BIRD-PLANT MUTUALISMS: ARE THEY BROKEN AND CAN WE FIX THEM?

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This is a short written version (with references) of the talk I gave to Canterbury Botanical Society on 7 September 2015. For full scientific names of plants and animals, and further details of sites and statistical tests, please refer to the cited references.

The key question is whether bird pollination and seed dispersal of native plants is currently working adequately in New Zealand with the current reduced densities of birds. Pollination and dispersal are two of the most important ecosystem services provided by birds, along with carrion removal, insect pest control, nutrient enrichment, and a few others (Wenny et al. 2011). It is important to ask whether bird services are working here, because New Zealand birds have suffered heavily from human impacts. We have lost 48% of land birds off the main North and South Islands, including some species that are important pollinators or dispersers, particularly hihi (stitchbirds) and saddleback (Kelly et al. 2010). Some of the remaining birds have restricted distributions, including kaka and kokako.

Pollination

For pollination, quantitative observation of flower visitors to bird-visited native plants found that three native birds do the vast majority of pollinator visits: bellbirds, tui and silvereyes (Kelly et al. 2006). Introduced birds made <5% of visits to native plants. Silvereyes are very widespread, but each of the other two has gaps in their distribution (bellbirds are absent from the northern North Island and tui from drier parts of the eastern South Island). Three other native birds with brush tongues (for nectar uptake) would have been important pollinators but now have restricted distributions (hihi, kaka and kokako).

Lists of which native plants have bird-visited flowers have increased as better observations have been made, with the tally now including 29 ornithophilous-flowered species and 85 species in total (Kelly et al. 2010). Ornithophilous flowers are those that look like they are adapted to birds (large, usually red or yellow, with copious nectar). New Zealand ornithophilous species are found in the genera *Alepis*, *Alseuosmia*, *Clianthus*, *Fuchsia*, *Knightia*, *Metrosideros*, *Peraxilla*, *Phormium*,

Rhabdothamnus (Fig. 1), *Sophora*, *Trilepidea*, *Vitex*, and *Xeronema*. Birds also commonly go to native plants with small apparently-entomophilous flowers such as *Griselinia* and *Pseudopanax* spp. Despite the small flowers having little nectar per flower, the birds can forage profitably on them (Castro & Robertson 1997). In total, bird-visited flowers make up 5% of the entire native flora and 29% of the trees, which are unusually high numbers for the temperate zone (Kelly et al. 2010).

Figure 1 A *Rhabdothamnus* flower from below, showing the fused anthers and long floral tube, which is too long for silvereyes to reach the nectar legitimately.

Measurements of pollen limitation (when seed set is limited by a shortage of pollen) are carried out by calculating the Pollen Limitation Index (PLI), which is [1 – (natural fruit set / hand pollinated fruit set)]. Measurements of native ornithophilous species show widespread pollen limitation on the New Zealand mainland at multiple sites in *Peraxilla* spp. (Kelly et al. 2007) and *Fuchsia excorticata* (Robertson et al. 2008; van Etten et al. submitted). A review of 10 species found that seven showed a PLI of at least 0.33, and that the mean PLI for New Zealand was significantly higher than average in a global survey of pollen limitation studies across all plants (Kelly et al. 2010). Evidence that this was caused by decreased bird numbers came from a study on the forest shrub *Rhabdothamnus solandri* (Anderson et al. 2011). This study showed strong pollen limitation on the mainland around Auckland, while on bird reserves nearby (Little Barrier, Tiritiri Matangi and Lady Alice Islands) there was no pollen limitation. Mainland populations of the plant were also seed-limited (adding seeds produced extra seedlings) and surveys showed a significant shortage of smaller plants, indicating that plant density is gradually declining from pollination failure.

All those data showing pollen limitation come from open flowers where insects and exotic birds were not excluded. So the overall message is that bird-pollinated native plants are often doing badly on the mainland

(North and South Islands) because there are too few native birds, and that insects and exotic birds are not filling this gap.

