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Mutualisms with the wreckage of an avifauna: the status of bird pollination and fruit-dispersal in New Zealand

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Abstract: Worldwide declines in bird numbers have recently renewed interest in how well bird–plant mutualisms are functioning. In New Zealand, it has been argued that bird pollination was relatively unimportant and bird-pollination failure was unlikely to threaten any New Zealand plants, whereas dispersal mutualisms were widespread and in some cases potentially at risk because of reliance on a single large frugivore, the kereru (*Hemiphaga novaeseelandiae*). Work since 1989, however, has changed that assessment. Smaller individual fruits of most plant species can be dispersed by mid-sized birds such as tui (*Prothemadera novaeseelandiae*) because both fruits and birds vary in size within a species. Only one species (*Beilschmiedia tarairi*) has no individual fruits small enough for this to occur. Germination of 19 fleshy-fruited species, including most species with fruits >8 mm diameter, does not depend on birds removing the fruit pulp. The few studies of fruit removal rates mostly (7 out of 10) show good dispersal quantity. So dispersal is less at risk than once thought. In contrast, there is now evidence for widespread pollen limitation in species with ornithophilous flowers. Tests on 10 of the 29 known native ornithophilous-flowered species found that in 8 cases seed production was reduced by at least one-third, and the pollen limitation indices overall were significantly higher than the global average. Birds also frequently visit flowers of many other smaller-flowered native species, and excluding birds significantly reduced seed set in the three species tested. So pollination is more at risk than once thought. Finally, analyses of both species numbers and total woody basal area show that dependence on bird pollination is unexpectedly high. Birds have been recorded visiting the flowers of 85 native species, representing 5% of the total seed-plant flora (compared with 12% of those with fleshy fruit) and 30% of the tree flora (compared with 59% with fleshy fruit). A higher percentage of New Zealand forest basal area has bird-visited flowers (37% of basal area nationally) than fleshy fruit (31%). Thus, bird pollination is more important in New Zealand than was realised, partly because birds visit many flowers that do not have classic “ornithophilous” flower morphology.

Keywords: dispersal; frugivory; germination; *Hemiphaga novaeseelandiae*; honeyeater; kereru; Meliphagidae; mutualisms; pollination; pollen limitation.

Introduction

There has been considerable interest in how well bird–plant interactions are functioning in the face of declines in birds worldwide (Sekercioglu et al. 2004; Peh et al. 2006; Corlett 2007). This is especially so in New Zealand, which Jared Diamond (1984) famously said no longer has an avifauna, just the wreckage of one. A series of papers, beginning with McEwen (1978) and Godley (1979), but developed most comprehensively by Clout and Hay (1989), argued that bird pollination is rare and unimportant in the New Zealand

flora, but that bird-dispersal is widespread and important. In particular, they argued that large-fruited trees “now depend almost entirely on kereru [the New Zealand pigeon, *Hemiphaga novaeseelandiae*] for their dispersal... this is a precarious situation” (Clout & Hay 1989: 32). Their paper raised some important concepts that are still valid, especially in relation to dispersal. However, since 1989, evidence has been accumulating that pollination is actually more at risk than dispersal.

The emphasis on dispersal as being at risk came from a consideration of the numbers of large native frugivorous

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birds which have become extinct or very restricted in range. McEwen (1978) said the kereru is the most important disperser of miro (*Prumnopitys ferruginea*) and “is the only [extant] common forest bird able to disperse the large seeds of tawa [*Beilschmiedia tawa*], taraire [*B. tarairi*] and karaka [*Corynocarpus laevigatus*]. Therefore, the pigeon is essential for the continued natural regeneration of these trees” (McEwen, 1978:107). Clout and Hay (1989: 31) extended McEwen’s idea to say kereru were now “virtually the sole dispersers” for 11 species of native plant with fruits >10 mm diameter. This idea has been widely accepted (e.g. Lee et al. 1991; Clout & Tilley 1992; Webb & Kelly 1993; Craig et al. 2000; Southward et al. 2002; Wilson 2004; Norton 2009), but recent information questions the fruit size range over which it applies. Clout and Hay (1989) showed kereru was (then) the only recorded disperser for the five trees with fruits >14 mm diameter: tawa, taraire, karaka, tawapou *Planchonella costata*, and puriri *Vitex lucens*; they included *Beilschmiedia tawaroa*, but it is now considered synonymous with *B. tawa* (Webb & Simpson 2001). The reliance on kereru was less absolute for the six species with fruit in the 10–14 mm range (miro, swamp maire *Syzygium maire*, kohekohe *Dysoxylum spectabile*, mangeao *Litsea calicaris*, hinau *Elaeocarpus dentatus*, and supplejack *Ripogonum scandens*). However, more recent evidence sheds light on which plant species are being dispersed by other birds, and how essential dispersal is for continued natural regeneration, as discussed below.

Arguments for the unimportance of bird pollination in the New Zealand flora date originally from Thomson (1881), but were best developed by Godley (1979) and Clout and Hay (1989). Godley showed that eight native bird species were recorded visiting the flowers of 30 species of native plant. The 30 species did not all have classic “ornithophilous” flowers (i.e. those that resemble typical bird-visited flowers: red or yellow, large, and with copious nectar). About half had small open flowers that appeared to be better suited to insect visitors (“entomophilous”) and even the ornithophilous flowers were also visited by insects such as bumblebees. This led Godley to dismiss bird pollination and suggest that insects could well be effective pollinators. He argued the bird visits were likely to be “incidental” and result in geitonogamy (self-pollination of a flower with pollen from a different flower on the same plant). Godley did say birds could be important in species with sexually dimorphic flowers in the genera *Fuchsia*, *Pittosporum*, *Melicytus*, *Cyathodes* and *Nestegis*, while Clout and Hay (1989) said that bird pollination may be important in *Fuchsia*, *Sophora*, *Phormium* and perhaps a few other species. Finally, Godley said that the number of native bird species involved in pollination in New Zealand (8 total, only about half of which commonly visit flowers) was very small compared with Australia (with 70 species of Meliphagidae (honeyeaters) alone). Both Godley (1979) and Clout and Hay (1989) concluded it was unlikely a lack of bird pollinators threatened any native plant. However, even though both papers said a definitive evaluation of the importance of bird pollination requires information on seed set rather than simply on flower visitation, that caveat has since been largely ignored.

In this paper we review recent relevant studies on bird–plant mutualisms using the framework of Bond (1994). Bond argued that, for mutualism failure to affect plant populations, four things have to be shown; (1) there are too few visits by the native mutualists to provide the required services; (2) introduced animals are not substituting for the native animals; (3) reproduction by seed is dependent on mutualist visits; and (4) maintenance of the plant population depends on seed

production (rather than, say, vegetative resprouting) and seed densities are limiting. We examine bird pollination and dispersal in New Zealand using this framework to assess the level of risk, and show that the new data suggest bird pollination is more at risk of failure than bird dispersal.

In particular, we will argue that:

- (1) Bird pollination has been systematically discounted in the past, but is now known to be important to a large number of native plant species, including many that do not fit the typical ornithophilous flower syndrome.
- (2) The fundamentally correct idea that only kereru can disperse large fruits has been frequently misapplied to even medium-fruit-size species, whereas field data now suggest it applies to only the three largest-fruited species.
- (3) There is now good evidence bird pollination is frequently failing on the New Zealand mainland, whereas there is little evidence so far that the same is true for bird dispersal.

This paper presents a logical framework for evaluating current knowledge of the importance of birds as pollinators and dispersers of New Zealand plants. In doing so we present a review of the post-1989 literature, along with new primary data, in three sections: dispersal, pollination, and the frequency of each of these in the New Zealand flora. In each case we acknowledge some limitations in the available data. For dispersal, we are largely limited to data on fruit removal rates, and on the effect of frugivores on germination rates. A thorough assessment of dispersal would include information on establishment and survival of the subsequent seedlings as a function of dispersed microsite (Kelly et al. 2004), but such data are not available. For pollination, our analysis is largely limited to fruit set data, i.e. pollination quantity. A consideration of pollen quality (e.g. inbreeding vs. outcrossing) and its effects on offspring fitness would be desirable but is currently possible for very few species.

Methods

Dispersal in *Beilschmiedia tawa*

Since 1994, dispersal quantity (fruit removal rates) of tawa fruits by birds has been monitored in nine seasons at Blue Duck Scientific Reserve (42°14' S, 173°47' E, 430 m elevation) 20 km north of Kaikoura, near the southern distribution limit of this species. Kereru and tui are present in Blue Duck reserve, although there is no management of mammalian carnivores there. In seven of the nine years, on one or several days in the middle of the fruiting season (usually April), plots of 1 x 5 m were placed under the canopy of mature tawa trees and all current-season fruits on the ground were classified as clean (flesh removed by passing through a bird) or fleshy (at least some fruit pulp still adhering). The number of plots varied (11 in 1994, 14 in 1997, 13 in 1999, 8 in 2003, 9 in 2005, 18 in 2007 and 15 in 2008). In 2004, the sampling used one plot of 1 m² placed under each of 10 different trees, and in 2006, it was based on the fruit caught between 28 February and 4 April in 3 seed traps of 0.1 m² under each of 10 trees. The total number of seeds m⁻² was used as an index of fruiting intensity, and the percentage of the total seed crop that had been through a bird was used as an index of the quantity of dispersal.

Fruit size distributions and germination

We measured the diameter (being the dimension that limits ingestion by birds) of fresh fruit samples for all native woody species with fruits >8 mm mean diameter that occur on the North

and South Islands, except for two species we have not been able to measure (*Litsea calicaris* and *Nestegis cunninghamii*) and three species with multiple small seeds in a large fruit that we excluded (*Freycinetia baueriana*, *Solanum laciniatum*, *Gaultheria antipoda*). This gave a total of 15 species, and we also included three smaller-fruited species (5.5–8 mm) that were readily available. Nearly all species were collected from at least two different sites, with up to nine site-year combinations for the most-collected species. At each site, we collected fresh intact ripe fruit from the ground, normally collecting 10 fruit from under each of 10 different trees. We searched systematically to avoid bias towards larger and more visible fruit. The fruit diameter (and length) were measured with digital callipers to 0.01 mm.

We then set up germination trials with these fruits to test the effect of flesh removal on germination. Following Robertson et al. (2006) we compared hand-cleaned fruits with intact ones, usually in both the glasshouse (with fruits placed on potting mix) and in the field at the site of collection (with fruits placed on the soil surface with leaf litter over the top). For full details of methods see Robertson et al. (2006). Where possible, we also included a through-bird treatment in the glasshouse, with variable numbers of seeds, as available. In a few cases, bird-cleaned fruits were used instead of hand-cleaned because we had insufficient intact fruits for hand cleaning. Germination was scored for up to 4 years until germination had ceased, although we include interim results for some cases set up in the last two years where germination is continuing. In total we ran 160 different trials (species, site, year, treatment combinations), usually with 100 fruits per trial (mean 93.6, range 13–252), giving a total of 14 983 fruits tested. For comparison, we also included in the analyses published germination data for *Nestegis cunninghamii* from Robertson et al. (2006).

Germination analysis followed Robertson et al. (2006) in use of the natural log of the odds ratio to measure effect sizes. In each trial the odds ratio (OR) was the number of germinated seeds divided by the number of seeds that failed to germinate. Where germination is 0% or 100% the odds ratio is undefined, so we added 0.5 to any zeros before calculating the ratio, hence we have conservative estimates of the effect sizes. We tested for effects of germination conditions (glasshouse vs. field) and treatment (intact vs. cleaned, bird-cleaned vs. hand-cleaned) using either binomial GLMs using all replicate trials, or paired t-tests on the subset where two treatments were applied to the same species-condition (glasshouse/field)-site-year combination. For the paired t-tests we excluded trials where germination was still continuing.

Bird gape sizes and feeding records

Bird gapes (the width across the outside of the bill at the base of the upper mandible) were measured on live birds mist-netted on Tiritiri Matangi Island and at Wenderholm (Anderson 1997) and on skins collected in New Zealand held by the Canterbury and Auckland Museums. Juveniles and specimens from offshore islands were excluded.

Records of birds feeding on different sized fruit were collated from the literature and our observations. The published records usually do not say explicitly that birds were swallowing whole fruit, but in general we make that assumption. Two cases, where birds were feeding on the flesh but not confirmed to ingest seeds, were excluded (both silvereyes *Zosterops lateralis* on *Alectryon excelsus*). One of the two records of silvereyes on *Dysoxylum spectabile* may also represent consumption of only the flesh.

