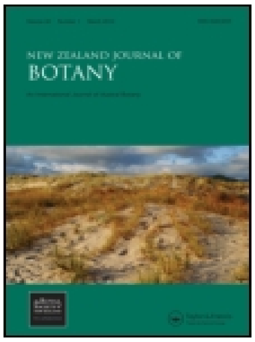

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Progress in understanding pollination systems in New Zealand

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Godley Review

Progress in understanding pollination systems in New Zealand

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Abstract Pollination in New Zealand, an isolated oceanic archipelago in the Southern Hemisphere, has previously been characterised as having low rates of self-incompatibility and a lack of specialised pollination, as well as little pollinator dependence. These features have been interpreted as supportive of "Baker's Rule", which suggests that long-distance colonisation selects for breeding systems that do not require biparental mating. However, we show that recent studies of the angiosperm flora reveal sexual systems (sexual dimorphism, self-incompatibility, monoecy, dichogamy, and herkogamy) that usually involve a dependence on pollen vectors. The level of self-incompatibility in the flora, though still poorly known, should be regarded as moderate rather than unusually low (about 36% of hermaphrodite populations tested are strongly or partially self-incompatible), though many more species remain to be tested. As found elsewhere, incompatibility is higher in the trees and shrubs (around 80%) compared with herbs (21%). Moreover, high rates of autonomous selfing have been demonstrated empirically in only 21% of the self-compatible species, demonstrating that they are not regular selfers. The pollinator dependence that these features impose makes much of the flora vulnerable to declines in pollinator service.

Pollination systems in New Zealand have been characterised as unspecialised, imprecise entomophilous systems that correspond to the predominance of small white or pale flowers with dish or bowl shapes. We use a two-tiered conceptual framework incorporating a coarse-scale blossom class analysis and a finer scale syndrome concept analysis to assess the level of specialisation in plant–pollinator relationships of New Zealand. Within each of the syndromes is a continuum of blossom classes: open-, directed-, and closed-access. Highly specialised systems are found in closed-access blossoms but they are not common in New Zealand (e.g., *Solanum*, *Carmichaelia*, orchids, and mistletoes). Large directed-access blossoms are primarily associated with bird pollination but certain small entomophilous blossoms, called "knob" blossoms (*Pseudopanax*, *Geniostoma*), are also important for perching birds and may be considered ornithophilous. Bats and lizards play a minor role in pollination. Moth pollination is not well studied and may reveal cryptic specialisation based on scent. The majority of pollination systems in New Zealand correspond to the "small bee syndrome", which is a generalised bee-pollinated system common elsewhere and includes visits from flies and other diverse insects. Naturalised exotic bees may have both positive and negative effects on indigenous pollination systems and could play a significant role in invasive mutualisms in which some weeds are specialised to their services. Future research in New Zealand pollination and breeding systems needs to focus on endangered mutualisms, particularly in birds; on invasive mutualisms, particularly for offshore islands; and on community analyses that evaluate exotic-indigenous interactions and the potential for specialisation in the poorly known insect pollination systems.

Keywords autonomous selfing; blossom class; community analyses; functional pollinator group; breeding system; New Zealand; pollen limitation; pollination syndrome; pollinator dependence; pollinator; self-compatibility; sexual system

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> *There is a grandeur in this view of life, with its several powers, having been originally breathed by the Creator into a few forms or one; and that, whilst this planet has gone cycling on according to the fixed law of gravity, from so simple a beginning endless forms most beautiful and most wonderful have been, and are being evolved.*" (Darwin *Origin of Species* 1859 cited in Barth 1985, p. 268)

INTRODUCTION

The beautiful and wonderful forms of flowers have fascinated pollination biologists for centuries and shaped fundamental concepts in pollination biology such as the syndrome and blossom class (Sprengel 1793 (1996); Darwin 1877a; Stebbins 1974; Faegri & van der Pijl 1979; Proctor et al. 1996). Pollination biologists have used these concepts to understand the evolution of floral diversity and predict reciprocal relationships in plant–pollinator interactions. When applied to the New Zealand flora, they portray a predominance of rather unspecialised entomophilous* pollination (Godley 1979; Lloyd 1985). However, pollination has not been well studied in New Zealand so assumptions based on these concepts bear further examination, particularly since the validity of the syndrome concept has recently been questioned (Herrera 1996; Ollerton 1996; Waser et al. 1996). Both concepts, if predictive, are important for understanding the conservation and restoration of pollinator mutualisms and the ecological impacts of exotic plants and pollinators.