Dispersal

Studies of which birds disperse the fruits of native plants shows that four native birds do the vast majority (85%) of all visits: silvereyes, bellbirds, kereru and tui (Kelly et al. 2006). Introduced birds were numerically unimportant in that survey, with the most common exotic bird being the blackbird, which made <4% of visits. A study in the Zealandia sanctuary in Wellington (Burns 2012) found blackbirds to be much more important, but this appears to be a product of higher densities of blackbirds in urban areas (around 1-5 blackbirds per ha) than in native forest away from towns (around 0.1 blackbirds per ha; van Heezik & Seddon 2012; Wilson et al. 2014).

Although there has been long-standing concern about whether decline in kereru (New Zealand pigeon) might cause problems for dispersal of large-seeded native plants, this concern has lessened recently for three reasons. Firstly kereru appear to be generally increasing rather than decreasing in density and range. Although kereru are slow-breeding and susceptible to nest predation and adult mortality (Clout et al. 1995), widespread community pest control of possums, stoats and sometimes rats are probably benefitting them, and kereru range increased between the 1984 and 2007 Bird Atlases (Robertson et al. 2007). Secondly, only one species of native plant (taraire) appears to be entirely dependent on kereru for seed dispersal (Kelly et al. 2010). Thirdly, germination trials show that all tested native plant species can germinate perfectly well in the absence of dispersers (Kelly et al. 2010).

However, there has been some concern about the importance of dispersers for moving seeds away from the vicinity of the parent trees, because a recent study found that mortality rates were much higher there for karaka (Fig. 2, p. 15) and taraire, the two largest-fruited native plants (Wotton & Kelly 2011). Survival of seedlings to two years old was 66-81% lower for seeds that fell off undispersed under the parent tree than for seeds that were treated as frugivores would treat them (pulp removed, placed at low density away from conspecific trees).

This means that it is important to know whether dispersal is sufficient or not. A survey of 10 studies found that in all but one case, fruit removal was rapid or at least adequate (Kelly et al. 2010). The only species that had documented dispersal failure was *Pittosporum crassifolium* around Auckland, ironically one of the smallest-seeded species that has been studied. Studies of fruit removal rates for tawa (the third-largest fruit in the New Zealand flora) at Blue Duck reserve near Kaikoura found most

years at least 50% of the seeds on the ground under the canopy had been through a bird (Kelly et al. 2010). More recent work measuring how many tawa seeds were moved up to 50 m away from the parents showed that an overall mean of at least 80% of the seed crops were being dispersed by birds, which seems like a very good number for that large-seeded tree in Blue Duck reserve (Tarryn Wyman unpublished PhD thesis).

Figure 2 The range of fruit sizes off a single karaka tree (from Akaroa, February 2009). Only kereru can swallow the larger fruits, but smaller fruits can be dispersed by birds like tui.

Another question around dispersal is whether exotic birds or mammals might be useful in dispersing fruits, possibly replacing locally absent native birds. A study was carried out at Kowhai Bush near Kaikoura, in secondary forest where the two largest common native frugivores are absent: common frugivores in the reserve were silvereyes, bellbirds, and exotic blackbirds and song thrushes. All four birds ate a range of fruiting species. However, there were five plant species in the reserve with fruits too large for silvereyes and bellbirds to swallow. Of these, neither of the two native plants (pigeonwood and supplejack) were dispersed by blackbirds and thrushes, but all three invasive exotic weeds (hawthorn, yew, and grapevine) were dispersed by the exotic birds (MacFarlane et al. in press). Therefore it seems that exotic birds may be causing problems with weed invasion rather than helping the large-fruited native plants to be dispersed.

Mammals might spread larger fruited native plant species, but again it appears that they are not being very useful. Possums do not swallow any fruits larger than about 9 mm, which is the upper size limit for silvereyes. Possums also damage many of the seeds they swallow, as well as

predating native birds and eating native plants. Work by Tarryn Wyman at Kowhai Bush (unpublished PhD thesis) also showed that there are too few possums per hectare to move a numerically important fraction of the total available fruits, so they appear to be of little value as dispersers. Feral pigs can move some matai seeds intact, but they destroy most matai fruits they eat (O'Connor & Kelly 2012), and also move weeds like banana passionfruit (Beavon & Kelly 2015). In the subalpine zone at Cass near Arthur's Pass, the most important and effective frugivore was the kea (Young et al. 2012). Mammals, including possums, sheep and rabbits moved many seeds around in their faeces, but these were either eaten incidentally (by sheep and rabbits) or moved to places (by possums) unsuitable for the plants to survive as seedlings (Laura Young unpublished PhD thesis).

