sites were at 10 locations, in fenced sanctuaries (Maungatautari, Bushy Park near Wanganui, Zealandia in Wellington, and Orokonui near Dunedin), unfenced mainland sites with intensive predator control (Boundary Stream in Hawke's Bay, Rotoiti Nature Recovery Project at Nelson Lakes, and Eglinton Valley), and islands lacking some major predators (Matakohe Island in Whangarei Harbour, Stewart Island, and D'Urville Island in the Marlborough Sounds). Matakohe Island is free of possums (King 2005); and stoats, rats (*Rattus* spp.) and mice were kept to low levels with intensive trapping at the time of the pollination measurements (B. Buhler, Matakohe Island Ranger, pers. comm.). Stewart Island has ship rats, Norway rats (*Rattus norvegicus*), kiore (*Rattus exulans*) and possums, but not stoats (Harper 2009). D'Urville Island has stoats and kiore, but not possums, ship rats or Norway rats (King 2005; Veale et al. 2012).

Most sites were surveyed using a single visit during the flowering season. However, five sites were surveyed twice within a given year (two dates separated by 2–4 weeks) and 10 were surveyed in more than one year (seven sites surveyed in two years, and three sites in three years). One site, Maungatautari, was surveyed once in 2008 and twice in 2010. Data were analysed using linear mixed models in the



**Figure 1.** Locations throughout New Zealand of National Pollination Survey sites in all five years (2007–2011). Grey triangles show low-predator sites (fenced, islands, and intensive pest control sites), and black triangles are all other sites. Some sites are obscured by other sites (e.g. there are six sites on Stewart Island).

'lme4' package (Bates et al. 2011) in R. Models were fitted using maximum likelihood and Gaussian error distribution. The use of maximum likelihood allows comparison of models with different fixed-effect structures. As for the Maungatautari data, a mean pollen score was calculated for each plant (the response variable), and then region (the three geographic regions and all the low-predator sites as a fourth 'region'), plant sex, number of flowers scored, and first-order interactions were fitted as fixed effects. To account for multiple measurements at sites within and among years, random effects were fitted for year and visit nested within site. The maximal model was simplified using backward selection to obtain final models. The effect of removing each fixed effect from the maximal model was compared using likelihood ratio tests. Fixed effects that did not significantly improve model fit were removed from the final model. As models with Gaussian error distribution in the lme4 package do not provide significance testing,  $P$ -values were generated using the 'pvals.fnc' function in the 'languageR' package (Baayen 2011), which uses Markov chain Monte Carlo (MCMC) simulations. Confidence intervals (95%) were calculated using the 'arm' package (Gelman et al. 2011).