Measuring pollen limitation

Pollen limitation is measured experimentally by comparing fruit set (fruits per flower) for hand-cross-pollinated flowers and unmanipulated (natural) flowers, quantified with the Pollen Limitation Index (PLI) as $(1 - (\text{natural fruit set} / \text{hand fruit set}))$ (Larson & Barrett 2000). We collated all available field data on pollen limitation in ornithophilous-flowered native plants in New Zealand, excluding data from bird sanctuaries, based on the summary in Robertson et al. (2008) but with the following changes. We excluded four data sets; *Cordyline australis* because the hand-pollinated and natural treatments were from different sites, and *Alseuosmia pusilla*, *A. turneri* and *A. quercifolia* as we consider the flowers are too small (<20 mm) to call ornithophilous (see Table 5 below). Arithmetic errors in calculating the PLIs for *Fuchsia excorticata* hermaphrodites and *Metrosideros excelsa* in Robertson et al. (2008) were corrected. Additional unpublished sites and years were included for *Peraxilla tetrapetala* and *P. colensoi*, as were unpublished data for *Sophora prostrata*. We included the ornithophilous *Alepis flavida* even though it is routinely self-pollinating (Ladley et al. 1997). The data for *Peraxilla* spp. included only flowers not attacked by *Zelleria maculata*, an endemic moth florivore which greatly reduces fruit set (Kelly et al. 2008). In *M. excelsa*, the PLI was based on fruit set \times seeds per fruit, but all other species used only fruit set. To compare the degree of pollen limitation in New Zealand with the rest of the world, we calculated the fruit-set natural-log odds ratios (i.e. $\ln(\text{hand-crossed} / \text{natural})$) and compared these against a global compilation of 482 studies (Knight et al. 2005).

List of plants with fleshy fruited or bird-visited flowers

We used Janice Lord's compilation of all the native plant species with fleshy fruit (Lord et al. 2002) to tabulate species numbers. Fruits were classified by diameter, using our measurements where available and Lord's measurements otherwise. We also checked the McGlone et al. (2010) list of 188 tree species against the list of dispersal modes given by Thorsen et al. (2009).

To update a list given in Newstrom & Robertson (2005) of the plant species with bird-visited flowers, we searched the literature, including the extensive compilations in the Handbook of Australian, New Zealand and Antarctic Birds (Higgins et al. 2001), but excluding rare records of birds visiting flowers of four plant species that are wind-pollinated and nectarless (*Coprosma foetidissima*, *C. rotundifolia*, *Coriaria arborea*, *Dodonaea viscosa*). We also compiled a second list of plant species that are worth closer study as possible bird-visited species. This list includes 79 species which have definitely bird-visited congeners with similar flower morphology, and six additional species in five genera (*Ackama*, *Alectryon*, *Litsea*, *Mida*, *Neomyrtus*) which we have listed on the basis of flower morphology alone.

To work out the percentage of the flora dependent on bird pollination, we used a list of the 1976 currently accepted native seed-plant species in the NZ Plant Names Database (<http://nzflora.landcareresearch.co.nz/>) on 23 September 2008, and excluded species that occur in the New Zealand botanical region only on the Kermadec (19 spp.), Chatham (36 spp.), and subantarctic islands (32 spp.), leaving 1889 species. We also looked at the subset of these that are trees (maximum height >6 m) and other woody plants (shrubs, climbers and hemiparasites) using the categorisation of McGlone et al. (2010). For comparisons with Australia, we used the entire

vascular floras, including ferns and species from offshore islands.

Lists of birds

We tabulated lists of native land bird species from field guides for New Zealand (Heather & Robertson 1996), and Australia (Simpson & Day 1996). We excluded seabirds (penguins, albatrosses, petrels, shearwaters, tropicbirds, gannets, waders, and gulls) and non-breeding species. For New Zealand, we included five species which became extinct after 1890, but excluded seven self-introductions which established after 1930, and, to match the plant compilation above, we excluded species found only on offshore islands (Kermadecs, Chathams and subantarctic islands). Recent changes to the New Zealand list (Tennyson 2010) were not included. Bird names follow Heather & Robertson (1996).

Basal area from National Vegetation Survey

To calculate the relative importance of birds for pollination and dispersal, taking plant species abundance into account, we calculated basal area data from forest plot data archived in the National Vegetation Survey (NVS) databank. A nationally representative set of 1381 plots was selected, as it was estimated that at least 1050 plots are needed to estimate species basal area to $\pm 10\%$ of the true mean at 95% confidence (Bellingham et al. 2000). To remove spatial bias from the data, a 3-km grid was superimposed across the North and South Islands, and then a random plot was selected from the nearest survey line occurring in the square region around each grid intersection. Variable-area, exclosure, and restricted-data-access plots were excluded. Then, for each plant species in the plot, its total basal area was calculated. These species (total 209 taxa across the 1381 plots) were then classified by fruit size (Lord et al. 2002) and flower type (Table 5, including only ornithophilous and definitely bird-visited species). Basal area by species was then summed in four regions selected to align with the geographic patterns of plant distribution: Northern North Island (Department of Conservation conservancies Northland, Auckland, Waikato and Bay of Plenty), Southern North Island (Hawkes Bay, Tongariro, Wanganui and Wellington conservancies, prior to 2009 conservancy boundary changes), Western South Island (Nelson-Marlborough, West Coast, Southland), and Eastern South Island (Canterbury, Otago). We calculated a national

average as the mean of the four regional means, because the number of plots from the northern North Island (89) was lower than for the other three regions (402, 493 and 397 for southern NI, western SI and eastern SI respectively). However, individual species totals are presented as simple totals from the combined 1381-plot dataset.

Results

Evaluating dispersal

Which animals act as dispersers?

Numerically, across 32 studied species of native fleshy-fruited plants, the majority (84%) of fruit dispersal was by four birds – kereru, tui, bellbirds (*Anthornis melanura*) and silvereyes – although another 11 native and 7 introduced bird species took small quantities of fruit (Kelly et al. 2006). When considering large-fruited species, Clout and Hay (1989) showed that the only bird recorded as feeding on fruits >14 mm diameter was the kereru, and it was also the only bird commonly seen taking fruits in the 10–14 mm size class. However, more observations since then have filled in some of the blanks in the matrix (our Table 1). Of particular interest are the records of birds other than kereru feeding on and swallowing fruits from species with mean fruit diameter >14 mm. Kokako (*Callaeas cinerea*) have been reported feeding on tawa, taraire and puriri, but are of restricted distribution. Tui are much more widespread and have been reported to feed on tawa, karaka and puriri. Several birds too small to be included in Clout and Hay's (1989) table have also been seen feeding on fruits in the 10–14 mm size class, with bellbirds being particularly noteworthy given their wide distribution. Both bellbirds and silvereyes swallow fruit in the 7–10 mm size class. The latest information therefore widens the list of reported dispersers of most of the large-fruited native plants.

Many of these new records in Table 1 show birds eating whole fruits larger than their measured gape, which ought to be difficult, although it has long been known for kereru (Clout & Hay 1989). Backing up these foraging observations on large fruits are records of excreted seeds (Table 1, last row). Williams (2003) reported silvereyes excreting seeds of *Prumnopitys taxifolia* (mean fruit diameter 9.5 mm) and

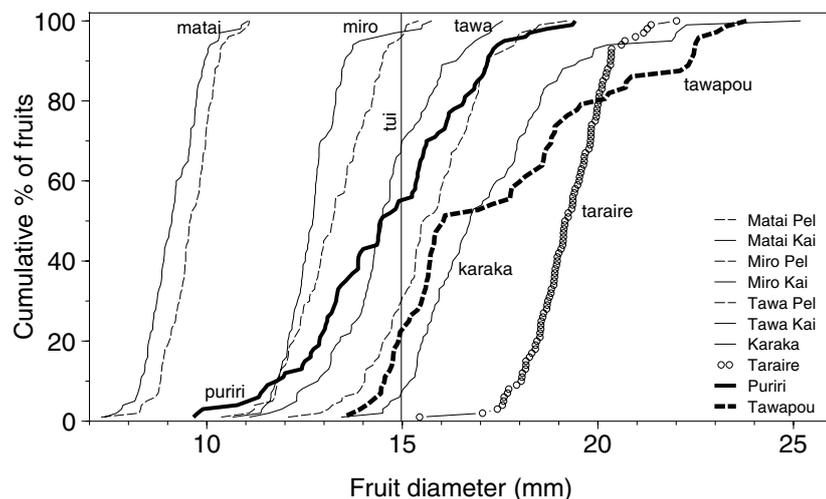


Figure 1. Examples of cumulative distributions of fruit diameters for seven important medium- and large-fruited native trees. Three species (matai *Prumnopitys taxifolia*, miro *Prumnopitys ferruginea*, and tawa *Beilschmiedia tawa*) are shown from two sites (Pelorus and Kaikoura, all 2004 except matai Kaikoura in 2003). The other species are shown for one site each (karaka *Corynocarpus laevigatus*: Auckland 2004, taraire *Beilschmiedia tarairi*: Whangarei 2004, puriri *Vitex lucens*: Wenderholm 2005, tawapou *Planchonella costata*: Whangarei 2005). The possible upper limit for consumption by tui (15 mm) is indicated; bellbirds and silvereyes are limited to c. 10 mm, and kereru c. 25 mm.

Table 1. Bird species recorded feeding on fruits of large-seeded plant species in New Zealand, and sizes of bird gapes and fruit diameters, updated after Clout and Hay (1989). A blank means no data. Shaded squares to the lower right are those where the mean gape size is larger than the mean fruit diameter. Feeding is thought to represent swallowing whole fruit, see text.

Plant species	Clout & Hay size class	Fruit diam (mm)	Silvereye	Bellbird	Stitchbird	Saddleback	Blackbird	Tui	Starling	Song thrush	Myna	Kokako	Weka	Kereru*	Brown kiwi
<i>Beilschmiedia tarairi</i> (taraire)	>14	19.6										g		aq	
<i>Planchonella costata</i> (tawapou)	>14	18.3												a	
<i>Corynocarpus laevigatus</i> (karaka)	>14	17.5			k	B	bde							a	
<i>Beilschmiedia tawa</i> (tawa)	>14	15.5					f					fh		aq	
<i>Vitex lucens</i> (puniri)	>14	15.3					el				l	A		aq	
<i>Syzygium maire</i> (swamp maire)	>10	13.1													
<i>Prumnopitys ferruginea</i> (miro)	>10	13.0		i		aip	eikt					ahx	a	aq	au
<i>Alectryon excelsus</i> (titoki)	>7	13.0				aoC	ao	o	a			a		a	
<i>Listea calicaris</i> (mangeao)	>10	12.5										a		aq	
<i>Ripogonum scandens</i> (supplejack)	>10	10.5		i	k	avr	abikt		a			ah		aq	
<i>Hedycarya arborea</i> (pigeonwood)	>7	9.7		i		a	a	a				ah		aq	
<i>Nestegis cunninghamii</i> (black maire)	>7	9.6				a	a	a				a		a	
<i>Prumnopitys taxifolia</i> (matai)	>7	9.4		tx		apx	aetx	ao				ax	a	a	
<i>Elaeocarpus dentatus</i> (hinau)	>10	9.2										ah	a	aq	au
<i>Rhopalostylis sapida</i> (nikau)	>7	9.1				avwz		a				an		aq	anu
<i>Dysoxylum spectabile</i> (kohekohe)	>10	9.0		s	jk	s	ejs	s	s			afz	a	aq	
Bird gape (mm) Clout & Hay			5	6	7	8	9	9	9	10	10	13	13	14	24
Bird gape mean (mm)			5.1	6.5	7.1	7.1	9.7	9.7	9.8	12.2	13.0	15.3	15.3	14	
maximum			6.3	8.5	8.6	9.0	13.0	11.0	12.7	14.6	14.5	16.5	16.5		
SD			0.37	1.03	0.64	1.42	1.22	0.93	1.19	1.53	0.78	0.79	0.79		
N			21	22	14	9	19	12	24	21	12	16	16		
Largest fruit reported swallowing (mm diameter, and source)			9.9 ^m	9.7 ^m			13.0 ^y								25 ^c

Plant species are as in Clout and Hay (1989) but minus "*B. tawarua*". Species are arranged by fruit diameter as in Table 2, Robertson et al. 2006, and Lord et al. (2002), which do not exactly match the fruit size categories of Clout and Hay. Bird gapes are from Clout and Hay (1989), and from our work (Anderson 1997 and SHA & JIL unpubl.). References: a, Clout & Hay (1989); b, Oliver (1955); c, Gibb (1970); d, Falla et al. (1978); e, Stewart (1984); f, Booth (1984); g, Myers (1984); h, Flux (1994); i, O'Donnell & Dilks (1994); j, Anderson (1997); k, Higgins et al. (2001); l, Dijkgraaf (2002); m, Williams (2003); n, Cowan (1991); o, Williams & Karl (1996); p, Beveridge (1964); q, Higgins & Davies (1996); r, Burrows (1994); s, David Mudge pers comm.; t, St. Paul (1975); u, Reid et al. (1982); v, Burrows (1996c); w, McNutt (1998); x, Burrows (2001); y, Williams (2006); z, S. Anderson unpubl.; A, Lee et al. (1991); B, Moncrieff (1929); C, JIL unpubl. *For full details on kereru feeding see Wilkinson & Wilkinson (1952); Merton (1966); St. Paul (1977); Clout et al. (1986); Clout et al. (1991); Burrows (1995, 1996b, 1999); Baker (1999); Gibb (2000).

hawthorn (*Crataegus monogyna*) (fruit diameter 9.9 mm, 1.9 times their gape of 5.1 mm), and bellbirds excreting seeds of fruits up to 9.7 mm diameter (1.5 times their gape of 6.5 mm). Blackbirds excreted seeds of *Alectryon excelsus* (fruit diameter 13.0, gape 9.7, ratio 1.34) (Williams & Karl 1996). Although we lack comparable data for tui, we estimated they should be able to consume up to about 15 mm diameter – the mean of the three ratios above is 1.58 times the gape, which, applied to the tui gape of 9.7 mm (Table 1), gives a maximum fruit size of about 15 mm. There are records of tui eating karaka (Table 1), consistent with this predicted maximum size.