New Zealand has a distinctive and subtle assemblage of plant–pollinator relationships (Godley 1979; Lloyd 1985) because it has a combination of both relict and dispersed flora with a restricted suite of pollinators (Webb & Kelly 1993). A large percentage (83%) of indigenous plant species are endemic to New Zealand (1566/1896) but this is offset by an extremely large addition of naturalised exotic plant species (53% of all plant species in the flora (2109/4005) (Wilton & Breitwieser 2000)). New Zealand has a low diversity of indigenous pollinators, some relatively primitive, and a small but pervasive, and highly effective, group of exotic pollinators (Donovan 1980).

These characteristics reflect the geographical isolation from other elements of Gondwanaland, variable oceanic climate, and an unusual combination of ancient Gondwanan, tropical, and more recently arrived elements in the flora (Webb & Kelly 1993). Lloyd (1985) noted that Hooker (1853) and Wallace (1880) both remarked on the disparity between the Australian and New Zealand indigenous floras in spite of their overall affinity. Lloyd (1985) explained the anomalies that puzzled Wallace by invoking the concept of immigration selection, i.e., all possible arrivals from nearby land masses are filtered at the species level due to adaptations promoting their long-distance dispersal and subsequent ability to establish and radiate. Since a large majority of New Zealand's indigenous plant species have immigrated from overseas (Lloyd 1985; Winkworth et al. 2002a), adaptations promoting dispersal and colonisation should be evident in breeding and sexual systems as well as in pollination.

Plant breeding and sexual systems have been relatively well studied in New Zealand (reviewed by Godley (1979), Lloyd (1985), Webb & Kelly (1993), and Webb et al. (1999)), but studies of pollination systems have focused primarily on bird pollination leaving insect pollination poorly understood. In a comprehensive review of 100 years of reproductive biology in New Zealand, Godley (1979) emphasised the need for more observations on pollination especially nocturnal pollinators and the role of scent. Later, Lloyd (1985) presented an evolutionary interpretation of the role of pollinators in shaping the flora and also highlighted the need for more data on pollination. Apart from Webb & Kelly's (1993) brief update on the topic, there has been no review of pollination for two decades.

Several trends in plant–pollinator evolution are evident in New Zealand. To understand these trends, Godley (1979) stressed the plant genus as the appropriate unit of analysis; based on this, Lloyd (1985) outlined a research programme for estimating the evolution of floral traits. Today, these analyses are typically conducted by mapping characters onto phylogenies, which have revealed repeated global trends of convergent evolution to more specialised pollination (e.g., Armbruster 1993; Hodges 1997; Johnson et al. 1998) but also recently discovered trends to more generalised pollination, i.e., despecialisation (Armbruster & Baldwin 1998), or to autogamy (i.e., self-pollination) (Barrett et al. 1996). Given the depauperate pollinator fauna in New Zealand, despecialisation is expected to be more prevalent than specialisation.

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*Terms are defined in the Glossary at the end of the paper.

Indeed, the prevailing view of New Zealand pollination systems is one of extreme generalisation with extensive pollinator sharing, and unpredictable, imprecise pollinator service; several aspects of the breeding systems of the flora have been interpreted in this context (Wallace 1880; Thomson 1927; Heine 1937; Godley 1979; Lloyd 1985; Webb & Kelly 1993). It was suggested that outcrossing was more commonly promoted by sexual dimorphism rather than by self-incompatibility (Baker 1967); that herkogamy (i.e., spatial separation of anthers and stigma) and dichogamy (i.e., temporal separation of male and female function) in outbreeding hermaphrodites were means of separating male and female function to increase the efficiency of otherwise imprecise and unspecialised pollination processes (Lloyd & Webb 1986; Webb & Lloyd 1986); and, finally, that there was a strong trend towards autogamy (i.e., self-pollination), particularly in alpine herbs (Raven 1973; Wardle 1978).

This view of breeding systems and pollination in New Zealand raises several questions. If mainly self-compatible and autonomously selfing species (i.e., self-pollinating without the need for pollen vectors) with few specialised pollination systems predominate in New Zealand, are exotic plants and pollinators likely to have little impact? Are the systems so generalised that all pollinators are equally likely to visit and pollinate all plant species whether they are exotic or indigenous? If so, what impact does this have on sustainability of indigenous pollination systems? If there are any specialised pollinator-dependent plant species, are they vulnerable?