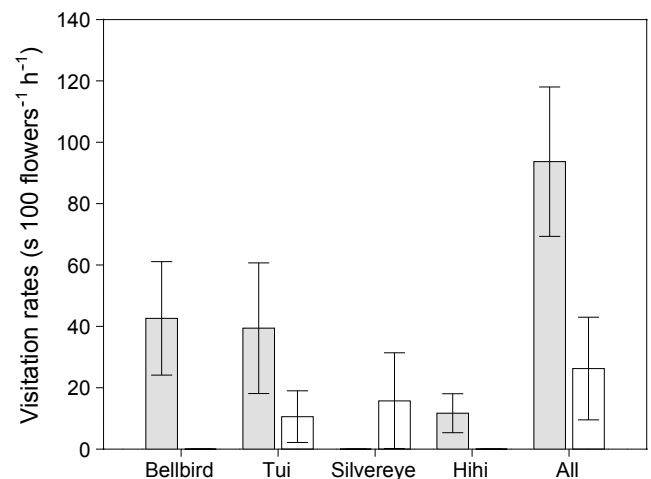
## Results

Five-minute bird counts showed that tūī and bellbirds were more abundant at Maungatautari than Pirongia, while silvereye abundance was similar at both sites (Fig. 2). The difference between sites was significant for tūī (Poisson GLM:  $\chi^2 = 66.88$ , d.f. = 1,  $P < 0.001$ ) and bellbirds ( $\chi^2 = 24.68$ , d.f. = 1,  $P < 0.001$ ), but not for silvereyes ( $\chi^2 = 0.72$ , d.f. = 1,  $P = 0.397$ ). At Maungatautari, although hihi are present and were observed visiting *F. excorticata* flowers (see below), they were not detected in the five-minute counts. Hihi are found predominantly on the lower slopes of Maungatautari, especially near the northern and southern gates where birds were initially released, and less frequently on the ridges where most of the five-minute bird counts were conducted. At Pirongia hihi are not present.

Flower visitation rates by all pollinating birds to *F. excorticata* flowers were 3.6 times higher at Maungatautari than Pirongia (Fig. 3). At Maungatautari, tūī made the most visits (13), but bellbirds, which only made nine visits, had longer visits and so provided more seconds of visit per 100 flowers per hour. Hihi were also recorded visiting flowers (three visits), and five visits by silvereyes were seen but all

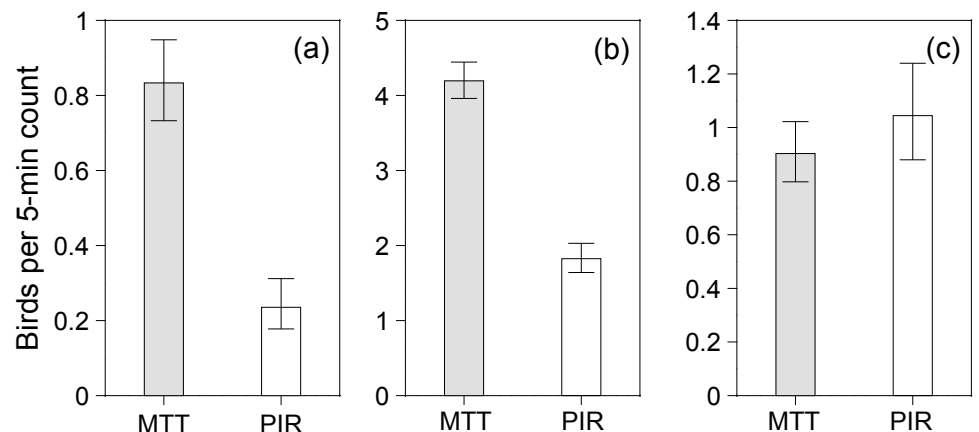
were to hermaphrodite plants so are not included here. At Pirongia, silvereyes made three visits to females and provided 59.7% of all pollinating time on flowers, while the three tūī visits provided the remaining 40.3% of visitation time (Fig. 3). Seven silvereye visits to hermaphrodite plants at Pirongia are not included. Using Wilcoxon rank sum tests, the visitation rate was significantly higher at Maungatautari for all birds combined ( $W = 22$ ,  $P = 0.029$ ;  $n_1 = n_2 = 10$  for each test) and bellbirds ( $W = 80$ ,  $P = 0.006$ ) but not for tūī ( $W = 61$ ,  $P = 0.328$ ), silvereyes ( $W = 45$ ,  $P = 0.368$ ) or hihi ( $W = 65$ ,  $P = 0.078$ ). At Maungatautari, aggression between pollinators was observed; tūī displaced feeding bellbirds and hihi, and bellbirds displaced hihi. At Pirongia, no aggression was observed.