There are two factors that allow birds to eat whole fruits larger than their gape. The first is that soft fruit may be malleable, and birds can stretch their jaws to swallow larger items, a behaviour that is well-known in fruit pigeons. So, a bird may be able to ingest a fruit that is larger than its gape. The second is that both fruits and gape sizes have not just a mean, but also a variance. Therefore, some of the larger individual birds of a small species may be able to eat the smaller fruits of a large-fruited plant. The mean gape for tui was 9.7 mm, but the maximum from a sample of 12 birds was 11.0 mm (Table 1). Similarly bellbirds had a mean of 6.5 mm but a maximum of 8.5 mm ($n = 22$).

For fruits, we have measured the variation in fruit sizes for nearly all the large-fruited native species, sometimes for multiple sites and years. Cumulative size distributions show smaller fruits overlapping the upper feeding limits of the key bird species (Fig. 1). Several key features emerge. Firstly, there is variation within species among sites and also among years (Table 2). Secondly, there can be very wide variation within a site. For example, for karaka at Auckland, while the mean width in Figure 1 was 17.2 mm, the range for individual fruits at this site was 13.4 to 25.2, the 5th percentile was 14.7 and the 95th percentile was 21.9 mm. The ranges were particularly broad in the larger-fruited species with variable numbers of seeds per fruit (tawapou, puriri and supplejack; standard deviations and coefficients of variation (CVs) are given in Table 2). In tawapou and supplejack, much of the size variation was related to the number of seeds per fruit (Fig. 2); comparable data could not be collected for puriri without interfering with the germination trials.

Because of the wide size distributions, the smallest fruits are within the likely ingestion ranges of birds too small to eat average-sized fruits. The mean for puriri (14.6 mm) is far beyond the ability of bellbirds to swallow, but 3% of fruits at the site plotted in Fig. 1 were smaller than the 10 mm that bellbirds might be able to eat. If tui could eat fruits up to 15 mm, they would be able to consume 70% of the tawa from Kaikoura, 30% of the tawa from Pelorus, 55% of the puriri, 22% of the tawapou, and 7% of the karaka in these examples – all species that an analysis based on means would conclude tui could not disperse, but consistent with the records in Table 1 of tui feeding on tawa, karaka and puriri. These percentages of fruits below a specified diameter also vary among years and among sites, as tabulated for 41 datasets on 18 different species in Table 2. For example, for tawa the percent <15 mm ranged from 70% to 14%.

Karaka is often described as New Zealand's largest fruit, which is true for length and probably mass, but both taraire and tawapou have fruits with a wider mean diameter (and hence harder for birds to swallow). Moreover, taraire is less variable in size, and is the only native species that has almost no individual ripe fruits of less than 15 mm diameter. Therefore, taraire is the species most dependent on kereru for dispersal because it has the largest **small** fruits, even though karaka

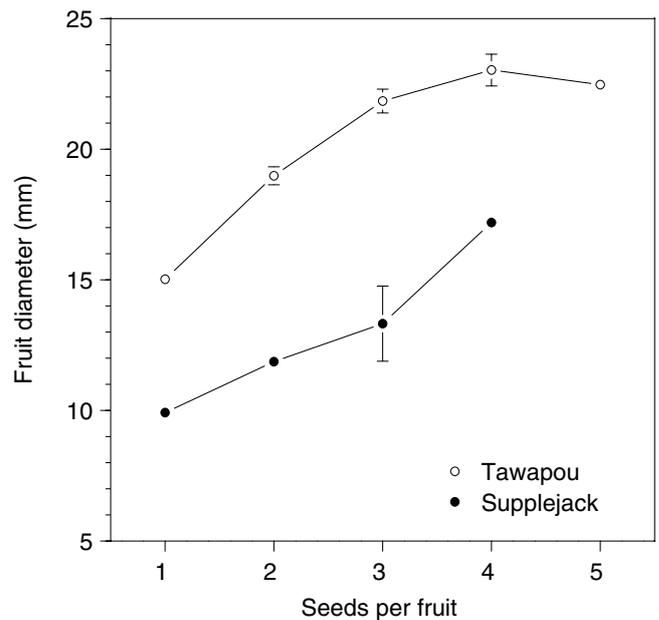


Figure 2. Diameter of ripe fruits of tawapou (*Planchonella costata*, open symbols) and supplejack, (*Ripogonum scandens* filled symbols) as a function of the number of developed seeds per fruit, from several sites combined (listed in Table 2). Means \pm 95% CIs are plotted, except for the largest size category for each species where there were too few seeds ($n = 51, 50, 28, 5$ and 1 fruits for tawapou and 142, 62, 9, 2 fruits for supplejack with 1–5 seeds), but many of the CIs are smaller than the symbols.

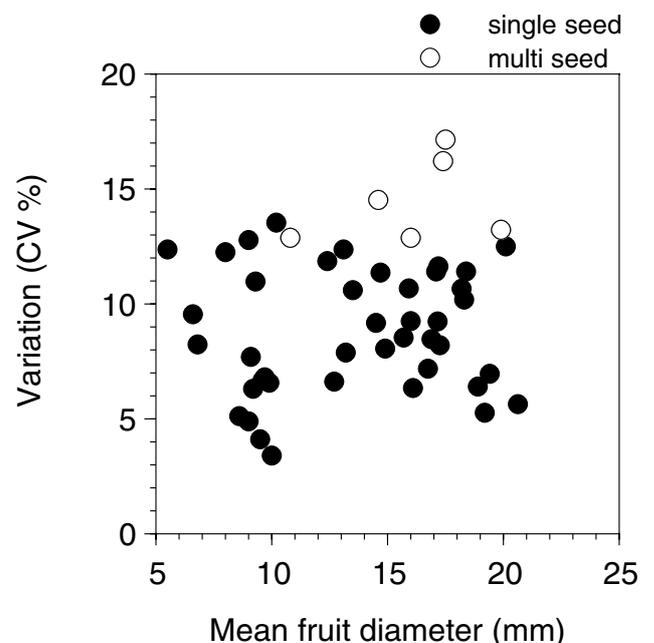


Figure 3. Variation in fruit diameter within a fruit crop (coefficient of variation for a site/year combination) versus mean fruit diameter in that dataset for 48 datasets from 18 New Zealand species. Species with variable numbers of seeds per fruit (*Dysoxylum spectabile*, supplejack, puriri and tawapou) were more variable than single-seeded species, but within the latter group there was no effect of fruit diameter (see text).

Table 2. Fruit sizes and germination (with and without flesh) for fleshy-fruited native plants, ordered by mean fruit diameter. Year is that of fruit collection. Mean fruit width (mm) and coefficient of variation ($CV = SD/mean \times 100$) are given, along with the percentage of fruits that were <10 mm or <15 mm diameter. Germination % is under the specified conditions (placed in field or glasshouse; bird-cleaned, hand-cleaned or intact fruit). An asterisk means germination had not finished. The data for *Nestegis cunninghamii* are from Robertson et al. (2006).

Species	Site	Year	Fruit width			% <10	% <15	Field bird	Field hand	Field intact	G/house bird	G/house hand	G/house intact
			Mean	SD	CV								
<i>Beilschmiedia tarairi</i> (taraire)	Wenderholm	2004	20.6	1.12	5.4	0	0	90.0		76.0		90.8	
	Whangarei	2004	19.2	1.01	5.3	0	0					85.0	
	Whangarei	2005	18.9	1.21	6.4	0	0		76.0	24.0		100.0	
<i>Planchonella costata</i> (tawapou)	Whangarei	2005	17.4	2.82	16.2	0	22	45.0		33.6	81.4*	48.7*	70.0*
	Whangarei	2006	19.9	2.63	13.2	0	22		45.0	43.0	51.4*	61.4*	6.5*
	Wenderholm	2004							2.0	2.0			
<i>Beilschmiedia tawa</i> (tawa)	Wenderholm	2007	17.5	3.00	17.1	0	30					61.8*	48.0*
	Kaikoura	2004	14.5	1.33	9.2	0	70		92.0	68.0	73.0	92.9	
	Kaikoura	2005	16.9	1.43	8.5	0	14		98.0	90.0	99.0	99.0	91.0
	Kaikoura	2006	16.1	1.02	6.3	0	14				90.4	88.0	34.0
	Kaikoura	2007	16.0	1.48	9.3	0	20		70.0	66.0	96.4	100.0	65.0
	Kaikoura	2008						24.0	52.0		92.0	99.0	96.0
	Pelorus	2004	15.7	1.34	8.5	0	30		94.0	98.0		98.0	
	Pelorus	2005	14.9	1.20	8.1	0	53		6.0	10.0		97.0	
	Nga Manu	2007	14.7	1.67	11.4	0	56		78.0	22.0	96.6	92.0	74.0
<i>Corynocarpus laevigatus</i> (karaka)	Palm. North	2008									78.0	98.0	62.0
	Kaikoura	2004	17.1	1.95	11.4	0	10		86.0	68.0		100.0	
	Kaikoura	2005	18.2	1.94	10.7	0	7		86.0	84.0		56.0	84.6
<i>Vitex lucens</i> (puriri)	Wenderholm	2005	14.6	2.12	14.5	3	55					43.0	
	Wenderholm	2007	16.0	2.06	12.9	0	32					8.8	5.8
	Wenderholm	2007	16.0	2.06	12.9	0	32					7.9	17.9
<i>Syzygium maire</i>	Nga Manu	2006	13.1	1.62	12.4	5	91		57.0	35.0	77.4	76.0	74.0
<i>Prumnopitys ferruginea</i> (miro)	Kaikoura	2004	12.7	0.84	6.6	0	97		0.0*	0.0*		76.0*	
	Pelorus	2004	13.2	1.04	7.9	0	96		4.0*	0.0*		80.0*	
<i>Elaeocarpus dentatus</i> (hinau)	Palm. North	2005	9.3	1.02	11.0	69	100		16.0*	14.0*		4.0*	
	Pelorus	2005	9.0	0.44	4.9	100	100		0.0*	0.0*		0.0*	0.0*
<i>Alectryon excelsus</i> (titoki)	Kaikoura	2005	12.4	1.47	11.9	5	97		85.0	85.0		91.0	93.3
	Wakefield	2007	13.5	1.43	10.6	0	83		0.0	0.0		61.0	40.7
<i>Ripogonum scandens</i> (supplejack)	Kaikoura	2004										96.7	92.9
	Kaikoura	2005	10.8	1.39	12.9	23	98		88.2	87.6	83.9	95.0	73.5
	Palm. North	2004							99.3	94.0			
	Palm. North	2005	10.2	1.38	13.5	54	100		98.4	90.1		91.9	
<i>Hedycarya arborea</i> (pigeonwood)	Palm. North	2005	10.0	0.34	3.4	46	100					83.0	71.8
	Kaikoura	2005	9.2	0.58	6.3	91	100		73.0	64.0	94.2	96.0	87.8
	Northland	2005	9.7	0.66	6.8	74	100				86.8	91.0	56.5
	Akaroa	2007	9.9	0.65	6.6	62	100				94.0	96.0	90.9
<i>Nestegis cunninghamii</i>	Ohakune	2000						64.6	58.0				
<i>Prumnopitys taxifolia</i> (matai)	Kaikoura	2004	9.1	0.70	7.7	91	100		40.0	32.0		63.0	
	Pelorus	2004	9.6	0.64	6.7	73	100		49.0	56.0		64.0	
<i>Dysoxylum spectabile</i>	Wenderholm	2004						76.0		81.2	87.5		
	Whangarei	2005	9.0	1.15	12.8	87	100		16.0	4.0	89.0	45.8	1.4
<i>Rhopalostylis sapida</i>	Palm. North	2005	8.6	0.44	5.1	100	100		87.0	76.0		80.0	87.1
	Akaroa	2005	9.5	0.39	4.1	94	100		18.0	24.0	93.1	89.0	88.6
<i>Myoporum laetum</i>	Akaroa	2005	8.0	0.98	12.3	94	100		0.0	0.0	9.0	7.0	12.0
<i>Coprosma lucida</i>	Port Hills	2005	6.8	0.56	8.2	100	100		31.5	18.0		48.8	24.0
<i>Coprosma grandifolia</i>	Kaikoura	2005	6.6	0.63	9.5	100	100		40.0	41.5		80.2	100.0
<i>Myrsine salicina</i>	Hunua Ranges	2005	5.5	0.68	12.4	100	100	72.0		35.0		71.7	

and tawapou have larger **large** fruits than taraire. If it was advantageous to large-fruited species to have some smaller individual fruits that could be dispersed by mid-sized birds, we would predict that the CV would be greater for large-fruited than small-fruited species. This was not the case (Fig. 3): once multi-seeded species were excluded, there was no relationship with mean fruit diameter (linear regression, $n = 42$, $F_{1,40} = 0.06$, $P = 0.80$).

