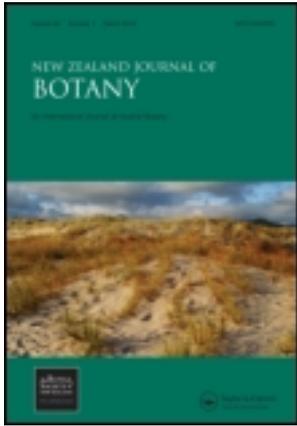


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RESEARCH ARTICLE

Comparative ecology of bird-pollinated and bird-dispersed New Zealand plants

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I observed birds forage for flowers and fruits for six consecutive years in a North Island forest to compare patterns in nectivory and frugivory in plants that rely on birds for both mutualistic services. Birds visited fewer flowering plant species ($n = 9$) than fleshy fruited plant species ($n = 23$). Four ‘bird plant’ species were identified (i.e., plant species that are co-dependent on birds for both pollination and seed dispersal). Visitation rates to flowers produced by bird plants were correlated with visitation rates to fruits, indicating that if a bird plant relied heavily on a particular bird species to visit its flowers, it tended to rely on the same bird species to visit its fruits. Coupled rates nectivory and frugivory raises a significant conservation concern, as it indicates that the loss of specific bird species may have a two-fold, negative effect on the reproductive fitness of plants that rely on birds for both pollination and seed dispersal.

Keywords: conservation; flower; fruit; frugivory; nectivory; mutualism; New Zealand

Introduction

New Zealand is home to many distinctive evolutionary lineages of birds. However, none of our distinctive bird species superficially resemble specialist pollinators that inhabit other biogeographic regions (e.g., hummingbirds). Instead, larger-bodied species that frequently consume fruits are also known to visit flowers (Kelly et al. 2010). For example, stitchbirds (*Notiomystis cincta*) and saddlebacks (*Philesturnus carunculatus*), which are in the endemic families Notiomystidae and Callaeidae, respectively, visit flowers in addition to consuming fleshy fruits. Similarly, kākā (*Nestor meridionalis*) and whiteheads (*Mohoua albicilla*), both in endemic genera, are nectivorous and frugivorous. Honeyeaters (Meliphagidae) and silvereyes (*Zosteropidae*) in Australasia are known to visit both flowers and fruits, and the New Zealand representatives of these families do as well (bellbird: *Anthornis melanura*, tūī: *Prothemadera novaeseelandiae*, silvereye: *Zosterops lateralis*).

Nearly half of New Zealand’s avifauna has gone extinct since the arrival of humans less than 1000 years ago (Tennyson & Martinson 2006) and many of the bird species listed above now occur only in a small number of intensively managed locations (see Innes et al. 2010). This situation may have serious implications for successful reproduction in many New Zealand plant species (Anderson et al. 2011). Because New Zealand birds interact with plants as both pollinators and seed dispersers, the loss of a single bird species may have a two-fold effect on plant reproduction. Similarly, the benefit of reintroducing rare, threatened or endangered birds to plant reproduction may extend beyond a single type of mutualistic service. However, the extent to which New Zealand birds provide dual mutualistic services for plants as pollinators and seed dispersers has never been investigated directly.

Here, I test whether native New Zealand plants are similarly reliant on native birds as pollinators and seed dispersers at the initial stage of mutualistic interactions. I observed birds forage

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for flowers and fruits in 627 h of observations within an intensively managed forest on the North Island (Zealandia). Results from long-term observations were then used to answer four related questions:

- (1) Do more plant species rely on birds as pollinators or seed dispersers?
- (2) How many plant species are co-dependent on birds for both pollination and seed dispersal (i.e., bird plants)?
- (3) Are visitation rates to flowers produced by bird plants higher than fruits?
- (4) Do bird plants rely on similar suites of bird species for both pollination and seed dispersal services?