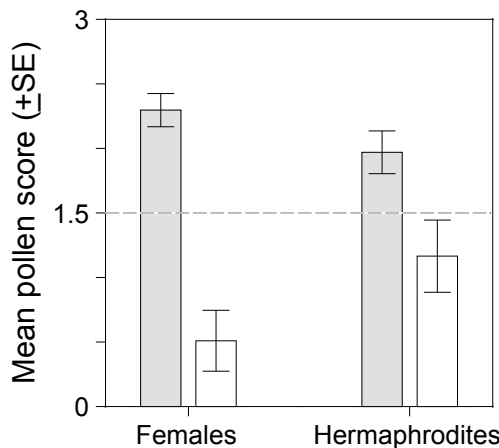
*Fuchsia excorticata* pollen scores were significantly higher at Maungatautari than Pirongia for both female and hermaphrodite plants (Fig. 4). Analysis of variance showed significant effects of site and the interaction between site and sex (Table 1), with the lowest pollen scores found for females (which cannot self-pollinate) at Pirongia (which had lower bird numbers). Pollen scores of both female and hermaphrodite plants at Pirongia are below the level of pollination (pollen score index of 1.5) that indicates good pollination service based on the relationship between pollen load and fruit set



**Figure 3.** Visitation rates of pollinating birds to *Fuchsia excorticata* flowers (mean seconds of bird activity per 100 flowers per hour with SEM) at Maungatautari (grey bars) and Pirongia (open bars). Visits by silvereyes to hermaphrodite flowers are excluded.

**Figure 2.** Mean number ( $\pm$ SEM) of (a) bellbirds, (b) tūī, and (c) silvereyes per five-minute bird count at Maungatautari (MTT) and Pirongia (PIR) in December 2010. Note different scales on y-axes. Values are fitted means from Poisson GLMs.





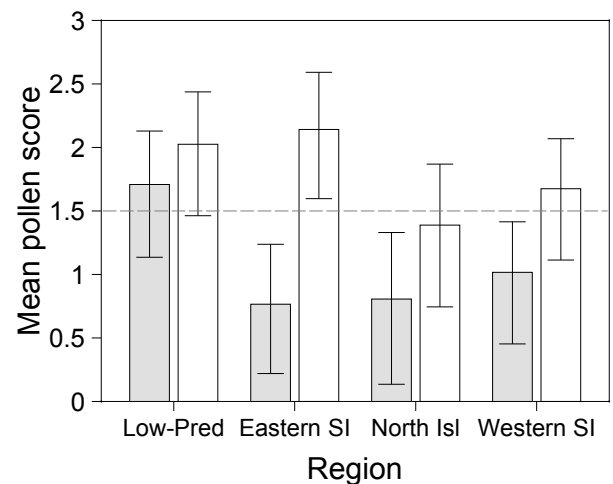
**Figure 4.** Fitted values for pollen scores of female and hermaphrodite *Fuchsia excorticata* plants at Maungatautari (grey bars) and Pirongia (open bars). A pollen score index of at least 1.5 (dashed line) indicates good pollination service, based on the relationship between pollen load and fruit set (Robertson et al. 2008).

**Table 1.** Split-plot analysis of variance of *Fuchsia excorticata* mean pollen scores at Maungatautari and Pirongia. The significance of each predictor was calculated when it was last in the model. Significant effects are in bold type. SS = sum of squares; MS = mean square.

	d.f.	SS	MS	F	P
<i>Error: plant</i>					
Site	1	31.32	31.32	<b>61.385</b>	<b>&lt;0.001</b>
Sex	1	0.01	0.01	0.018	0.893
Sex:Site	1	4.59	4.59	<b>8.999</b>	<b>0.004</b>
Residual	57	29.09	0.51		
<i>Error: within</i>					
Visit	1	1.16	1.16	3.595	0.064
Visit:Sex	1	0.37	0.37	1.130	0.293
Visit:Site	1	0.26	0.26	0.804	0.374
Residual	49	15.86	0.32		

(Robertson et al. 2008), whereas both sexes at Maungatautari received good pollination service.