Table 1 alters the conclusion of Clout and Hay (1989): they said kereru were "virtually the only disperser" of ten species with fruits >10 mm diameter, whereas tui and/or blackbirds feed on 6 of the 10 species (including 6 of the 7 common species). Probably only for taraire are kereru truly virtually the only disperser. However, if some of the bird-plant combinations in Table 1 happen only infrequently, this reduces the contribution

of the bird to regeneration of the plant species. This may be an issue for tui, the second-largest common frugivore, which nationwide have a diet that is usually dominated by nectar, with only about 10% fruit (Murphy & Kelly 2001). Even so, undispersed fruits are able to germinate under the parent (see below), and even low levels of dispersal could allow sufficient colonisation of new habitats and maintenance of gene flow between parts of a meta-population (Kelly et al. 2004). Thus, kereru certainly remains the main disperser for fruits >14 mm, but the absence of kereru would be unlikely to induce local regeneration failure. We need more study on whether in the absence of kereru, occasional long-distance dispersal by other birds would be sufficient to maintain plant populations.

Finally, can introduced mammals serve as substitute dispersers for the seeds of native plants? So far, only the

smaller introduced mammals have been tested (Williams et al. 2000; Dungan et al. 2002; Dungan & Norton 2003; Williams 2003). In general, mice (*Mus musculus*) and rats eat many seeds and fruits, but grind up all (mice and *Rattus exulans*) or nearly all (*Rattus rattus*) the seeds, so they act largely as seed predators. Brushtail possums (*Trichosurus vulpecula*) also eat many fruits and are confirmed to disperse some seeds up to about 10 mm, including frequent pigeonwood (9 mm mean fruit diameter), occasional matai (*Prumnopitys taxifolia*) (9.5 mm) and one supplejack seed (10.6 mm), whereas with miro (12.3 mm) possums eat only the flesh and with tawa (18.8 mm) they chew and destroy the kernel (Williams 2003). Larger mammals have not yet been tested.

Studies of dispersal rates

There have been few studies documenting dispersal quantity (removal rates) of New Zealand species, and the only study on fruits >14 mm diameter is on tawa. Over nine seasons at Blue Duck Scientific Reserve near Kaikoura, an average of 50% of tawa seeds underneath parent canopies had passed through a bird (Fig. 4). There was variation among years, with a minimum of 13% in 1999 and a maximum of 80% in 1997, but no significant relationship to size of the fruit crop (linear regression, $F = 0.44$, $n = 9$, $P = 0.53$, $R^2 = 0.06$). These numbers will under-estimate the percentage of the total seed crop processed by birds, as many seeds swallowed by birds are dropped away from parent canopies (Wotton 2007). However, poor dispersal service would show up as large numbers of fleshy fruits falling under the parents. Overall, the Blue Duck data seem to represent reasonably good dispersal, since some fleshy fruits will always fall from the trees due to handling errors by birds, the feeding activities of possums (Knowles & Beveridge 1982), and fruit dislodged by wind. However, in two of the nine years less than a third of fruits under the parents had been eaten by birds, so data from a single year should be treated with caution.

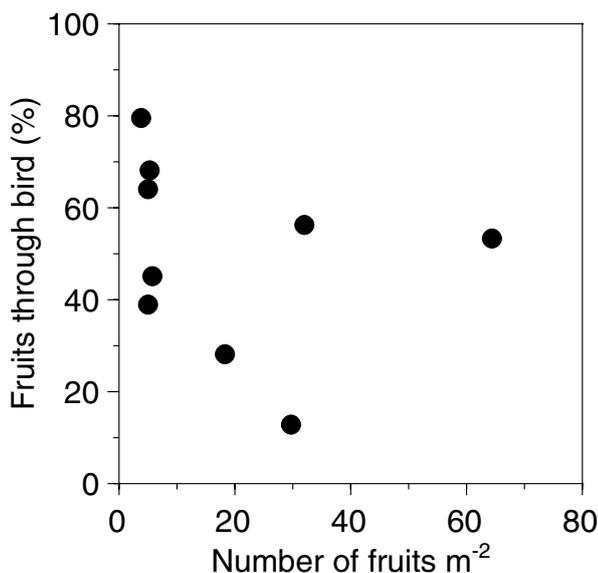


Figure 4. Dispersal of *Beilschmiedia tawa* fruits by birds over nine seasons at Blue Duck Scientific Reserve, Kaikoura. Fruits were collected off the ground under the canopies of mature tawa trees and classified as clean (through bird) or flesh intact. There was no significant relationship with fruit crop size (see text).

Including the Blue Duck tawa study, we know of dispersal studies for 10 New Zealand plant species (Table 3). Most studies use the rates that fruits were removed from plants, or the percentage of fruits on tagged branches that had time to go over-ripe before being removed by dispersers. There was wide variation in the level of replication in these studies; from no replication when data come from a single tree in one season, through to a high level in multi-site multi-year studies.

Summarising the results is difficult as studies use different methods, and there is no objective definition of what represents “good” or “poor” dispersal service (Kelly et al. 2004), so the ratings in the table are our interpretations. We conclude that seven of the ten studies (including both studies on fruits >10 mm) show reasonably good dispersal service, two show slower (but still nearly complete: Robertson et al. 2008) fruit removal on the mainland, and only one shows major problems with dispersal. Oddly, the worst dispersal was found for the second-smallest dispersal units in this table (*Pittosporum crassifolium*, where birds take individual seeds from the open fruit), well within the gape size of even the smallest frugivorous birds.

Germination consequences of not being dispersed

Next we consider the consequences of dispersal failure: can plants still regenerate (germinate and establish) locally if fruits are not dispersed? After a series of studies by Burrows (1995, 1996a & b, 1999), reviewed in Kelly et al. (2004), which showed many New Zealand plant species failing to germinate from whole fruits, concern was raised that seeds in undispersed fruits may die without germinating. This implies that dispersers are essential for regeneration, because without them the fruit flesh would not be removed and germination would not occur. However, the lack of germination from whole fruit was later found to be an artefact of using Petri dishes for the germination trials (Robertson et al. 2006), presumably because germination inhibitors cannot leach away in a Petri dish. Robertson et al. (2006) showed that three large-fruited New Zealand species (karaka, tawa, supplejack) germinated well from whole fruit in the field and in pots in the glasshouse, in contrast to the failure of all three species to germinate from whole fruits in Petri dishes.

We extended the Robertson et al. study by testing germination from whole fruits and cleaned seeds for almost all native species with fruits >8 mm diameter (Table 2), each usually at several different sites. Four conclusions emerge from these results:

(1) Two species (miro *Prumnopitys ferruginea*, hinau *Elaeocarpus dentatus*) have restricted germination with long delays before first germination, germination continuing over many years, and low percentages germinating. This has been previously reported for miro (Clout & Tilley 1992) but not to our knowledge for hinau. Miro and hinau are two of the four native species with very thick endocarps, which Thorsen et al. (2009) speculated may have been for protection against damage in moa gizzards. The third thick-endocarp species, puriri, also showed relatively low germination percentages, while the fourth (matai) germinated normally. Perhaps the poor germination of these three species is the first evidence for an ‘anachronistic’ adaptation in the flora to dispersal by moa (cf. Lord et al. 2002 and Thorsen et al. 2009), which are known to have eaten matai and *Elaeocarpus hookerianus* fruit (Lee et al. 2010). Testing the effect of simulated moa gut passage on germination in miro, hinau and puriri would be worthwhile. Tawapou germination was initially delayed, but then showed good germination in the second or third year.

Table 3. Studies of dispersal service to fleshy-fruited New Zealand plants.

Species	Fruit diam (mm)	Dispersal adequacy and details	Reference
<i>Beilschmiedia tawa</i>	18.8	Good: over 9 seasons mean 50% of fruits under parent have been through bird; range 13–80%	this paper
<i>Prumnopitys ferruginea</i>	12.3	Good: in one season kereru 'G' ate 85% of crop on one tree at Pelorus	Clout & Hay 1989
<i>Rhopalostylis sapida</i>	7.9	Slow: two mainland sites showed higher % ripe and overripe fruits than seen on Kapiti Island	McNutt 1998
<i>Peraxilla colensoi</i>	6.9	Good: in one season only 0.3% of fruits seen over-ripe	Ladley & Kelly 1996
<i>Alepis flavida</i>	6.1	Good: over two seasons \leq 8.0% of fruits fell off undispersed (mean 4.7%)	Kelly et al. 2004
<i>Ileostylus micranthus</i>	5.5	Good: in one season no fruits seen over-ripe	Ladley & Kelly 1996
<i>Fuchsia excorticata</i>	5.1	Slow: seven mainland sites, some over two seasons, showed higher % ripe and overripe fruits than seen on Kapiti Island	Robertson et al. 2008
<i>Peraxilla tetrapetala</i>	4.2	Good: over three seasons \leq 6.5% of fruits fell off undispersed (mean 4.6%)	Kelly et al. 2004
<i>Pittosporum crassifolium</i>	4.0*	Poor: only 20% of seeds dispersed on mainland, compared to 94% on bird sanctuary	Anderson et al. 2006
<i>Tupeia antarctica</i>	3.6	Good: in one season no fruits seen over-ripe	Ladley & Kelly 1996

*diameter of the dispersal unit (single seed)

(2) Germination failed in some trials, but not others from the same collection (e.g. *Myoporum laetum* from Akaroa 2005 in the field but not the glasshouse, puriri from Auckland 2005 in the glasshouse but not the field). In some cases, this was due to dry conditions in the field causing seeds to go into dormancy: the *M. laetum* Akaroa 2005 collection had zero germination over two years in the field, but then the remaining intact seeds ($n = 59$) were brought into the glasshouse where 24 germinated (41%; no difference between hand-cleaned vs. whole-fruit treatments, Chi-square = 1.49, $df = 1$, $P = 0.22$). There was also some variation among years, for example tawa normally germinated well in both field and glasshouse, except for seeds from Pelorus in 2005 which in the field (but not in the glasshouse) suffered high levels of attack by invertebrates, probably the tortricid moth *Cryptaspasma querula* (Knowles & Beveridge 1982), with consequent very low germination.

(3) There was no significant difference in germination percentage between hand-cleaned and bird-cleaned seeds across the 17 collections (all in the glasshouse) where we could test this using ln odds ratios with a paired t-test matched for species, site and year ($t = 1.02$, $df = 16$, $P = 0.32$). The sign of the effect was inconsistent, with seven cases where bird-cleaned seeds had higher germination than hand-cleaned, one where they were equal, and 10 where bird-cleaned had lower germination. This was even true within a species (the 7 cases for tawa: Table 2). In other words, the scarification effect of gut passage was small and inconsistent (Robertson et al. 2006). Therefore, we combined bird-cleaned and hand-cleaned seeds for subsequent analyses.

(4) There were no species which showed consistent germination failure in whole fruits compared with cleaned seeds. Germination from whole fruits was often slower than from cleaned seeds, but the differences in germination percentages reduced over time. When analysing final germination, including both field and glasshouse, and testing with a binomial GLM with species fitted first, there were significant effects of species, condition (field vs. glasshouse), treatment (intact vs. cleaned), and the condition \times treatment interaction; these effects were found when the analysis included unfinished trials (Table 4) and when they were excluded (not shown). Germination was higher in the glasshouse than the field, and higher for cleaned than intact seeds, especially in the glasshouse (Fig. 5). The

increased germination of cleaned seeds was higher in the glasshouse (85.1 vs 68.6% for cleaned and intact fruits) than the field (64.9 vs 57.7% respectively). Since the treatment effect was smaller in field conditions, which is the biologically relevant case, we used a paired t-test to determine whether this effect was significant in the field with intact and cleaned seeds matched for site and year. Excluding studies where germination had not finished, we had 28 cases drawn from 15 species (Table 2). Final germination was significantly lower from intact fruits (using ln odds ratio, $t = -2.69$, $df = 27$, $P = 0.012$), though the effect was quite small (mean germination from cleaned fruits was 65.5%, compared to 58.6% for intact fruits). We therefore conclude that under field conditions for large-seeded New Zealand plants, the deinhibition effect is statistically real, but biologically not very important (about a 10% reduction in germination).

These results confirm and extend the conclusions of Robertson et al. (2006) that fruit ingestion by a frugivore is not necessary for germination in the larger-fruited New Zealand flora. Undispersed fruits of all tested large and medium-fruited New Zealand trees can germinate well without first passing through a bird gut, so germination is not reliant on frugivorous birds as the studies by Burrows had initially suggested. The only caveat to this conclusion is that we have not yet tested *Litsea calicaris* (fruit diameter approx 12.5 mm).

