IS INTER-DEPENDENCE OF NATIVE FAUNA AND FLORA AN ISSUE FOR FUTURE SURVIVAL OF NATIVE PLANTS?

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INTRODUCTION: CONDITIONS FOR MUTUALISMS TO MATTER

In this paper we consider to what extent the persistence of the native flora is dependent on persistence of native animals (birds and invertebrates). In other words, to what extent does reproduction by native plants rely on pollination and/or dispersal by native animals? Bond (1994) identified three conditions which must be met for a mutualism like pollination or dispersal to have a negative impact on the plant population: (1) plants must need visitors to reproduce; (2) the visitation rate must have declined; and (3) production of seeds must be important for maintenance of the plant population. In this paper we review all three of these conditions, and collate some data relevant to the second (visitation rate).

First, do plants need visitors to reproduce? Some plants can reproduce via seed independently of visitors, by virtue of alternative mechanisms (such as self-pollination or abiotic dispersal) that bypass the failure of the animal-mediated process. One key test of this condition is to measure the success of reproduction where animal visitors are excluded. This is easily done for pollination by bagging flowers, and recording whether the flowers ripen seeds. The other key treatment is to hand-pollinate some flowers, to provide a measure of the maximum possible fruit set rate (since it cannot be assumed that the plant has enough reserves to ripen all flowers into fruits). In a global review, Burd (1994) showed that many plant species require outcross pollen, or require an agent to move pollen onto the stigma, so pollen limitation (fruit set being restricted by an inadequate supply of suitable pollen) was widespread.

The New Zealand flora has some characteristics that influence the dependence on visits by pollinators. New Zealand has a low number of plant species known to be self-incompatible (only 11 species cited in Webb and Kelly 1993), although this low number probably partly reflects incomplete information, not just a low frequency of self-incompatibility. The New Zealand flora does have the world's highest frequency of separate sexes (18% of genera have dioecy and 7% gynodioecy: Webb et al. 1999). Dioecy, like self-incompatibility in hermaphrodites, makes cross-pollination essential. However, many of the important dioecious genera are wind pollinated (e.g. *Coprosma*, *Podocarpus*, *Dacrydium*, *Dacrycarpus*, *Prumopitys*) rather than animal-pollinated (Webb et al. 1999). Some of the gynodioecious genera have self-compatible pollen and hence the hermaphrodite plants are able to self-pollinate (e.g. *Fuchsia*: Godley and Berry 1995).

Of course, plants may be self-compatible but not capable of routinely autonomously selfing, i.e. they still need a vector to move compatible pollen (their own or from another plant) from anthers to stigma. For example, the beech mistletoes (*Peraxilla tetrapetala*, *Peraxilla colensoi*, and *Alepis flavida*: Loranthaceae) are all self-compatible, but only *Alepis* is able to routinely autonomously self-pollinate (Ladley et al. 1997; Robertson et al. 1999). Both *Peraxilla* species have very low fruit set rates inside bags, showing that they depend on animals as pollen vectors despite being self-compatible.

It is much less easy for dispersal to quantify the success of dispersed and undispersed fruits, as the seeds are very hard to follow individually. Seeds that are not dispersed usually still have some non-zero probability of success in the vicinity of the parent. The locations of particular seeds are usually unknown, and their success or failure at producing adult plants in the next generation (dispersal quality: Schupp 1993) may have to be measured over timescales of years or decades. Only one part of this overall success can be readily measured, and this is the germination rate for seeds that have, or have not, been passed through the gut of a disperser (usually a bird). In a global review, Traveset (1998) showed that there is often, but not always, an advantage to seed germination percentages after removal of the fruit flesh. An extensive series of papers on the New Zealand woody flora by Colin Burrows (e.g. 1999) generally showed that native woody plant species show low germination percentages unless the seeds are removed from the fruit flesh (reviewed by Trass 2000). However, these experiments were largely carried out in artificial conditions, which may seriously alter the rates of leaching and breakdown of germination inhibitors in the fruit flesh (Robertson and Trass, in prep.).

Overall, it seems that the New Zealand flora is generally dependent on animal visitors for high levels of fruit set or seed germination, but that often some lower level of reproduction is possible without any animal visitors present.

Second, have visitation rates declined? This can be broken into two parts: have visits by native animals declined, and have introduced animals become important visitors which may to some extent substitute for native animals? At first glance, it might be thought that introduced animals could have become important in New Zealand. It is clear that there have been extensive declines in density, and range, of important elements of the native bird fauna (Bull et al. 1985). For example, stitchbirds and saddlebacks (bird names follow Heather and Robertson 1996) were important flower and fruit visitors respectively, yet both are now found essentially only on offshore islands. Numbers of introduced animals have the potential to replace some of the lost native flower and fruit visitors. Several introduced birds that visit flowers and fruits, such as blackbirds and chaffinches, are now among the most widespread and common birds in New Zealand (Bull et al. 1985). Introduced birds have been frequently listed as visiting the flowers and fruits of native plants (O'Donnell and Dilks 1994; Burrows 1994). The introduced honeybee, a highly competent generalist pollinator, is one of the most widespread insects in the country (Donovan 1980). However, we will consider this point more fully below, using data from a survey of the literature on New Zealand plants.