The best model for the National Pollination Survey data included plant sex, region, number of flowers scored, and the sex by region interaction as fixed effects (Table 2a). Pollen scores were higher for hermaphrodite plants than female plants in each region (Table 2a; Fig. 5). Female plants at low-predator sites had significantly higher pollen scores than females at unmanaged sites in any region (Table 2a; Fig. 5), and only at low-predator sites was the mean above the level (1.5) indicating good pollination service. Hermaphrodite plants had high pollen scores in all regions, except for North Island, and only hermaphrodites at North Island sites had significantly lower pollen scores than those at low-predator sites when examined alone (Table 2b). Further sampling of *F. excorticata* pollen scores is needed from the North Island region, as only seven unmanaged sites were sampled there. The number of flowers scored had a significant effect on pollen scores of both female and hermaphrodite plants, with higher pollen scores on plants that had more flowers sampled (Table 2a), perhaps because birds are attracted more to large floral displays.



**Figure 5.** Back-transformed mean pollen scores (with 95% confidence intervals) on stigmas of *Fuchsia excorticata* female plants (grey bars) and hermaphrodite plants (open bars) within each region. A mean score of  $\geq 1.5$  indicates good pollination, see text.

**Table 2.** Linear mixed models testing (a) the effects of region, plant sex, number of flowers examined, and the interaction between region and sex on mean pollen scores of female and hermaphrodite plants in the National Pollination Survey, and (b) the effects of region on hermaphrodite plants only. Sites, visit nested within sites, and years were included as random effects in each model. Significant effects (generated using Markov chain Monte Carlo) in bold.

Model	Fixed effects	Estimate	Std error	t-value	P
(a) Females and hermaphrodites	Intercept (Females at low-predator sites)	1.0877	0.3567	3.049	0.002
	Region(Eastern SI)	<b>-0.9665</b>	<b>0.2618</b>	<b>-3.692</b>	<b>&lt;0.001</b>
	Region(North Island)	<b>-0.8878</b>	<b>0.3296</b>	<b>-2.694</b>	<b>0.007</b>
	Region(Western SI)	<b>-0.7076</b>	<b>0.2237</b>	<b>-3.163</b>	<b>0.002</b>
	Sex(Hermaphrodite)	<b>0.3083</b>	<b>0.0779</b>	<b>3.956</b>	<b>&lt;0.001</b>
	Number of flowers	<b>0.0637</b>	<b>0.0277</b>	<b>2.303</b>	<b>0.021</b>
	Region(Eastern SI):Sex(Hermaphrodite)	<b>1.0705</b>	<b>0.1281</b>	<b>8.356</b>	<b>&lt;0.001</b>
	Region(North Island):Sex(Hermaphrodite)	0.2808	0.1589	1.767	0.078
	Region(Western SI):Sex(Hermaphrodite)	<b>0.3439</b>	<b>0.1036</b>	<b>3.321</b>	<b>0.001</b>
(b) Hermaphrodites only	Intercept (Low-predator sites)	2.0571	0.2316	8.884	<0.001
	Region(Eastern SI)	0.0654	0.2735	0.239	0.811
	Region(North Island)	<b>-0.7607</b>	<b>0.3098</b>	<b>-2.455</b>	<b>0.014</b>
	Region(Western SI)	-0.4158	0.2347	-1.772	0.077

## Discussion

Results from this study are consistent with the idea that higher abundances of key pollinating birds at Maungatautari have improved the pollination service to *F. excorticata*. All parameters examined (pollinating birds, visitation, and pollen loads) were higher at Maungatautari compared with Pirongia. Furthermore, data from throughout New Zealand from the National Pollination Survey suggest that female *F. excorticata* had improved pollination service at low-predator sites.

### Status of pollination service

Bird pollination was previously thought to be unimportant in the New Zealand flora (Clout & Hay 1989). However, a growing body of literature challenges this view (e.g. Ladley & Kelly 1995; Anderson 2003; Newstrom & Robertson 2005; Anderson et al. 2006; Robertson et al. 2008; Kelly et al. 2010). It now appears that seed set in ornithophilous (bird-pollinated) flowers is frequently being reduced by insufficient visitation by birds on the New Zealand mainland. Of the 10 ornithophilous species examined so far, most species had strong pollen limitation with over a third of potential fruits lost due to inadequate pollination service (Kelly et al. 2010). Only *Alepis flavida* and hermaphrodite *F. excorticata* did not have substantial pollen-limitation: both are self-compatible, allowing some fruit set in the absence of pollinating birds (Ladley et al. 1997; Robertson et al. 2008). However, selfed seeds may suffer from inbreeding depression, as has been confirmed for *F. excorticata* and *Sophora microphylla* (Robertson et al. 2011). Our study supports the findings of Robertson et al. (2008), with pollen scores below the level required for adequate fruit set in *F. excorticata* females over much of the mainland, while hermaphrodite *F. excorticata* generally have pollen levels that indicate adequate fruit set (albeit with an unknown level of futile selfing).