Methods

All observations were made in Zealandia, a forest reserve on the North Island of New Zealand (41°18.3'S, 174°44.8'E), which is surrounded by a predator-proof fence that excludes all introduced mammals except for mice (*Mus musculus*). Zealandia supports mid-successional broadleaf-conifer forest comprised of evergreen trees, tree ferns and lianas. Since the construction of the predator-proof fence, much of what remains of the New Zealand avifauna has become established within its boundaries. Many species that were rare or absent in the Wellington region have been translocated within the boundaries of the fence since its construction, including bellbirds, kākā, saddlebacks, stitchbirds and whiteheads. Tūi were present within the reserve prior to the construction of the fence and their numbers have since grown appreciably. Silvereyes (waxeyes) colonized New Zealand from Australia in the recent past (<200 years ago) and have also increased in abundance without specific management intervention.

To quantify bird-flower and bird-fruit interactions, I walked a circular trail that took ca. 1 h to traverse and observed birds forage on flowers and fruits. Observations were made approximately every 5 days for six consecutive years (2006–2011). Accurate observations of the total number of fruits consumed or flowers probed

during foraging bouts were infeasible logistically, due to the often rapid movements of birds in dense foliage. Therefore, I quantified bird-plant interactions more broadly following Burns (2006). I scored a feeding 'visit' when a bird approached a plant and consumed at least one fruit or inserted its bill within at least one flower. To avoid multiple observations of the same bird during each census, observations were halted after each visitation event and then resumed 10 m down the trail.

A total of 627 one-hour observation periods were accumulated across the study period, and a total of 3293 foraging visits were observed between 7 species of native birds and 28 species of native plants. However, bird-flower and bird-fruit interactions were not sampled with equal intensity. Distinct fruiting and flowering seasons occur in Zealandia and sampling intensity varied seasonally. Although somewhat variable annually, the flowering season generally occurred between August and January, while the fruiting season generally occurred between February and July (Burns unpubl. data). A total of 266 h of observations were accumulated between August and January, while 351 h of observations were accumulated between February and July. Therefore, bird-fruit interactions were sampled more insensitively than bird-flower interactions.

To test whether more plant species relied on birds as pollinators than as seed dispersers, the total number of plants species whose flowers were visited by birds on three or more occasions throughout the study period were tallied. Analyses were restricted to common bird-flower interactions because birds were sometimes observed inspecting flowers that do not produce nectar and are obviously wind-pollinated (e.g., *Coprosma robusta*). To facilitate unbiased comparisons, the total number of fruit species that were visited by birds three or more times were also tallied. To test for differences in the total number of plant species whose fruits and flowers were visited by birds, I conducted a binomial test assuming that the probability that a plant species will be bird-pollinated ($p=0.5$) is equal to the probability that it will be bird dispersed ($p-1=0.5$).

To compare visitation rates to flowers and fruits produced by bird plants, and to test whether they tend to rely on the same bird species for both pollination and seed dispersal services, I conducted a general linear mixed-model. Flower visitation rate (number of visits to flowers \div number of hours of observations during the pollination season) for each bird species was used as the dependent variable. Plant species was considered a fixed-factor with four levels (*Fuchsia excorticata*, *Geniostoma rupestre*, *Pseudopanax arboreus*, *Schefflera digitata*). Fruit visitation rate (number of visits to fruits \div number of hours of observations during the fruiting season) for each bird species was included as a covariate. To control for the independence problem generated by including flower and fruit visitation rates from the same bird species for all four plant species, bird species was included in the model as a random factor with seven levels (bellbird, kākā, saddleback, stitchbird, tūi, silvereye, whitehead). Fruit and flower visitation rates were square-root transformed prior to analyses to improve normality and homoscedasticity.

Results

The flowers of nine native plant species were visited by birds. Conversely, 23 native species produced fleshy fruits that were visited by birds. The observed ratio of bird-pollinated to bird-dispersed plant species numbers differed significantly from unity ($p[x \leq 9] = 0.010$), indicating that there were significantly more bird-dispersed plant species. Four bird plant species were observed (*F. excorticata*, *G. rupestre*, *P. arboreus* and *S. digitata*, see Table 1).