Third, we need to ask is the plant seed-limited? In other words, does the maintenance of plant population density depend on continued seed production and dispersal? Bond (1994) reasoned that clonal plants may persist mainly by vegetative sprouting rather than by seedling establishment. Also, plants which have strong density-dependent seedling mortality may show little evidence of increased numbers at the population level if extra seed is added (Andersen 1989; Crawley 1990), i.e. they are not seed-limited. However, Turnbull et al. (2000) found some evidence for seed limitation in about half of the 100 worldwide cases they reviewed, especially in short lived plants and plants of open habitats. Unfortunately, seed limitation has been rarely tested for in New Zealand.

The aim of this paper is to evaluate the extent of dependence of native plants on native and introduced animals for pollination and dispersal, mainly based on the frequency of visits to flowers and fruits. Counting the frequency of visits by each animal species is a more accurate representation of the importance of native visitors than simply tallying a species list of visitors, and calculating what percentage of all the species are native ones. Ideally, this assessment would be based not on frequency of visits, but on effectiveness, as some flower visitors may be nectar robbers or seed predators, etc. However, there are few data on the effectiveness of individual animals as pollinators or dispersers. Hence, this paper is restricted to frequency of visits.

IS BIRD POLLINATION CURRENTLY ADEQUATE IN NEW ZEALAND?

The first way to test whether native plants are dependent on native animals is to measure whether seed production is currently adequate on the mainland of New Zealand, despite the large changes in the avifauna mentioned above. A recent review (Anderson et al. in press) summarises pollination experiments on seven bird-pollinated plant species on the North and South Islands. Only one of these seven (the self-compatible *Alepis flavida*) did not have sites where pollination was failing. Inadequate pollination was defined as where unmanipulated fruit set was closer to that for pollinator-excluded flowers (the worst-case scenario) than to that for hand-pollinated flowers (the best case). Overall, pollination was inadequate at about half the sites. In many cases there was evidence that low bird densities were the primary cause.

For example, the bird-pollinated forest shrub *Rhabdothamnus solandri* (Gesneriaceae) has been studied at two mainland sites near Auckland where only tui are present, and one offshore bird sanctuary (Little Barrier Island) where native bird pollinators are abundant (Anderson et al. in press). Natural fruit set was very low at both mainland sites, but was high on Little Barrier. Signs left on flowers by visiting birds showed that these fruit set differences were caused by differences in visitation rates. Overall, on the mainland, seed production per flower in *Rhabdothamnus* was only c. 10% of that found on Little Barrier. Recent work on *Rhabdothamnus* by Sue Molloy (*unpublished data*) near Whangarei and on Lady Alice Island found the same pattern.

Therefore, at least for bird-pollinated native plants, there is evidence that reproduction is not currently functioning well.

HOW IMPORTANT ARE NATIVE AND INTRODUCED BIRD POLLINATORS?

Our approach was based on Kelly et al. (in press), where fuller details of methods and species studied are included. Briefly, we collated all published studies where the percentages of visits made by all different birds (or insects, see below) to native plants were given. Studies that listed the species visiting flowers or fruits without numerical estimates of their importance were not included. We supplemented the literature with our own unpublished data. Generally, the proportion of "visits" made by each group was measured by the relative length of time spent foraging on fruits and flowers.

In total for birds visiting flowers we found 52 cases covering 18 native plant species from 31 sites (Table 1). A full listing of the sites and species is given in Kelly et al. (in press). Almost one-third of the 16 bird species seen visiting flowers were introduced taxa; however, the introduced birds made far less than one-third of all visits. More than half the sites recorded no visits at all by introduced birds, the mean contribution of all introduced birds combined was only 5%, and three native species (silvereye, tui and bellbird) jointly made up 89% of all recorded visits (Table 1, Fig. 1). Kereru do sometimes visit flowers, but to eat them (O'Donnell and Dilks 1994) so are counted here as making zero contribution to successful pollination – in fact they probably reduce fruit set rather than increasing it.

Table 1. Importance of native and introduced animals as visitors to flowers and fruits of native plants (measured as % of all visits). Note that bird visitors were identified to species, while insect visitors were sometimes only identified to genus or higher categories. Based on Kelly et al. (in press).