To determine if reduced seed set caused by inadequate pollination will have population-level consequences, it is necessary to examine whether the population is seed-limited (Bond 1994). Seed limitation is difficult to measure for long-lived plants and at present has only been examined for three ornithophilous New Zealand species. Kelly et al. (2007) found *Peraxilla tetrapetala*, a stem hemiparasite, to be seed-limited. However, this species is entirely reliant on bird dispersal to attach seeds to host branches and undispersed seeds perish; consequently this species is more likely to be seed-limited than non-parasitic plants for which some undispersed seeds can still germinate (Kelly et al. 2007). A study of *Rhabdothamnus solandri* showed that on the New Zealand mainland this species was not only severely pollen-limited but was also strongly seed-limited, resulting in a reduction of juvenile plants in the population (Anderson et al. 2011). *Fuchsia excorticata* is also sometimes seed-limited (despite it having a persistent soil seed bank); Bell (2010) found seed-limitation in *F. excorticata* on the mainland was related to mammalian pest control, with lower seed-limitation at sites with pest control compared with sites without pest control, probably because increased bird densities at sites with pest control resulted in improved pollination. Further studies are required to test whether other pollen-limited ornithophilous plants are also seed-limited.

Additionally, experimental manipulations by Anderson (2003) showed that for three species assumed to be entomophilous (insect-pollinated), fruit set was considerably higher when flowers were accessible to both bird and insect pollinators than insects alone. Kelly et al. (2010) considered

bird pollination to be important for reproduction in 48 native plant species. Hence it seems that reduced bird densities on the New Zealand mainland are affecting the pollination of many ornithophilous and some non-ornithophilous flowering plants, with demographic consequences for at least some species. However, for some plant species, introduced animals such as chaffinches (Kelly et al. 2006) or ship rats (Pattimore & Wilcove 2012) may compensate to some extent.

### Pollination service and breeding systems

Pollination service should be examined in the context of plant breeding systems (Newstrom & Robertson 2005). Only hermaphrodite species without strong inbreeding depression can reproduce independent of pollinators (Newstrom & Robertson 2005). Although the National Pollination Survey data suggest that pollination of hermaphrodite *F. excorticata* plants is generally adequate, it is likely that seed set is maintained by increased self-pollination at low bird densities (Robertson et al. 2008). Since selfed offspring are known to have very low fitness due to strong inbreeding depression (Robertson et al. 2011), hermaphrodite reproduction may still be failing, in a way not detected by our measurements of pollen loads.

Pollen loads on female *F. excorticata* plants provide a better indication of current pollination levels and pollinator service than pollen loads on hermaphrodites. Females are not able to self-pollinate, thus pollen loads on female plants are always out-crossed and offspring of female plants have no inbreeding depression (Robertson et al. 2011). Our study showed that female *F. excorticata* are more vulnerable to mutualism failure than hermaphrodites are, indicated by females having lower amounts of pollen on stigmas at low abundances of birds (Pirongia) or where there is insufficient mammalian predator control (National Pollination Survey). This is consistent with Robertson et al.'s (2008) findings that females are more pollen-limited than hermaphrodites and that females therefore provide a more sensitive visual indicator of pollinator attention.