The general linear mixed-model showed that after controlling for bird species ($F_{6,14} = 3.897$, $p = 0.017$), flower visitation rates were generally associated with fruit visitation rates ($F_{1,14} = 35.973$, $p < 0.001$). However, a significant interaction between the covariate and fixed-factor was observed, indicating that the relationship between flower and fruit visitation rates differed among species ($F_{3,14} = 6.529$, $p = 0.005$). The effect of plant species was insignificant ($F_{3,14} = 0.494$, $p = 0.692$). These results indicate that

Table 1 The total number of visits made by birds to the flowers and fruits of 28 species of woody plants during 617 h of observations in a forest reserve on the North Island.

Species	Visits to flowers	Visits to fruits
<i>Aristotelia serrata</i>	–	39
<i>Coprosma grandifolia</i>	–	197
<i>Coprosma robusta</i>	–	338
<i>Coriaria arborea</i>	–	82
<i>Elaeocarpus dentatus</i>	–	12
<i>Fuchsia excorticata</i>	597	42
<i>Geniostoma rupestre</i>	28	346
<i>Hedycarya arborea</i>	–	22
<i>Knightia excels</i>	8	–
<i>Meliccytus ramiflorus</i>	–	374
<i>Metrosideros excelsa</i>	5	–
<i>Metrosideros fulgens</i>	3	–
<i>Muehlenbeckia australis</i>	–	47
<i>Myoporum laevigatum</i>	–	81
<i>Myrsine australis</i>	–	150
<i>Passiflora tetrandra</i>	–	9
<i>Phormium tenax</i>	134	–
<i>Piper excelsum</i>	–	79
<i>Pittosporum eugenioides</i>	–	103
<i>Pittosporum tenuifolium</i>	–	9
<i>Podocarpus totara</i>	–	29
<i>Pseudopanax arboreus</i>	128	311
<i>Pseudopanax crassifolius</i>	–	9
<i>Ripogonum scandens</i>	–	10
<i>Rubus cissoides</i>	–	4
<i>Schefflera digitata</i>	21	272
<i>Solanum aviculare</i>	–	6
<i>Sophora microphylla</i>	110	–

No entry (–) denotes species that were visited fewer than three times.

visitation rates to flowers and fruits produced by bird plants were generally similar. They also indicate that bird plants tended to rely on the same bird species for both pollination and seed dispersal services (Fig. 1).

Discussion

Long-term observations of bird–plant interactions revealed that fewer plant species utilized