Category	Bird visits to flowers	Bird visits to fruits	Insect visits to flowers
No of cases	52	39	15
No of plant spp	18	32	12
No of sites	31	10	10
No of animal spp	16	22	no data
% species introduced	31%	32%	no data
Mean % visits by introduced species	5%	5%	29%
Cases with no introduced species	69%	56%	20%
Most frequent introduced species	sparrow	blackbird	*Bombus* spp
% visits by most frequent introduced species	3%	4%	12%
% visits by key natives*	89%	84%	63%

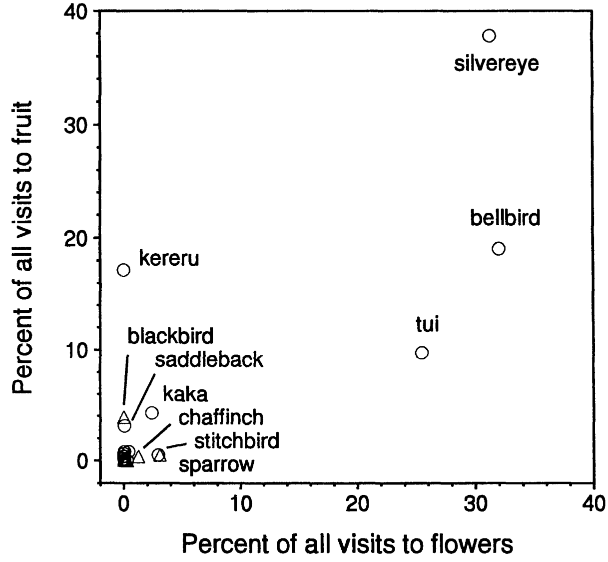
*for birds = silvereye + bellbird + tui + kereru; for insects = native bees + Diptera

HOW IMPORTANT ARE NATIVE AND INTRODUCED BIRD DISPERSERS?

The picture for bird dispersal was very similar to that for bird pollination. We found slightly fewer datasets (39 cases from 10 sites: Table 1) but covering more plant species (32) and more fruit visitors (22) than were found for flower visitors. Again one-third of the bird species were introduced, but again these introduced birds made only 5% of all visits. The four most important native birds (silvereye, bellbird, tui, kereru) made 84% of all visits.

The most important introduced bird fruit visitor was the blackbird, which is very widespread throughout New Zealand, but rarely goes to native plants (Table 1 and Fig. 1), apparently preferring introduced plant species (Williams and Karl 1996).

Fig. 1. The overall mean contribution by different bird species to flower visits and fruit visits on native plants throughout New Zealand. Introduced birds are marked with triangles, native birds with circles. Kereru are marked as doing zero pollination, but probably have a negative effect by eating flowers (see text). Adapted from Kelly et al. (in press).



HOW IMPORTANT ARE NATIVE AND INTRODUCED INSECT POLLINATORS?

The first point to note is that insect pollination has been less widely studied (at least with respect to quantitative visit information) than bird pollination and dispersal. Also, because of the greater difficulty with identification of invertebrate species, many of the studies use broader groupings. We grouped flower visitors into honeybees (*Apis mellifera*), bumblebees (*Bombus* spp), Vespulid wasps (*Vespula* spp) – all introduced – and native groupings at higher taxonomic levels (native bees, other native Hymenoptera, Diptera, Lepidoptera, Coleoptera, and Others). The last four groupings are predominantly native, but may include a few introduced species.

Altogether we found 15 cases covering 12 plant species (Table 1). The contribution by introduced species was higher than for birds, with a mean of 29% of all visits made by the introduced bees and wasps (compared to 5% for birds). Only 20% of cases had no recorded visits by introduced insects, and the most important group (*Bombus* spp) made 12% of visits, higher than the 3-4% made by the most important birds (Table 1). The two predominant native groups (native bees and Dipterans) made 63% of all visits. All this shows that introduced insects are more significant flower visitors to their respective native plants than introduced birds are to theirs.

Some of the important information available for bird-pollinated native plants is not available for insect-pollinated plants. For example, there is very little information about whether native insect-pollinated plants are pollen limited or not. One study on the mistletoe *Ileostylus micranthus* found no significant pollen limitation at two sites near Christchurch (von Tippelskirsch 2001), but clearly more studies are needed. Until we know the frequency of pollen limitation in such plants, we cannot tell if the visits being made by introduced insects (Table 1) are superfluous (perhaps the visits by native insects are enough for adequate pollination), essential (perhaps natives and introduced insects combined just reach the threshold for sufficient pollination), or still not enough.

Another important set of information that is not available is whether native invertebrate flower visitors have declined. We have very little information about changes in densities of native invertebrates over time. There are no known extinctions in New Zealand of native invertebrate pollinators (John Dugdale, pers. comm.) but our knowledge of the pre-human and post-human insect pollinators is very sketchy so losses may have gone unrecorded.