Table 4. Analysis of effects of condition (glasshouse vs. field) and treatment (intact fruit vs. cleaned of flesh) on germination in 160 trials of 19 species of fleshy-fruited New Zealand plant. Analysis used a binomial GLM on the proportion of seeds germinating. Significant effects are in bold type.

	df	Deviance	P
Species	18	4811.9	<0.001
Condition (field/glasshouse)	1	535.3	<0.001
Treatment (whole/clean)	1	230.6	<0.001
Condition \times treatment	1	62.2	<0.001
Residual	138	2751.7	

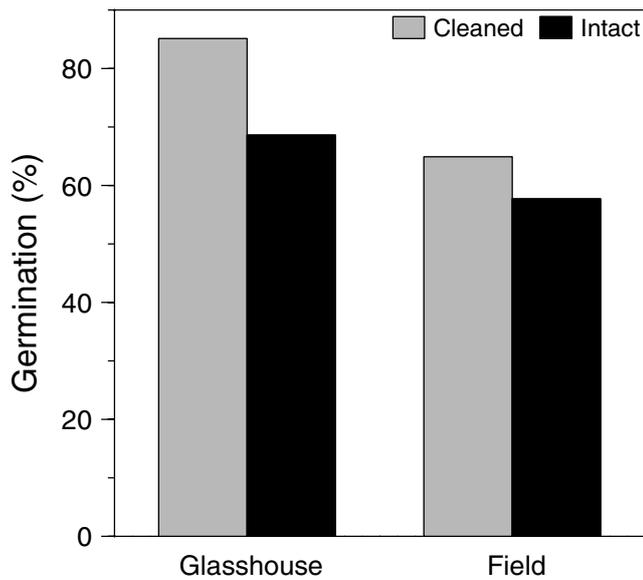


Figure 5. Germination of seeds in intact fruits or cleaned of fruit pulp, in glasshouse or field conditions, for 47 collections of 19 native large-fruited species (listed in Table 2). There were significant effects of cleaning, condition, and cleaning \times condition (see Table 4). Limiting the analysis to the 28 collections from 15 species with paired cleaned and intact treatments germinated in the field showed the cleaning effect was significant under field conditions, with very similar means to those shown here (see text).

Evaluating pollination

Which birds act as pollinators?

Godley (1979) listed the eight native birds known at that time to visit flowers (tui, bellbird, silvereye, kaka *Nestor meridionalis*, stitchbird *Notiomystis cincta*, saddleback *Philesturnus carunculatus*, red-crowned parakeet *Cyanoramphus novaezelandiae*, yellow-crowned parakeet *C. auriceps*), plus two introduced birds (house sparrow *Passer domesticus* and starling *Sturnus vulgaris*). Kelly et al. (2006) added another four natives (kea *Nestor notabilis*, whitehead *Mohoua albigilla*, yellowhead *M. ochrocephala*, fantail *Rhipidura fuliginosa*, but we exclude the rare record for insectivorous fantails as probably hawking on flowers) and three exotics (chaffinch *Fringilla coelebs*, eastern rosella *Platycercus eximius*, myna *Acridotheres tristis*). Thorogood et al. (2007) added the native kokako for a total of 12 natives and 17 species altogether. Kereru were excluded because they are flower predators (Kelly et al. 2006). The same is at least partially true for the parrots: we have watched red-crowned parakeets destroying flowers of *Peraxilla tetrapetala*, *Geniostoma rupestre* and *Pittosporum umbellatum*, yellow-crowned parakeets obliterating entire flower crops in *Phormium tenax*, and kaka damaging *Pittosporum crassifolium*, while Wilson (2004: 199) reports kea damaging flowers. However, we have also seen kaka and kea treating *P. tetrapetala* flowers carefully.

The vast majority (89%) of visits to native flowers were made by just three birds; bellbirds (32% of all visits), silvereyes (31%) and tui (25%). No other bird made more than 3.1% of visits (Kelly et al. 2006), and only 5.0% of all visits were made by the five introduced species combined. Although only three natives were frequently seen visiting flowers, it is likely

another three species (stitchbirds, kaka, kokako) were also important before they suffered severe reductions in range and density. All three have brush tongues, well suited to taking up nectar (Heather & Robertson 1996; Thorogood et al. 2007). Stitchbirds made 15.4% of flower visits in the 10 studies carried out on island sanctuaries where they still occur (Little Barrier and Tiritiri Matangi).

Degree of pollen limitation

Godley (1979) thought flower visits by birds were likely to be incidental, but field studies on pollination of bird-visited New Zealand plants since 1995 have shown this is not the case. These studies have documented widespread pollen limitation and dependence on birds. Since the first concerns were raised in relation to *Peraxilla* spp. (Ladley & Kelly 1995; Kelly et al. 1996), the level of pollination has been measured in 10 species with ornithophilous flowers (one with 2 sexes), most over multiple sites or years (Fig. 6). Most of these species (80%, including *Fuchsia excorticata* females) had mean Pollen Limitation Indexes (PLIs) that indicate substantial pollen limitation (at least one-third of potential fruits lost) including two species with severe limitation (more than two-thirds lost). Moreover, one of the two species with mean $PLI < 0.33$ still had some sites where pollen was limiting (*P. colensoi*, where 4 of the 12 sites had $PLI > 0.33$ with a maximum of 0.82). Also, for some species, there are additional effects beyond fruit set, such as reduced numbers of seeds per fruit in natural versus hand-crossed fruits of *F. perscandens* (Montgomery et al. 2001) and *S. microphylla* (our unpublished data). Thus, pollen limitation appears to be widespread for ornithophilous-flowered plants on the New Zealand mainland.

The magnitude of pollen limitation was assessed by comparing the mean effect sizes (ln odds ratio) for each species to the global compilation of Knight et al. (2005). Only 2 of the

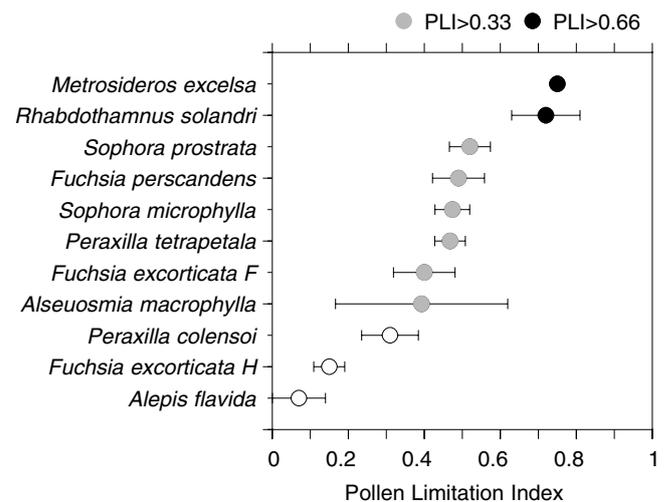


Figure 6. Degree of pollen limitation in field measurements on ornithophilous-flowered indigenous plants in New Zealand, measured as the mean Pollen Limitation Index (1–(hand-cross-pollinated fruit set/ natural fruit set)) \pm SEM. Number of replicate site-season combinations, and sources when different from Robertson et al. (2008): *M. excelsa* (1), *R. solandri* (2), *S. prostrata* (7, unpubl. data), *F. perscandens* (3), *S. microphylla* (10), *P. tetrapetala* (31), *F. excorticata* females (F, 10), *A. macrophylla* (4), *P. colensoi* (12), *F. excorticata* hermaphrodites (H, 12), *Alepis flavida* (2, Ladley et al. 1997).

11 cases (*Alepis flavida* and *F. excorticata* hermaphrodites) had effect sizes (Fig. 6) that would have put them in the bottom half of the global compilation. *Peraxilla colensoi* was in the 58th percentile, the next six cases (*Alseuosmia macrophylla* to *S. prostrata*) fell between the 70th and 75th percentiles, and the last two (*Rhabdothamnus solandri* and *Metrosideros excelsa*) were around the 85th percentile. Hence, 73% of the New Zealand cases (8/11) were in the top 30% of effect sizes globally. The mean of the New Zealand ranks was significantly higher than the null hypothesis of 50% (one-tailed t-test, $df = 10$, $t = 2.28$, $P = 0.023$). This shows that pollen limitation in New Zealand ornithophilous-flowered plants is relatively high.

Godley (1979) and Clout and Hay (1989) thought insects, which visit many ornithophilous flowers, would be sufficient for pollination. This is clearly not the case, because all the above natural fruit-set rates were for flowers accessible to all pollinators, including insects. Insects are specifically disproved as adequate pollinators in *Sophora microphylla*, the example mentioned by Godley (1979). Insects appear to be inefficient pollinators largely because of a size mismatch on ornithophilous flowers, so they either do not make contact with the stigma, or can only access the nectar by robbing at the base of the flower. In *Peraxilla* spp. small native bees were found to be less effective than birds, but better than nothing (Robertson et al. 2005). Anderson (2003) tested two ornithophilous species (*S. microphylla*, *M. excelsa*) and three species with “entomophilous” flowers (*Pittosporum crassifolium*, *Geniostoma ligustrifolium* (now *G. rupestre*), *Pseudopanax arboreus*) on a bird sanctuary, and showed that in all five cases, fruit set was significantly reduced by enclosing flowers in wire bird-exclusion cages, despite free access by insects. This surprising result shows that birds are important not just for the ornithophilous-flowered species, but also for all three tested entomophilous-flowered species visited by birds (see below).

In theory, self-incompatible species should be more strongly pollen limited, but the degree of pollen limitation in Figure 6 is not closely related to level of self-incompatibility (Newstrom & Robertson 2005). Self-pollination is certainly involved in the lack of pollen limitation in *Alepis flavida* and probably also for *F. excorticata* hermaphrodites (Robertson et al. 2008), but there is little other obvious pattern. Some of the most highly pollen-limited species (*R. solandri*, *F. perscandens*, *P. tetrapetala*) are fully self-compatible. The wholly or partially self-incompatible or gynodioecious species (*M. excelsa*, *S. prostrata*, *S. microphylla*, *F. excorticata* females, *Alseuosmia macrophylla*) are spread throughout the range of PLI scores.

Degree of seed limitation

One important caveat from the above demonstrations of widespread pollen limitation is that unless the populations are seed-limited, rather than microsite-limited, there may be no population-level consequences from reduced fruit set (Bond 1994; Ashman et al. 2004). In other words, if more fruits were produced, there may simply be more seedlings to die in competition for the few “safe sites”. Testing seed limitation is difficult and has rarely been attempted for bird-visited species, but *P. tetrapetala* has been found to be seed-limited at two sites (Kelly et al. 2007), so pollen limitation does matter in this species. Further testing on other species would be worthwhile.

Inbreeding depression

The documented pollen limitation above is all based on fruit set, with in some cases information on seed set per fruit. However, for species with inbreeding depression, such data may underestimate the impact of reduced pollination service, because with reduced flower visitation rates some self-compatible species are likely to increase self-pollination rather than reduce fruit set, as shown experimentally in *Metrosideros excelsa* (Schmidt-Adam et al. 2009). This is probably one reason that *Fuchsia excorticata* hermaphrodites are less pollen-limited than females (Robertson et al. 2008), although hermaphrodites also produce more nectar per flower (Delph & Lively 1985) so may get visited more often. Few bird-visited New Zealand plants have been tested for inbreeding depression. There is inbreeding depression in *Metrosideros excelsa* (Schmidt-Adam et al. 2000), but not in *Peraxilla* spp. (Robertson et al. 1999). Our unpublished studies still under way on *F. excorticata* and *S. microphylla* suggest both species may have substantial inbreeding depression. This topic clearly requires further study.

Characteristics of the New Zealand flora

Numbers of bird-visited species

The number of ornithophilous-flowered species in New Zealand has been given as around 13–15 (Clout & Hay 1989; Castro & Robertson 1997; Newstrom & Robertson 2005). These tallies are conservative; they list only species where bird visits have been observed, rather than all species with an ornithophilous flower structure (e.g. Godley included only one *Phormium* species). Several ornithophilous endemic plants were omitted, such as *Trilepidea adamsii* (sadly now extinct, but still counted in the flora tallies) and *Xeronema callistemon* (Poor Knights lily). Our total number of ornithophilous-flowered species (Table 5) is 29, about double previous tallies. Our tally is higher because it includes a more thorough listing within genera (c. 7 spp.), newly-described species (6 spp., including 5 in *Sophora*), and previously-ignored genera (2 spp.).