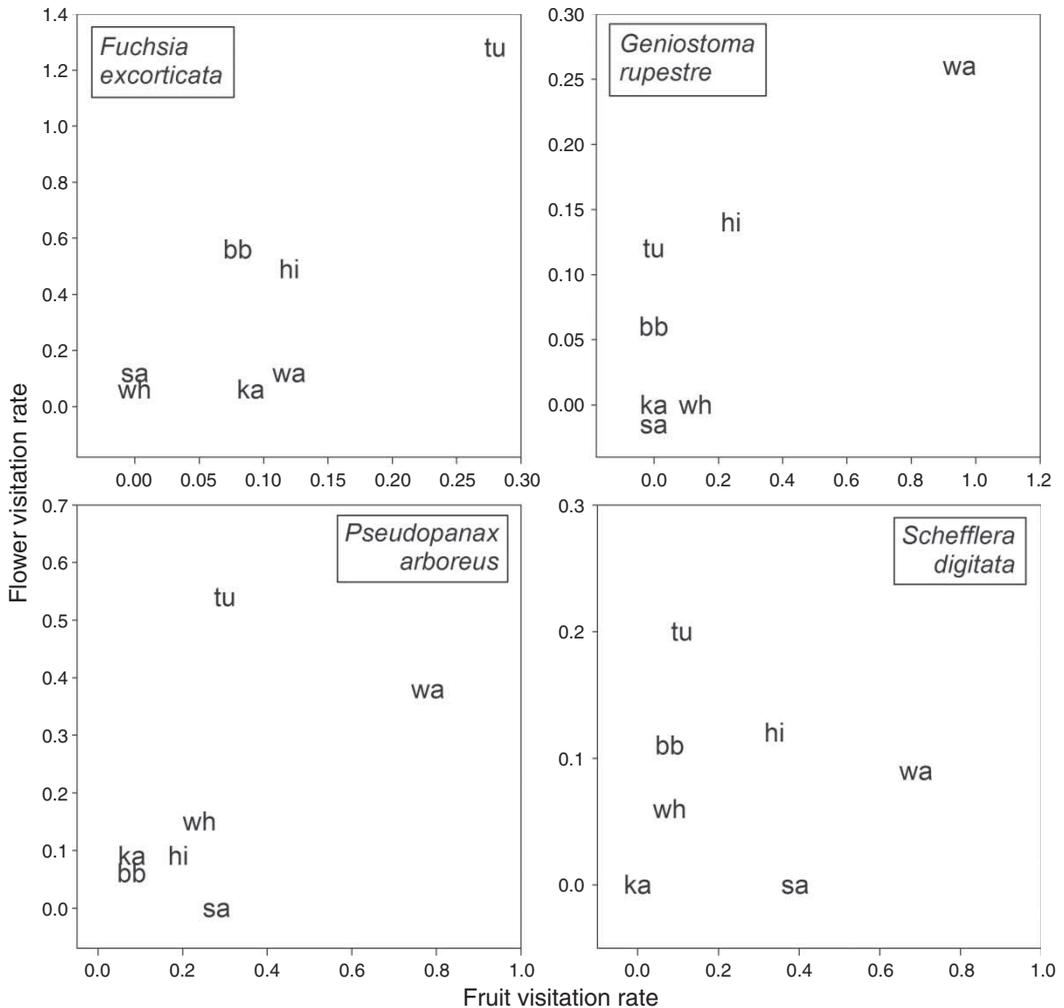


Figure 1 Relationships between fruit visitation rates and flower visitation rates (number of visits \div number of observation hours, square root transformed) in four plant species. Points represent individual bird species that both consume fruits and visit flowers (bb, bellbird; ka, kākā; sa, saddleback; st, stitchbird; tu, tūī; wa, silvereye; wh, whitehead).

birds as pollinators than as seed dispersers and that four plant species utilized birds for both pollination and seed dispersal. The flowers and fruits produced by bird plants were generally visited at similar rates by birds. Furthermore, if they were visited more frequently by a particular bird species as a nectivore, then they were also more likely to be visited more frequently by the same bird species as a frugivore.

Declines in native bird populations have been shown previously to lead to pollination failure, which in turn can lead to reduced seed set and ultimately declines in plant populations (Anderson et al. 2011). Similarly, the loss of particular frugivores can lead to recruitment limitations in particular types of trees (Wotton & Kelly 2011). By contrast, other studies have shown that introduced nectivore and frugivore

species sometimes visit native flowers and fruits and it is possible that they might compensate for the loss of native bird pollinator and seed disperser species to some degree (Pattemore & Wilcove 2012; Burns 2012; see also Wenny et al. 2011).

Bird plants may be particularly vulnerable to dispersal and pollination failure. Not only are they reliant on what is left of the dwindling New Zealand avifauna as potential pollination and seed dispersal vectors, they are sometimes reliant on the same bird species for both services. Under these circumstances, if an important pollinator species is lost, then an important seed disperser is also lost, which may compound the probability of reproductive failure. Results reported here identified four bird plant species. Similar observations in other localities are likely to uncover more (e.g., *Vitex lucens*).