Whether by loss of indigenous plants or pollinators, or gain of exotics, the potential for disruption of pollination services impinges on several areas of concern, e.g., biodiversity conservation (Kearns et al. 1998; Roubik 2000), ecological restoration (Montalvo et al. 1997; Neal 1998; Potts et al. 2003; Frankie & Vinson 2004), biosecurity protection (Goulson 2003a; Hanley & Goulson 2003), biosafety issues such as geneflow (Newstrom et al. 2003), and sustainable agriculture and horticulture (Allen-Wardell et al. 1998; Kevan & Imperatriz-Fonseca 2002). Changes in mating and pollination systems are not as obvious or immediate as other ecological processes at the community level; analyses and comparisons have used several different approaches (Jordano 1987; Momose et al. 1998; Memmot 1999; Dicks et al. 2002; Memmot & Waser 2002; Olesen & Jordano 2002; Frankie et al. 2004; Kay & Schemske 2004). It is in this area that the syndrome and blossom class concepts would be of most value as predictive tools.

The aims of this review are to:

1) Examine the view that self-compatibility and autonomous selfing predominates in the New Zealand flora. Do many species depend on pollinator service? Do we have evidence that any pollinator-dependent plant species are currently pollen limited and what factors contribute to the limitation?
2) Evaluate the syndrome and blossom class concepts as predictive tools to investigate the evolution (past) and ecology (present and future) of pollinator mutualisms in New Zealand. What are the limits to using these concepts? Does the syndrome concept need to be modified or completely supplanted by another conceptual framework?
3) Examine the view that pollination in New Zealand is predominantly unspecialised and entomophilous. Does this apply to all habitats and in all seasons? How many, if any, specialised pollination systems exist in New Zealand?
4) Apply, if possible, the syndrome or blossom class concepts to the problem of assessing and predicting ecological impacts due to losses or gains of pollinators or plants. What research priorities are needed to address current and future issues in pollination of the New Zealand flora?

We first review the evidence for breeding systems and pollinator dependency in New Zealand plant species, and then evaluate the relevance and usefulness of the syndrome concept for predicting plant–pollinator interactions. We next apply both the syndrome and blossom class concepts to review the major types of biotic pollination systems in New Zealand and evaluate potential for specialisation. Finally, we address potential positive and negative effects of exotic pollinators and plants on indigenous pollination systems.

BREEDING SYSTEMS AND THE NEED FOR POLLINATORS

Pollinator dependence

Darwin's realisation of the importance of outcrossing in plants and the mechanisms that promote it (Darwin 1862, 1876, 1877a,b) stimulated activity amongst New Zealand's botanists on the pollination and breeding systems of the New Zealand flora (Cheeseman 1873, 1875, 1877, 1878, 1881, 1882; Thomson 1879a,b, 1881a,b). Thomson (1881a) suggested that despite a depauperate pollinating fauna and the general dull coloration and the lack of

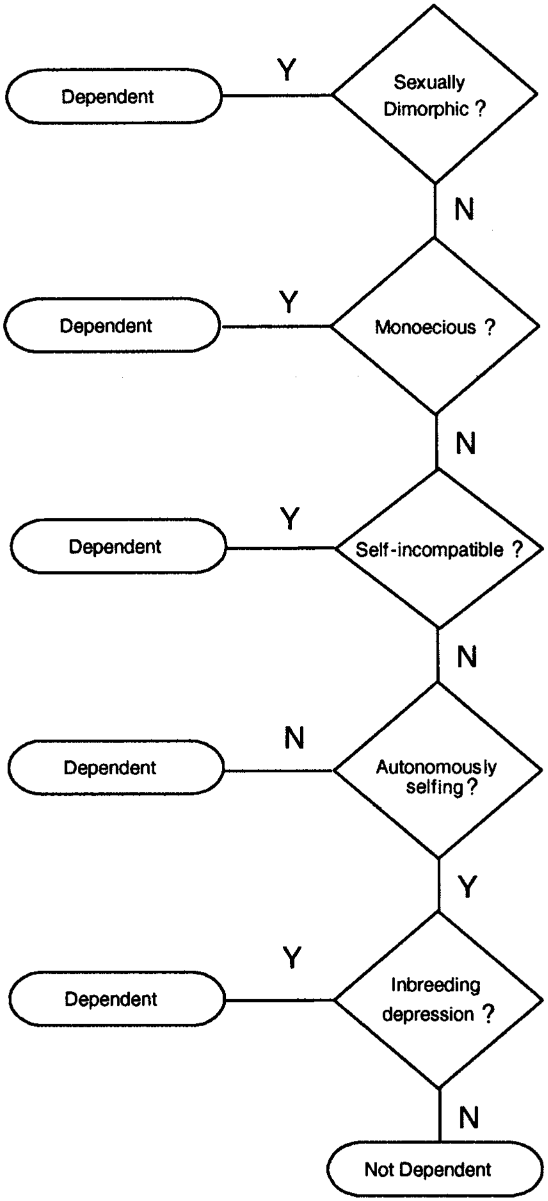

Fig. 1 Serial conceptual model of plant–pollinator dependence.

morphological complexity of the flowers, as much as 50% of the flora was adapted for cross-fertilisation, principally through having separate sexes or dichogamy.