### Silvereyes as pollinators of *Fuchsia excorticata*

This study, similar to previous studies (Robertson et al. 2008, 2011), assumed that silvereyes were robbers of hermaphrodite *F. excorticata* flowers but were legitimate pollinators of the smaller female flowers. For pollination to occur it is necessary for pollen to contact the bird in the correct position for deposition on a female stigma. Silvereyes have short beaks, of approximately 14.3 mm, and are usually unable to access nectar from hermaphrodite *F. excorticata* flowers using the flower opening and instead rob nectar by puncturing the corolla tube (Delph & Lively 1985; Robertson et al. 2008). While hermaphrodite corollas on average are approximately 20 mm in length (Delph & Lively 1985), lengths vary between 11 and 22 mm (Godley & Berry 1995), and silvereyes occasionally feed legitimately from hermaphrodite flowers with short corollas (J. Iles, pers. obs.). Therefore, although silvereyes feed from female flowers legitimately (corolla length: 6.5–13 mm; Godley & Berry 1995), they may have little or no pollen to deposit unless they had also previously legitimately visited a hermaphrodite flower. Further examination of silvereye feeding behaviour is necessary to determine how frequently visits to female flowers result in pollen deposition, and therefore whether they are actually useful pollinators of *F. excorticata* females.

## Restoration of mutualisms

Little attention has been focused on restoring animal-mediated pollination in natural ecosystems (Dixon 2009; Menz et al. 2011; but see Baskett et al. 2011), although ecosystem restoration in general may have unintended (or intended but usually unmeasured) benefits on pollination mutualisms. Given increases in native bird densities following mammalian predator control or eradication (Innes et al. 2010; O'Donnell & Hoare 2012), and that pollination functions better on island sanctuaries with elevated bird densities (Anderson 2003; Anderson et al. 2006, 2011), we would assume increased bird densities on the mainland would restore bird–plant mutualisms. The only direct attempt to restore a single pollination mutualism between native species (as opposed to an ecosystem-level restoration goal) in New Zealand failed. That attempt was based on the premise that pollination of *Peraxilla tetrapetala* was restricted by insufficient numbers of bellbirds, their sole bird pollinator at the study site (Kelly et al. 2005). In an effort to increase bellbird numbers, stoats were intensively trapped. This led to much higher bellbird nest success and increased bellbird numbers by 79%, but failed to improve pollination of *P. tetrapetala*. Reasons for the failure are unclear (Kelly et al. 2005).

Our study did not test whether the higher abundance of key pollinating birds at Maungatautari was a consequence of mammalian pest control there. However, pre- and post-eradication monitoring by Landcare Research since 2002 at Maungatautari and non-treatment blocks suggests that both tūi and bellbird five-minute bird counts increased due to pest eradication at Maungatautari (N. Fitzgerald, J. Innes, Landcare Research, pers. comms; Innes et al. 2006; Fitzgerald et al. 2009). Irrespective of cause, the higher abundance of tūi and bellbirds in 2010, and the presence of hihi, appears to have restored the pollination mutualism to *F. excorticata* at Maungatautari. It should be noted that hihi could not have been successfully reintroduced to Maungatautari without a very high level of mammalian predator control (Chauvenet et al. 2012). Additionally, considering pollination scores across the whole of New Zealand, female *F. excorticata* received better pollination at low-predator sites, presumably because a decreased abundance of mammalian pests at those sites allowed pollinating birds to reach higher densities. The National Pollen Survey analysis compared numerous intensively managed sites to many non-treatment sites, and thus supports a hypothesis that the better pollination found at Maungatautari is attributable to ecological restoration, rather than some pre-existing site effect.

It appears that increasing bird density and/or diversity (presence of hihi) may be important in restoring pollination mutualisms. Sites that have zero or near-zero pest densities, such as fenced sanctuaries like Maungatautari, are expensive (Scofield et al. 2011) but may provide conservation gains that cannot be achieved in cheaper pest management programmes (e.g. Kelly et al. 2005). Our study documents some positive ecosystem-level benefits gained from fenced sanctuaries, but further work measuring the size and uniqueness of those benefits is clearly needed (Burns et al. 2012; Innes et al. 2012).

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