Correlated dependencies on the same bird species for pollination and seed dispersal services varied among bird plant species. Joint dependencies were higher in *F. excorticata*, *G. rupestre* and *P. arboreus* than in *S. digitata*. *Fuchsia excorticata* was particularly reliant on tūī, bellbirds and hihi for pollination and dispersal services, whereas *P. arboreus* relied heavily on tūī and silvereyes, and *G. rupestre* relied heavily on silvereyes and hihi. Therefore, *F. excorticata*, *G. rupestre* and *P. arboreus* might be more susceptible to reproductive failure in regions without their key, dual-mutualist species. However, insect pollinators and seed dispersers are also known to visit the fruits and flowers of these species (Newstrom & Robertson 2005; Duthie et al. 2006; King et al. 2011). So other types of mutualists may well compensate for the loss of key avian mutualists.

Although rarely observed in continental settings, birds inhabiting isolated islands often visit flowers in addition to fruits. For example, populations of several species frugivorous European tits (Paridae) and warblers (Sylviidae) expand their diets to include nectar on Macronesian Islands (Dupont et al. 2004; Valido et al. 2004; see also Hansen et al. 2002; Micheneau et al. 2006). Island reptiles often show similarly expanded diets (Olesen & Valido 2003).

For example, a single species of gecko is the last remaining pollinator and seed disperser of *Rousea simplex*, a shrub endemic to Mauritius (Hansen & Müller 2009a). Unfortunately, this 'lizard plant' is now highly endangered, due both to declines in its single, effective mutualist, and to introduced ants that aggressively defend flowers and fruits, severely disrupting successful plant reproduction (Hansen & Müller 2009b).

Fleshy fruits consumed by birds in this study are phenotypically similar to bird-dispersed, fleshy fruits found elsewhere. Most are small, round and coloured reddish-orange or bluish-black (Burns & Lake 2009; Burns 2013). However, the morphology of many species of flowers that are visited by birds in New Zealand deviate strongly from those visited by birds in other biogeographic regions. Bird-dispersed flowers are usually red, tubular and comparatively large (see Pellmyr 2002). Although *F. excorticata* matches this description, the remaining bird plants (*P. arboreus*, *G. rupestre* and *S. digitata*) all produce small, more disk-shaped flowers that are either white or green. Why these species have not evolved flower morphologies that match those visited by birds in other biogeographic regions is unclear and worthy of further study (see also Kingston & McQuillan 2000; Dupont et al. 2004; Valido et al. 2004; Micheneau et al. 2006). One possibility is that although they are visited by birds, certain insects are more effective pollinators and therefore more important evolutionarily (see Newstrom & Robertson 2005).

Several methodological aspects of this study warrant a cautious approach to interpreting results. Although Zealandia is an ideal place to investigate bird–plant interactions, bird–flower and bird–fruit interaction patterns observed here may not be representative of other localities. Data only quantify the first stage in mutualistic interactions and processes operating at later stages, such as pollen presentation and seed deposition may counter gains made in reproductive fitness at the visitation stage (Schupp et al. 2010). How frequently bird visitation leads to successful pollination and seed dispersal remains unknown. Differences in visitation rates among bird and plant species might result from very different mechanisms. They could

arise from preferential foraging resulting from interspecific variation in food requirements, reward levels and morphology. However, they might also result from similar foraging preferences among randomly foraging, yet differentially abundant, bird species that interact with differentially abundant plant species (Zamora 2000; Burns 2006, 2013). Additional work is needed to discern between these two possibilities.

Results from this study provide some initial insight into the comparative ecology of bird–flower and bird–fruit interactions in the New Zealand flora. However, many important and interesting questions remain unanswered. Why are there comparatively few bird-pollinated plants in New Zealand? Why do birds visit flowers that differ markedly from the bird pollination ‘syndrome’? Are bird plants particularly vulnerable to reproductive failure in areas devoid of heavily managed bird populations?

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