Moreover, on both the mainland and on bird sanctuaries, birds regularly visit additional species of native plants that have flowers traditionally classified as entomophilous. Newstrom & Robertson (2005) listed 37 bird-visited “entomophilous” plant taxa including 4 genera, but argued for an additional floral category common in Australasia, of “generalist” flowers that are individually small in size but clustered in compact inflorescences with robust perches and often flowering in cooler seasons (e.g. *Pseudopanax arboreus*). Such flowers seem to be well adapted for pollination by both birds and insects, although the traditional classification would call them entomophilous. The bird visits are not incidental; Anderson (2003) showed the birds were necessary for good fruit set, and Castro and Robertson (1997) showed it was energetically profitable for birds to forage on them, despite the small nectar rewards per flower. Similarly, brush-blossoms in the Myrtaceae are traditionally assigned as bird or insect-adapted according to colour (red or white respectively), but work in Australia shows birds frequently go to the white blossoms (Ford et al. 1979; Hingston & McQuillan 2000), so we include these flowers in the generalist category.

The number of species where bird pollination seems to be important for reproduction is 48 (29 ornithophilous, 6 generalists, and 13 frequently-visited entomophilous species). The total number of bird-visited species is 85, considerably above the previous tally of 51 (Newstrom & Robertson 2005).

Table 5. Bird-visited species in the New Zealand flora (excluding the Kermadec, Chathams, and subantarctic islands). Plants are divided into ornithophilous, generalist (bird/insect), or entomophilous (frequently or infrequently bird-visited, largely following Newstrom & Robertson 2005). “Visited” species have definite records of bird visits, whereas “possible” species are all (except for *Ackama*, *Alectryon*, *Litsea*, *Mida* and *Neomyrtus*) species with similar flowers to a definitely bird-visited congener. Definite visitation records are from Newstrom & Robertson (2005) and additional sources: a Rasch & Craig (1988), b Peter Bellingham pers. comm., c Jenny Ladley unpubl., d Higgins et al. (2001), e Bergquist (1987), f Fani Venter pers. comm., g Rose Thorogood pers comm., h O’Donnell & Dilks (1994). Species are trees (based on McGlone et al. 2010), except where indicated: * shrubs (i.e. woody plants under 6 m), ** vines, ^ woody hemiparasites and # herbs.

Visited ornithophilous (n = 19)	Other ornithophilous (n = 10)
<i>Alepis flavida</i> ^, <i>Alseuosmia macrophylla</i> *, <i>Clianthus puniceus</i> (d), <i>Fuchsia excorticata</i> , <i>Knightia excelsa</i> , <i>Metrosideros excelsa</i> , <i>M. fulgens</i> ***, <i>M. robusta</i> , <i>M. umbellata</i> , <i>Sophora microphylla</i> (c), <i>S. tetraptera</i> (e), <i>S. prostrata</i> * (c), <i>Peraxilla colensoi</i> ^, <i>P. tetrapetala</i> ^, <i>Phormium cookianum</i> #(d), <i>P. tenax</i> #, <i>Rhabdothamnus solandri</i> *, <i>Vitex lucens</i> , <i>Xeronema callistemon</i> #(b)	<i>Clianthus maximus</i> , <i>Fuchsia perscandens</i> *, <i>Metrosideros carminea</i> ***, <i>M. parkinsonii</i> ***, <i>Sophora chathamica</i> , <i>S. fulvida</i> , <i>S. godleyi</i> , <i>S. longicarinata</i> , <i>S. molloyi</i> *, <i>Trilepidea adamsii</i> ^
Visited generalist (n = 6)	Possible generalist (n = 17)
<i>Carmichaelia williamsii</i> * (b), <i>Geniostoma rupestre</i> , <i>Metrosideros perforata</i> ***, <i>Pseudopanax arboreus</i> , <i>Tecomanthe speciosa</i> ***(e), <i>Weinmannia racemosa</i>	<i>Ackama nubicola</i> , <i>A. rosifolia</i> , <i>Alseuosmia pusilla</i> *, <i>A. turneri</i> *, <i>A. quercifolia</i> *, <i>Fuchsia procumbens</i> *, <i>Metrosideros albiflora</i> ***, <i>M. bartlettii</i> , <i>M. colensoi</i> ***, <i>M. diffusa</i> ***, <i>Pseudopanax discolor</i> , <i>P. ferox</i> , <i>P. gillesii</i> , <i>P. laetus</i> *, <i>P. lessonii</i> , <i>P. linearis</i> , <i>Weinmannia silvicola</i>
Frequently-visited entomophilous (n = 13)	Possible frequently-visited entomophilous (n = 15)
<i>Cordyline australis</i> (d), <i>Dracophyllum elegantissimum</i> (f), <i>D. latifolium</i> (f), <i>D. traversii</i> [includes <i>D. pyramidale</i>](f), <i>Dysoxylum spectabile</i> , <i>Elaeocarpus dentatus</i> , <i>Griselinia littoralis</i> , <i>Myoporum laetum</i> , <i>Pittosporum cornifolium</i> *, <i>P. crassifolium</i> , <i>P. eugenoides</i> , <i>P. tenuifolium</i> , <i>P. umbellatum</i>	<i>Cordyline banksii</i> *, <i>C. indivisa</i> , <i>Dracophyllum lessonianum</i> , <i>D. menziesii</i> *, <i>D. fiordense</i> *, <i>Elaeocarpus hookerianus</i> , <i>Griselinia lucida</i> , <i>Pittosporum colensoi</i> , <i>P. dalii</i> , <i>P. ellipticum</i> , <i>P. huttonianum</i> , <i>P. kirkii</i> *, <i>P. pimeleoides</i> *, <i>P. ralphii</i> , <i>P. virgatum</i>
Occasionally-visited entomophilous (n = 37)	Possible occasionally-visited entomophilous (n = 53)
<i>Aristotelia serrata</i> , <i>Astelia</i> spp. #, <i>Beilschmiedia tarairi</i> (d), <i>B. tawa</i> , <i>Carpodetus serratus</i> (d), <i>Clematis paniculata</i> ***(e), <i>Corynocarpus laevigatus</i> , <i>Dracophyllum longifolium</i> (d), <i>Earina autumnalis</i> #, <i>Freycinetia baueriana</i> ***(h), <i>Hebe</i> spp*, <i>Hedycarya arborea</i> (h), <i>Hoheria populnea</i> , <i>Ixerba brexioides</i> (e), <i>Kunzea ericoides</i> , <i>Laurelia novae-zelandiae</i> , <i>Leptospermum scoparium</i> (e), <i>Leucopogon fasciculatus</i> (g), <i>Lophomyrtus</i> spp. (h), <i>Melicytus ramiflorus</i> , <i>Myrsine australis</i> , <i>M. salicina</i> , <i>Nestegis lanceolata</i> , <i>Parsonia heterophylla</i> ***(d), <i>Passiflora tetrandra</i> ***, <i>Pennantia corymbosa</i> (h), <i>Pseudopanax colensoi</i> (d), <i>P. crassifolium</i> , <i>Pseudowintera colorata</i> (h), <i>Quintinia serrata</i> (d), <i>Raukaua simplex</i> (h), <i>Rhopalostylis sapida</i> , <i>Ripogonum scandens</i> ***, <i>Rubus cissoides</i> ***, <i>Schefflera digitata</i> , <i>Syzygium maire</i> , <i>Toronia toru</i>	<i>Alectryon excelsus</i> , <i>Astelia banksii</i> #, <i>A. fragrans</i> #, <i>A. grandis</i> #, <i>A. nervosa</i> #, <i>A. skottsbergii</i> #, <i>A. solandri</i> #, <i>A. trinerva</i> #, <i>Clematis forsteri</i> ***, <i>C. foetida</i> ***, <i>C. cunninghamii</i> ***, <i>C. afoliata</i> ***, <i>C. marata</i> ***, <i>C. marmoraria</i> ***, <i>C. petriei</i> ***, <i>C. quadriracteolata</i> *, <i>Earina aestivalis</i> #, <i>E. mucronata</i> #, <i>Hebe brevifolia</i> *, <i>H. elliptica</i> *, <i>H. macrocarpa</i> *, <i>H. salicifolia</i> *, <i>H. speciosa</i> *, <i>H. stricta</i> * (a), <i>Hoheria angustifolia</i> , <i>H. equitum</i> , <i>H. glabrata</i> , <i>H. lyallii</i> , <i>H. ovata</i> , <i>H. sextylosa</i> , <i>Kunzea sinclairii</i> *, <i>Leptecophylla</i> (<i>Cyathodes</i>) <i>juniperina</i> *, <i>Litsea calicaris</i> , <i>Lophomyrtus bullata</i> , <i>L. obcordata</i> , <i>Melicytus flexuosus</i> *, <i>M. lanceolatus</i> , <i>M. obovatus</i> *, <i>Mida salicifolia</i> (a), <i>Nestegis apetala</i> , <i>N. cunninghamii</i> , <i>N. montana</i> , <i>Neomyrtus pedunculata</i> , <i>Parsonia capsularis</i> , <i>Pseudowintera axillaris</i> , <i>P. insperata</i> , <i>P. traversii</i> *, <i>Quintinia acutifolia</i> , <i>Raukaua edgerleyi</i> , <i>Rubus australis</i> ***, <i>R. parvus</i> ***, <i>R. schmidelioides</i> ***, <i>R. squarrosus</i> **

There are another 85 species listed as “possibles”, which we consider species worth studying to see if birds visit. However, in subsequent sections we ignore all the “possible” species listed in Table 5 and consider only the 85 ornithophilous and definitely-visited species. The absence of records of birds visiting the “possible” species is not as yet conclusive, because there are still too few records of bird feeding behaviour. We are attempting to evaluate the likely pre-human importance of birds as pollinators. Where bird densities are reduced (as currently on the main islands), foraging is probably concentrated on the highest-reward species and visits to lower-reward species may be rarely seen, especially at sites lacking stitchbirds and/or bellbirds. Observations made on bird sanctuaries will be maximally informative.

As a percentage of the total seed-plant flora of the mainland (1889 species), the 85 definitely bird-visited species are 4.5%

of the total, and the 48 frequently-visited species are 2.5%. Considering only the 615 woody species (trees, shrubs, woody climbers and mistletoes), the 80 bird-visited woody species represent 13% and the 45 frequently-visited species represent 7.3% of this category. Among the 188 trees, the 56 bird-visited species make up 29.7% and the 27 frequently-visited species are 14.4% of this group.

It is difficult to assess the relative risks of mutualism failure for these pollination and dispersal categories. The largest-fruited plants were thought to be most at risk because their dispersal was thought to depend on a single bird species, but we have shown that this is completely true only for taraire. We have shown that bird pollination is frequently inadequate, reducing seed set, and most of the country now has a maximum of three effective bird pollinators (tui, bellbird and silvereye), but often only two or one of these is present (Robertson et al.

2007). Thus, the two most-specialised categories (fruit over 14 mm width, and ornithophilous flowers) may represent similar levels of risk of mutualism failure, and similarly for the second-most specialised categories (fruit over 10 mm, and generalist bird/insect flowers). When comparing these categories, there are many more plants in the most dependent category (29 ornithophilous-flowered species, vs. 5 species with fruit over 14 mm diameter), and the same is true when including the next most dependent category (48 ornithophilous plus frequently-visited generalist and entomophilous species, vs. 10 species with fruit over 10 mm). A plot of the geographic ranges within New Zealand of the most dependent groups (Fig. 7) shows the ornithophilous flower syndrome involves more plant species at every latitude and extends further south than does large-fruit dispersal.

Proportion of forest basal area

The previous section estimates importance from the percentage

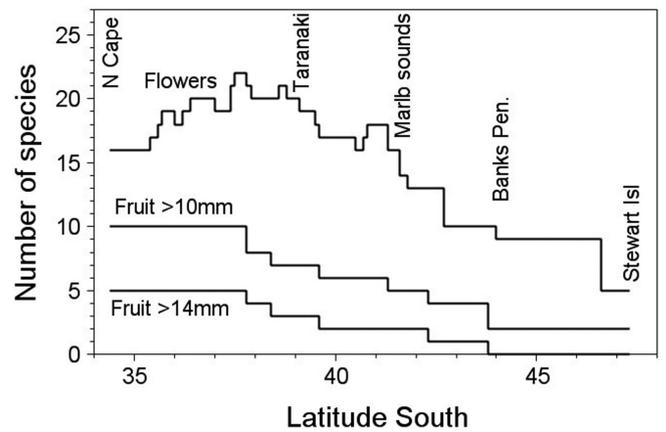


Figure 7. Numbers of plant species with ornithophilous flowers or large fruits present at different latitudes throughout New Zealand. Distribution data from Poole & Adams (1990).