Restoration

Another question then is whether conservation action is able to restore bird densities to a level where pollination and dispersal mutualisms will be reinstated. Experiments on this show it is easier to increase bird densities than to restore the mutualisms, for unknown reasons.

The first attempt was a stoat trapping experiment at Craigieburn, where the mistletoe *Peraxilla tetrapetala* is pollen-limited because of a shortage of bellbirds (Kelly et al. 2005). Stoat trapping was able to increase bellbird numbers by 80%, but this increased bellbird density did not translate into higher pollination success on the mistletoes. A similar experiment at Lake Rotoiti, Nelson Lakes National Park, found that *Peraxilla* mistletoe pollination at Lake Rotoiti (with intensive pest management and high bellbird densities) was no more successful than in farmland near Wakefield with no particular pest control (Kelly et al. unpublished).

However, work at Maungatautari mainland island near Hamilton did show that the pest-proof fence has been successful in restoring mutualisms. The reserve has higher bird densities (tui and bellbirds) than a similar nearby forest without intensive pest management, Pirongia (Iles & Kelly 2014). Hihi have also been successfully reintroduced to the mainland island. A study of pollination rates on *Fuchsia excorticata* found that bird visitation rates to flowers were more than three times higher in Maungatautari than at Pirongia. Female *F. excorticata* plants were getting sufficient pollen inside the reserve, but not outside (Iles & Kelly 2014). A wider survey throughout New Zealand showed that female *F. excorticata* plants were pollen-limited at nearly all sites except those with high bird densities (island reserves, and fenced and unfenced mainland islands with intensive pest control). So pollination was restored in this case by intensive management.

Conclusions

- Bird-pollination is frequently failing on the mainland, because native birds have declined and exotic birds and insects are not effective replacements.
- Seed dispersal is in better shape than pollination with less evidence for failure.
- For dispersal, exotic animals are again not providing much useful service, and they often act as weed vectors.
- Kereru are important dispersers, are not declining in numbers, and they are not the only, or even the most numerically important, native frugivore.
- Silvereyes are very widespread and important pollinators and dispersers, though they cannot handle the largest flowers and fruits.
- Restoration efforts are often effective at increasing bird densities, but less often effective at restoring pollination and dispersal service, although Fuchsia excorticata does show better pollination at sites with intensive pest management.

Acknowledgements

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THE ALPINE ENVIRONMENT UNDER ATTACK

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In 1975 when I immigrated to New Zealand and began wandering in the central South Island mountains, the landscape faced ongoing manageable pressures. The exotic weed *Hieracium* was spreading everywhere, a scourge of the High Country. Introduced game animals, though numerous, were culled, controlled or captured from the ground and in the air. The term "global warming" was not an everyday phrase and our weather patterns were generally settled. Plant studies for me in those early days were enjoyable and rewarding. Now, 40 years later, the alpine environment is under duress. What has happened to change my opinion?

I can vividly remember the spring of 1982 in the Hooker Valley at Aoraki Mount Cook National Park. Then in November *Ranunculus lyallii* exploded into bloom like never before. Whole hillsides and little vales turned profusely white, the spectacle was unbelievable. Up and down the Main Divide, the scene was similar. A once in a lifetime display, sadly never repeated. Perhaps ideal climatic conditions prevailed then. Who knows? Then too, *Anisotome pilifera* formed large clumps near raging wild water at the Hooker River. The flower heads were as large as garden cauliflowers, magnificent and conspicuous. These days it is hard to spot a single specimen plant. Up from the Stocking Stream in shaded rocks beneath Te Waewae Glacier grew numerous *Myosotis macrantha.* Now only small plants exist at the mercy of the next deluge. Have more intense rainstorms over the intervening years caused mini-landslides to obliterate these fine plants? Have foraging animals also had an impact? Noticeable on the Stairway to Heaven up towards Sealy Tarns are more and more fresh possum droppings. Are these creatures gaining easy elevation aided by the wooden staircase in their quest for a tasty morsel? Other climbers have intimated to me a similar conclusion. Stoats too are regularly sighted on daily walks. Perhaps it is too difficult to implement a