However what can be said is that for the data on hand to date, introduced insects are making a larger share of flower visits to insect-visited plants, than introduced birds are to bird-visited plants.

ARE NATIVE PLANTS SEED-LIMITED?

As noted above, seed limitation has rarely been studied in New Zealand. In considering the effects of pollen limitation in *Peraxilla tetrapetala*, Robertson et al. (1999) argued that the biology of the species suggests that seed limitation is likely. The plant germinates on host tree branches, with low probabilities both of being dropped onto an appropriate branch, and of establishment once dropped there, so they argued that self-thinning among mistletoe seedlings was very unlikely. If that is the case, then any increase in seed production would lead to an increase in adults in the next generation, and conversely for decreases in seed production.

An experiment currently under way at Lake Ohau is designed to test this hypothesis experimentally. Seeds of *P. tetrapetala* were planted onto branches at high densities (4 groups of 5 seeds per host branch) or low densities (three single widely spaced seeds per branch), and the fate of the seedlings followed. So far after 33 months, there is no indication that the high-density plantings produce seedlings with significantly lower survival than the low-density plantings (Chi-sq = 0.90, df = 1, $P = 0.34$, NS).

All this suggests that reductions in seed output because of failed mutualisms with pollinators and dispersers would probably result in reduced plant density. However, it would be very worthwhile to test a range of other native plants for seed limitation, especially non-mistletoe species.

CONCLUSIONS

Overall it seems that native bird mutualists have definitely declined since human arrival in New Zealand (except for the silvereye, which arrived naturally about 1856 and is now widespread). Pollination is often inadequate at many mainland sites for native bird-pollinated plants, and in some cases the pollen limitation has been shown to be due to insufficient visitation by native birds (Anderson et al. in press). Introduced birds are widespread in nearly all parts of New Zealand, but do surprisingly little visitation of native plants, either to flowers or to fruit.

For dispersal, there is some evidence that dispersal is less rapid or less complete on the mainland than on offshore islands, but dispersal limitation seems to possibly be less common than pollen limitation (Anderson et al. in press). Again, the native birds involved have declined (except for silvereyes), and introduced birds are very infrequent substitutes.

In fact, measured purely in terms of frequency of visits to flowers and fruits, four birds (silvereyes, bellbirds, tui and kereru) provide >85% of the service to native plants, and the silvereye is the single most frequent visitor. If it was not for the self-introduction of this species 150 years ago, both pollination and dispersal of native plants would be in a much more precarious position (Burrows 1994). Consideration of effectiveness, as opposed to frequency, of visits would lead to somewhat higher emphasis on tui for long-tubed flowers, and tui and kereru for larger single-seeded fruits, but there is no doubt that silvereyes are very important mutualists for native plants.

For both bird-pollination and bird-dispersal, the evidence suggests that for many native plant species lack of visitation reduces, rather than completely prevents, reproduction. There are some exceptions, such as the absolute requirement for dispersal by native mistletoes (Ladley and Kelly, 1996). However, even if some seed production can occur in the absence of visitors, the quantitative decline in reproduction can be large, so that we might expect quite large reductions in the population sizes of various native plant species over the medium term unless the four key mutualist birds can be protected.

The situation for insect-pollinated plants is much less clear, and more work is needed on various aspects of these species. In particular, we need to know the level of pollen limitation on insect pollinated plants. We also highlight several other key areas for further study. We need much better information under field conditions about the levels of germination of seeds inside undispersed fruits of native plants, and we need to know how widespread seed limitation is in the native flora.

But in conclusion, we have shown that many native plants are reliant on native animals to produce and disperse their seeds. The birds also rely on the native plants for food sources (e.g. Murphy and Kelly 2003), so that ultimately the conservation of one cannot proceed effectively without conservation of the other.

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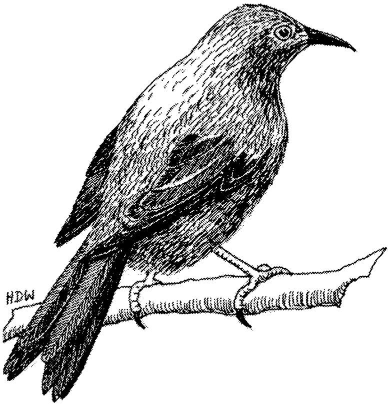

Bellbird, korimako (*Anthornis melanura*). Feeding on nectar, small fruit, insects and spiders, bellbirds are important pollinators and seed dispersers of many native and introduced plants. Native fuchsia, for example, provide bellbirds with nectar for up to 6 months each year, and fruit for up to 5 months, and in the process is both pollinated and dispersed, a nice example of co-dependence. (del. Hugh Wilson).