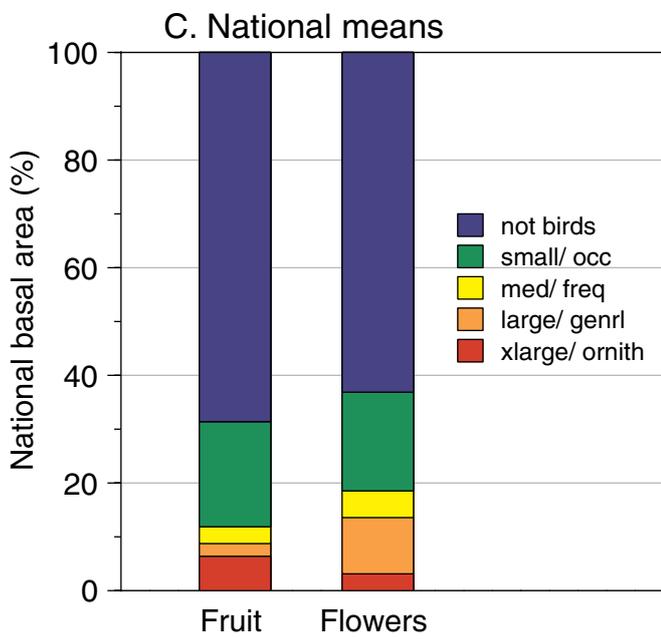
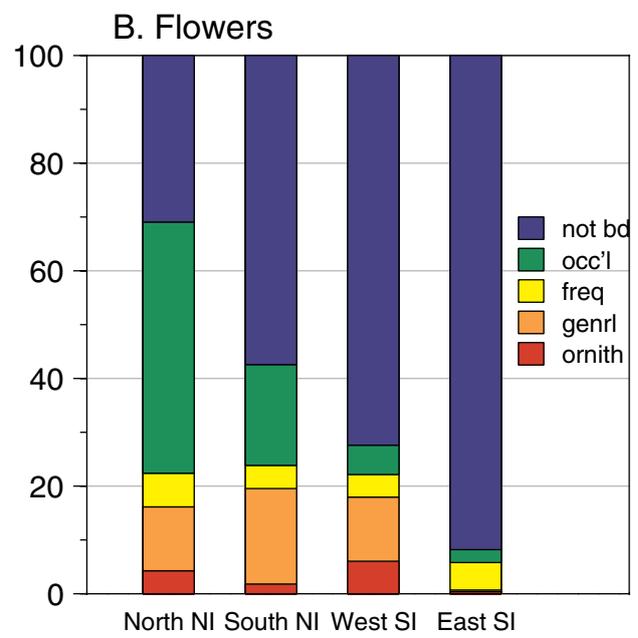
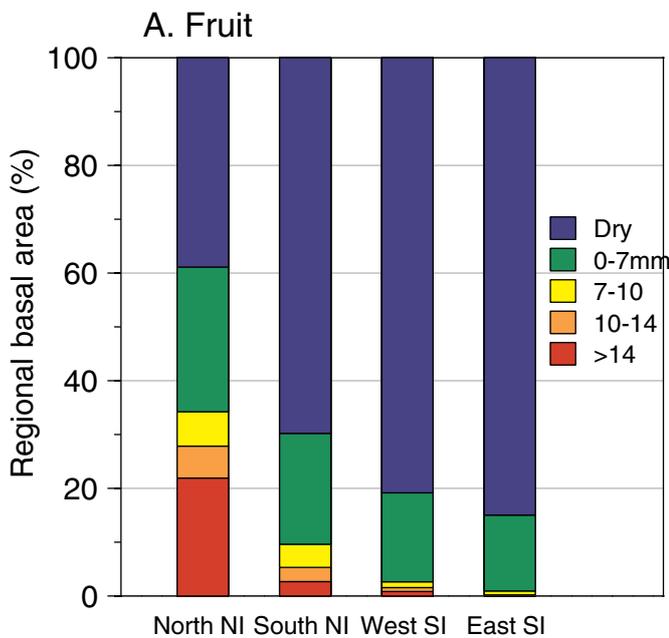


Figure 8. Proportion of the woody basal area made up of plants with bird mutualisms in 1381 nationally representative NVS plots. A: fruit by region, B: flowers by region, C: national averages (mean of the four regional means). Plants are categorised by fruit type (dry-fruited, or fleshy-fruited in different size classes from under 7 mm diameter to over 14 mm) and flower type (not visited by birds, occasionally visited, frequently visited, generalist bird/insect flowers, and ornithophilous flowers, see Table 5).

of species which are bird pollinated or fleshy-fruited. Another approach includes the relative abundances of species to find out what proportion of the plant biomass is bird pollinated or fleshy-fruited. The data from the 1381 nationally representative forest plots showed both fleshy-fruited species and bird-visited species are a decreasing proportion of the total basal area with increasing distance south and eastwards (Fig. 8). This is driven largely by the increasing dominance of *Nothofagus* spp. which are wind-pollinated and dry-fruited. However, several surprising points emerged. In the national average, and in every region except the eastern South Island, the percentage of basal area with bird-visited flowers was greater than the percentage with fleshy fruit. In the subsets for each mutualism that are most dependent on specialist service (fruits over 10 mm and ornithophilous plus generalist flowers), the percentage of basal area was greater for flowers than fruits in the national average and in every region except the northern North Island. Thus, the woody basal area is broadly more exposed to disruption by failure of bird-pollination mutualisms than by failure of dispersal of large fruit, contrary to the orthodox view of the New Zealand flora. The only major exception to this generalisation is found in the northern North Island where there is a higher relative basal area of large-fruited (>14 mm) species than ornithophilous flowers.

The plant species contributing to these patterns are listed in Table 6. Most of the categories were dominated by one or two common species: tawa for fruits over 14 mm, miro for fruits 10–14 mm, *Carpodetus serratus* and *Hedycarya arborea* for fruits 7–10 mm, *Metrosideros umbellata* (southern rata) for ornithophilous flowers, *Weinmannia racemosa* (kamahi) for generalist flowers and *Griselinia littoralis* (broadleaf) for frequently-visited flowers. Because there are relatively fewer plots in the northern North Island, the 1381 plot data set probably under-represents the basal area in the northern North Island for taraire, karaka and puriri, skewing the large-fruit percentages downwards. On the other hand, as this dataset is based on tagged stems >3 m tall, it excludes climbers, mistletoes, and herbaceous plants, three groups that include a number of widespread and/or locally dense ornithophilous species (e.g. *Metrosideros* spp., *Peraxilla* spp. and *Phormium* spp., respectively) as well as some fleshy-fruited species (e.g. supplejack, *Peraxilla* spp). It is unknown whether these two biases cancel each other out. Finally, vegetation samples taken throughout New Zealand even 50 years earlier would have had higher basal areas in *Metrosideros robusta* (northern rata) and *Fuchsia excorticata*, two once-abundant ornithophilous species which have suffered extensive mortality due to possum browse (Meads 1976; Batcheler 1983; Pekelharing et al. 1998). We are not aware of any equivalent selective loss of a common large-fruited species from native forests.

What we can conclude from this NVS plot sample is that the New Zealand woody flora has a surprisingly large percentage of its basal area in species that have bird-visited flowers. Much of this basal area is in generalist or frequently-visited entomophilous flowered species which have not been tested for pollination effectiveness when birds are present versus excluded. It would clearly be worthwhile to test this.

Discussion

Are large-fruited plants dependent on kereru?

It is often said that for species with fruits over 10 mm mean diameter, kereru are now “virtually the sole dispersers” (Clout

& Hay 1989: 31) or similar phrases (e.g. Lee et al. 1991; Wotton 2002; Kelly et al. 2004; Wilson 2004; Anderson et al. 2006). Our data show there is some dispersal by other still-widespread birds up to individual fruits of about 15 mm. Thus, only one plant species (taraire) cannot be actually or plausibly dispersed by other relatively widespread native birds, especially tui. There are observations of tui feeding on puriri, tawa and karaka, though this may not be frequent. We predict that tui should also be able to feed on some species they have not been recorded on, including tawapou and *Syzygium maire*; both plant species are now relatively uncommon and may not have been watched sufficiently often for dispersal events. With reduced bird densities at most remaining sites, birds may concentrate on the highest-reward plants and ignore plants that would be visited were birds more abundant. Clearly, quantitative data on the actual (rather than potential) contribution of tui to the dispersal of large fruit on mainland New Zealand would be valuable.

A second line of evidence also suggests that dispersal by birds other than kereru may be important for the large-fruited species. Lord et al. (2002) showed that New Zealand had generally small fruits (overall mean width 7.7 mm, the largest species averaging about 20 mm). Interestingly, smaller fruits were usually round, but larger fruits became increasingly elliptical, with width increasing more slowly than length. Also, New Zealand species had smaller fruits than their congeners in Australia. All this was interpreted as an adaptation to the generally smaller size of the volant (flying) frugivorous birds in New Zealand.

However the evolution of smaller, more elliptical fruit in New Zealand has probably not been driven by the kereru, which at 650 g body weight (Heather & Robertson 1996) is the fourth-largest extant pigeon in the world (Frances 2007) after three species of crowned pigeons in Papua New Guinea (*Goura* spp., 1.7–2.9 kg; Higgins & Davies 1996). Although the New Zealand spectrum of volant frugivorous birds is more skewed towards lighter birds than the Australian spectrum (Lord et al. 2002; Lord 2004), there is little deficiency at the top end, with kereru nearly as heavy as the largest Australian dispersers (figure 4.5 in Lord et al. 2002). Both countries have a similar percentage of their frugivores in the >560 g range (1 of 13 = 8% in New Zealand, 6 of 60 = 10% in Australia). Kereru swallow fruits to about 25 mm diameter (Gibb 1970; Clout & Hay 1989), which includes nearly all of the largest individual fruits of all native plants. Of the more than 4,000 fruits we measured of all species, only two individual karaka fruits exceeded 25 mm diameter, representing 0.4% of the karaka fruits measured. No other species had any fruits over 25 mm. The karaka fruits were quite elliptical (mean width = 18.2 mm, mean length = 31.0 mm), but if they had been spherical and contained the same volume 57 fruits (10.7%) would have been >25 mm diameter. Karaka seems to be the only native species where elliptical fruits are necessary to allow kereru to swallow this minority of very large fruits, but karaka alone cannot account for the significant relationships shown by Lord et al. (2002). In their figure 4.2, native fruits start to become elliptical above about 10 mm diameter.

Moreover, if kereru had any substantial difficulty swallowing the largest fruit, they would be expected to preferentially select smaller individual fruits from the larger-fruited species. Wotton & Ladley (2008) showed there was no significant trend in this direction. If kereru do not select smaller or narrower individual fruits they would not cause selection for reductions in fruit size or fruit width.

We therefore suggest the trends towards smaller and more

Table 6. Basal areas of fleshy-fruited and bird-visited plants (A, fleshy fruit and B, bird-visited flowers) from 1381 randomly selected NVS plots. N is the number of plots (of 1381) containing the species, and % BA is the percentage of the national total basal area. A. Fleshy fruit types, based on fruit diameter (Table 1 and Lord et al. 2002). B. Flower types, based on Table 5 including only the ornithophilous and definitely-visited species. Bold type indicates the highest-basal-area species. Species are not listed separately for fruits under 7 mm or occasionally-visited entomophilous flowers.

(A) Fruit type				(B) Flower type				
Fruit type	Species	N plots	% BA	Flower type	Species	N	% BA	
≥14 mm	<i>Beilschmiedia tarairi</i>	2	0.02	Ornithophilous	<i>Alseuosmia macrophylla</i>	2	<0.01	
	<i>Beilschmiedia tawa</i>	112	2.31		<i>Fuchsia excorticata</i>	47	0.24	
	<i>Vitex lucens</i>	2	0.01		<i>Knightia excelsa</i>	84	0.46	
	total		2.34		<i>Metrosideros fulgens</i>	22	0.01	
≥10 mm	<i>Alectryon excelsus</i>	18	0.04		<i>Metrosideros robusta</i>	16	0.25	
	<i>Elaeocarpus dentatus</i>	73	0.39		<i>Metrosideros umbellata</i>	103	2.20	
	<i>Gaultheria antipoda</i>	5	<0.01		<i>Sophora microphylla</i>	13	0.03	
	<i>Litsea calicaris</i>	16	0.06		<i>Sophora tetraptera</i>	2	0.01	
	<i>Nestegis lanceolata</i>	10	0.02		<i>Vitex lucens</i>	2	0.01	
	<i>Prumnopitys ferruginea</i>	142	0.87		total		3.21	
	<i>Ripogonum scandens</i>	6	<0.01		Generalist	<i>Geniostoma ligustrifolium</i>	21	<0.01
	<i>Syzygium maire</i>	2	0.04			<i>Metrosideros perforata</i>	10	0.01
	total		1.41			<i>Pseudopanax arboreus</i>	28	<0.01
	≥7 mm	<i>Carpodetus serratus</i>	299	0.67		<i>Weinmannia racemosa</i>	383	10.37
<i>Coprosma lucida</i>		39	0.01	total			10.46	
<i>Coprosma propinqua</i>		36	0.01	Frequently-visited	<i>Cordyline australis</i>	11	0.02	
<i>Coprosma spathulata</i>		6	<0.01		<i>Dracophyllum latifolium</i>	8	0.02	
<i>Coprosma tenuifolia</i>		25	0.01		<i>Dracophyllum traversii</i>	31	0.29	
<i>Dysoxylum spectabile</i>		16	0.09		<i>Dysoxylum spectabile</i>	16	0.09	
<i>Elaeocarpus hookerianus</i>		83	0.16		<i>Elaeocarpus dentatus</i>	73	0.39	
<i>Freycinetia baueriana</i>		6	<0.01		<i>Griselinia littoralis</i>	485	3.61	
<i>Hedycarya arborea</i>		131	0.63		<i>Myoporum laetum</i>	7	0.03	
<i>Lophomyrtus bullata</i>		1	<0.01		<i>Pittosporum crassifolium</i>	2	<0.01	
<i>Mida salicifolia</i>		6	<0.01		<i>Pittosporum eugenioides</i>	33	0.10	
<i>Myoporum laetum</i>		7	0.03		<i>Pittosporum tenuifolium</i>	40	0.05	
<i>Myrsine salicina</i>		109	0.42	<i>Pittosporum umbellatum</i>	1	<0.01		
<i>Nestegis cunninghamii</i>		29	0.11	total		4.59		
<i>Pseudopanax ferox</i>		4	<0.01	Occasionally-visited	29 spp.		10.76	
<i>Rhopalostylis sapida</i>		9	0.05					
total			2.20					
<7 mm	74 spp.		17.6					

elliptical fruits in the New Zealand flora are unlikely to be related to fruit consumption by kereru. The trends seem more likely to have been selectively favoured because they allow all the fruits of mid-sized plant species (mean diameters 10–14 mm), and the smaller fruits of the largest-fruited (mean >14 mm) species, to be dispersed by mid-sized native birds such as tui, kokako and saddlebacks. Importantly, for this to show up as a detectable trend in fruit size, dispersal by these mid-sized birds must have been relatively frequent and effective.

Relative frequency of bird dispersal and bird pollination in the New Zealand flora

For some reason, evaluations of the relative importance of bird pollination versus bird dispersal in New Zealand have often compared imperfectly matched numbers. Dispersal by birds is argued to be important because most (70%) native tree species have fleshy fruit, whereas bird pollination is argued to be unimportant because only a small percentage of the total flora (<1%) have ornithophilous flowers (Clout & Hay 1989). This comparison is mismatched in three ways. Firstly, the dispersal percentage is of the tree flora, not the entire flora where only 12% of species have fleshy fruit (Lord et al. 2002; Thorsen et al. 2009 give this as 13.5%), but the pollination

figure is for the entire flora, despite trees being more often ornithophilous. Secondly, the bird-dispersal figure is based on all fleshy-fruited plants, whereas the bird-pollination figure has been based only on plants with flowers that show the classic ornithophilous syndrome. Thirdly, even when all bird-visited flower species are considered, only those where birds were actually reported as visiting were counted, whereas all species with fleshy fruit were included, even though birds have only been recorded as feeding on about 50% of these (Lee et al. 1991). This has meant, for example, that *Phormium tenax* was counted as bird-visited but *P. cookianum* was not, and *Fuchsia excorticata* but not *F. perscandens*, even though within each genus the flowers are morphologically very similar.

We can make fairer comparisons in two ways: Firstly using the entire flora, fleshy fruit are found in 12%, and confirmed bird-visited flowers in 4.5% of species. Secondly considering only trees, Clout and Hay (1989) reported that 70% of 240 native woody species (probably mostly trees) had fleshy fruit, and Burrows (1994) used slightly different criteria to calculate that 72% of 96 tree species were fleshy-fruited. Our tallies show that bird-visited flowers are found in 30% of the 188 trees listed by McGlone et al. (2010), and fleshy fruit in 59% of them. In both the total and tree floras, fleshy-fruitedness is still more

common than bird pollination, but by a much smaller margin (2.0 to 2.5-fold) than previously implied (70-fold).

Why discount the importance of bird pollination?

There seem to be six possible reasons for the previous assumption that bird pollination should be discounted as unimportant in New Zealand.

First is the Eurocentric idea that birds are not important pollinators in the temperate zone, but Europe rather than New Zealand is odd in this respect. Europe is the only temperate area where bird pollination is not important (Ford et al. 1979; Ford 1985).

Second, it is often said that New Zealand has relatively few flower-visiting birds, implying perhaps that there are not enough species to matter. However, comparisons of the absolute number of New Zealand flower-visiting bird species with Australia's 111 flower-visiting birds (Godley 1979; Ford et al. 1979) are uninformative (Castro & Robertson 1997; Newstrom & Robertson 2005) unless they allow for the large differences in land area and total fauna size. Relative to its native land bird fauna, New Zealand has the same proportion of flower-visiting birds (12 of 60 species = 20.0%) as Australia (111 of 560 = 19.8%; Chi-sq = 0.00, df = 1, P = 0.97), while as a proportion of the native vascular floras bird-visited plants are actually significantly more common in New Zealand (85 of 2158 species = 3.9%) than in Australia (250 of 15 638 species = 1.6%; Chi-sq = 56.2, df = 1, P < 0.001) (Ford et al. 1979; Hnatiuk 1990; de Lange et al. 2006). Also, while the absolute numbers of bird species involved is smaller in temperate areas than in the tropics, the value of bird pollinators to the plants is higher compared with insect pollinators in colder areas, because birds are less deterred by inclement weather than insects (Castro & Robertson 1997).

Third, Godley emphasised that birds might only effect geitonogamous self-pollination, but work since 1979 has reduced this concern. Both birds and insects visit large floral displays on mass-flowering plants for much shorter bouts than expected (Augsburger 1980; Stephenson 1982; Frankie & Haber 1983; Biernaskie et al. 2002). High levels of pollen carryover, especially on large pollinators like birds, mean that outcrossed pollen is still being delivered to flowers visited later in a feeding bout (Robertson 1992).

Fourth, earlier work on bird visitation was based on the New Zealand mainland with low bird densities following the introduction of mammalian predators. Observing birds on island sanctuaries, where densities are higher and more similar to pre-human levels, gives a fairer picture of the original importance of birds to the New Zealand flora, especially on plants with smaller rewards (Castro & Robertson 1997; Anderson 2003).

Fifth, Godley argued that native silvereyes visited many native flowers, but as recent arrivals (establishing in 1856) they "have played no part in the evolution of whatever true ornithophily occurs here" (Godley 1979: 446). On the other hand, he argued that birds were not important for the pollination of *Sophora microphylla* because the flowers were also visited by honeybees and bumblebees, both of which were deliberately introduced by humans after the unassisted arrival of silvereyes. This seems to set a higher standard for evidence of bird importance than for evidence of insect importance. The conclusion of Kelly et al. (2006) was that the primary change in bird pollination since human arrival was the replacement of the now-rare stitchbird by the silvereye.

Finally, it was assumed that insect visitors to even

ornithophilous native plants would effect pollination, rendering any pollen movement by birds superfluous. The field data clearly disprove this hypothesis, with pollen-limited fruit set in a majority of species on the mainland where bird densities have been reduced, even in the presence of insects including honeybees and bumblebees. Moreover, both ornithophilous and entomophilous-flowered species showed reduced fruit set when birds, but not insects, were excluded.

We therefore consider these arguments are incorrect. There has been a tendency to discount the evidence (based on frequency of visits and levels of seed set) for the importance of bird pollination. It is time to accept that bird pollination is important in New Zealand. The contrast with frugivory is striking, because nearly all the above arguments could be – but have not been – applied to discount the importance of dispersal of large fruit by kereru: large frugivorous birds are more common in the tropics and Australia (Lord et al. 2002); we have few species of large frugivore and few species of large-fruited plants in New Zealand; kereru sit for long periods in the same tree (Pearson & Climo 1993; Wotton 2007) so probably often drop seeds under the parent (the dispersal equivalent of geitonogamy); and introduced mammals might disperse some seeds (Williams 2003). Rephrasing the arguments in this way shows they have correctly been given little weight in frugivory, and incorrectly given too much weight when considering pollination.

Important future work

This review has highlighted some areas where more work is required: First, we need more measurements of dispersal quantity on the mainland, especially for large-fruited species. Evidence of complete dispersal failure in these species would be obvious (undispersed fruit lying thickly under the tree with no evidence of bird-excreted seeds). There are unpublished reports of complete dispersal failure for tawa around Hamilton (Elizabeth Overdyck, pers. comm.) and we have seen partial dispersal failure in taraire near Whangarei and in tawa in the worst year at Blue Duck.

Second, there is a strong need for better quantitative measures of dispersal effectiveness, comparable to the Pollen Limitation Index for pollination failure. At present it is very hard to say that any measure of reduced dispersal unequivocally demonstrates a cost to the plant, because the safe sites for plant regeneration are so uncertain in time and space (Kelly et al. 2004). Possible higher seed or seedling mortality from pathogens or seed predators near parent trees (e.g. Packer & Clay 2000) could greatly increase the ecological and evolutionary importance of bird dispersal, and increase the negative consequences of its failure. Manipulative experiments planting whole fruits and flesh-removed seeds at various locations under and away from parent trees would provide an opportunity to quantify the consequences for germination and establishment in large-fruited species, with sometimes surprisingly large effects found (Wotton 2007).

Third, we need to test the effect on regeneration if larger frugivores become rare or locally extinct, and only smaller frugivores are taking the smallest individual seeds. Are the smallest seeds of large-seeded species still fit? This has not yet been tested in New Zealand, but it would clearly be interesting to do so. Overseas studies show variable results, with some finding relatively small differences in germination and establishment between large and small seeds from the same species (e.g. Pizo et al. 2006; Breen & Richards 2008; Susko & Cavers 2008).

Fourth, we have little idea of how much longer-distance dispersal is necessary for the maintenance of meta-populations at the landscape scale. Tui and other mid-sized birds are probably providing some dispersal of the largest-fruited species, but we have no way of knowing whether this is enough. Seed dispersal and pollination are both also important for gene flow among fragmented populations (Hamilton 1999; Garcia et al. 2007), and trees are particularly vulnerable to inbreeding depression (Scofield & Schultz 2006) which could be avoided by effective pollen and fruit dispersal. Modelling seems a likely way to get at these answers, combined with molecular work to quantify rates of immigration.

Fifth, we need to find out whether introduced mammals are achieving some dispersal, and whether this is sufficient to maintain native plant meta-populations. Jordano et al. (2007) showed that unlikely animals (in their case, foxes, badgers and martens) provided most of the long-distance seed dispersal in *Prunus mahaleb*. In New Zealand, we need to investigate the role of larger mammals, especially pigs, goats, deer, sheep, cattle, and horses, in dispersing the larger native seeds. Pigs are primarily seed predators, destroying seeds of taraire (Dawson & Sneddon 1969), hinau, matai and miro (Beveridge 1964), but they can also disperse some seeds intact (Beveridge 1964; Williams 2003).

Sixth, more observation of bird visits to flowers would be worthwhile to confirm or eliminate some of the additional 85 possible species in Table 5 (which have the potential to double the number of bird-visited plants to 9% of the entire flora). This seemingly descriptive task is important for understanding how the flora actually works, as opposed to how we assumed it ought to work. These observations should be made both on bird sanctuaries, to see the pre-human state, and on the mainland to see what we are left with now.

Finally, we need quantification on additional plant species of pollination service (fruit set) in the presence and absence of birds, extending the work of Anderson (2003). In particular, it would be good to have these data for *Metrosideros umbellata*, *Weinmannia racemosa*, and *Griselinia littoralis*, three species with bird-visited flowers that make up 16% of the current native forest basal area.

Conclusion

For a series of apparently historical reasons, evidence for the importance of bird pollination in the New Zealand flora has been frequently discounted. Both bird dispersal of fleshy fruit and bird pollination are important in the New Zealand flora. For both pollination and dispersal, there are a number of relatively specialised native plants that are dependent on a small number of native birds. Contrary to the orthodox view, there are more native plants reliant on specialist bird pollination than on specialist dispersal. By number of species, specialist bird-pollinated native plants are more numerous at all latitudes and extend much further south than the specialist large-fruited plants. In terms of percentage of basal area in forest plots, both total bird-visited flowers and specialist bird-visited flowers are more abundant in most areas than total and specialist fleshy-fruited species respectively. There are no cases of either pollination or dispersal where complete failure has been documented, but the closest to complete failure are in pollination (*Rhabdothamnus solandri* and *Metrosideros excelsa*). Pollination shows more frequent evidence for some failure of mutualist service than does dispersal, though data for dispersal are less complete.

In summary, the New Zealand flora is transparently reliant on bird dispersal (in the woody flora at least), but cryptically reliant on bird pollination. Most bird-plant mutualisms are still functioning, but the local maintenance of native bird numbers is important for this to continue. Silvereyes are widespread and, despite their recent arrival, are important for pollination of smaller flowers and dispersal of smaller fruits. The maintenance of kereru populations is important to ensure the effective dispersal (not germination or regeneration) of native plants with fruits over 14 mm mean diameter, for which they are the predominant (but not the only) disperser. However, even more important is the maintenance of local populations of tui and bellbirds, to ensure adequate pollination of the greater number of bird-dependent native species, and for their important contributions to dispersal of the many medium and small-fruited native plants.

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