Subsequent work emphasised several other evolutionary trends in the flora. Biogeographic and geological analyses suggested the recent colonisation by a large element of the flora, in particular by the alpine component (Raven 1973). Baker (1955) suggested that long-distance dispersal to islands would greatly favour autogamous species, since new populations could establish from a single successful propagule. Detailed work on several herbaceous genera, for example on *Cardamine* (Pritchard 1957), *Epilobium* (Brockie 1959; Raven & Raven 1976), and *Parahebe* (Garnock-Jones 1976), further established the predominance of autogamy and a lack of self-incompatibility in the flora (Rattenbury 1962; Wardle 1978; Godley 1979; Webb & Kelly 1993).

Despite these assertions about the importance of selfing in pollinator-depauperate New Zealand, it is clear that, as suggested by Thomson (1881a), an analysis of the breeding systems of New Zealand plants reveals a high degree of dependence on pollinators. The only plant species that are not pollen-vector dependent are autonomously selfing hermaphrodites that do not exhibit significant inbreeding depression. Although our knowledge of the breeding systems and mating patterns is far from complete, it is easy to show that the majority of New Zealand species are not likely to be autonomously selfing.

Wind provides an alternative to animals for vector-dependent species. Anemophily is predominant in groups such as gymnosperms, grasses, sedges, and rushes, and is scattered through other groups of flowering plants such as *Nothofagus*, *Coprosma*, and *Coriaria*. Overall, wind-pollination is assumed for 78 genera (29% of the total seed plant genera) (Webb et al. 1999).

A flow diagram (Fig. 1) illustrates sequentially the alternative breeding systems to autonomy, all of which require pollen vectors (animals, wind, or, rarely, water). Although presented here as a series of dichotomies, most of these conditions exist in intermediate forms that impart partial dependence. For example, the first dichotomy shown here is sexual dimorphism (dicliny). Strict dioecy (i.e., separate male and female plants) is the most extreme form of sexual dimorphism and requires pollen to be transferred from male plant to female plant by a vector. However, gynodioecy is a common variant (hermaphrodite and female plants), in which females are completely vector-dependent, while the hermaphrodites may not be. Other partial dependencies occur through andromonoecy or gynomonoecy (i.e., hermaphrodite and male or hermaphrodite and female flowers on one plant), partial self-compatibility, low levels of autonomous selfing, and weak inbreeding depression.

Sexual dimorphism

The high proportion of gender dimorphism (Hooker 1853; Thomson 1881a; Godley 1979) in the flora of New Zealand, along with the flora of Hawaii, provides a challenge to Baker's Rule (Baker 1955), which suggested that this strategy was unlikely to be successful in the colonisation of island groups. High rates of dioecy in Hawaii and New Zealand led Carlquist (1966), Baker (1967), and Gilmartin (1968) to suggest that sexual dimorphism may have frequently established following colonisation by a self-compatible hermaphrodite. Baker (1967) claimed that a change to dicliny is easier to achieve than the acquisition of the genetic architecture necessary for self-incompatibility, and may be favoured as a response to selection for pollination efficiency when small unspecialised pollinators are involved (Bawa & Opler 1975; Bawa 1980, 1982; Thomson & Barrett 1981; see Sakai & Weller (1999) for a review of this and of other ecological correlates of dioecy).

A recent review (Webb et al. 1999) documented gender dimorphism in 83 indigenous genera of New Zealand seed plants (23% of total): 65 genera are dioecious, 26 genera gynodioecious (some genera contain both forms of dimorphism). Significantly, only 17 of these are estimated to have arisen autochthonously in New Zealand (i.e., it evolved in New Zealand following colonisation, rather than preceding it). In Hawaii, this portion is estimated at 31.8% of the dimorphic species (Sakai & Weller 1999). The implication of these figures is that for the majority of cases, despite Baker's suggestion, sexual dimorphism was already present in the plant colonists that established on these islands (see Barrett (1996) for a discussion of this topic).

Monoecy, herkogamy, and dichogamy

Probably the most widespread cause of dependence on pollen vectors is the separation of male and female functions in space and/or time. Interfloral (monoecism) and intrafloral herkogamy effectively isolates pollen from stigma spatially. Alternatively, these functions may be separated in time (dichogamy). Although traditionally interpreted as an outcrossing mechanism, they may also have an explanation in preventing interference between functions, since these features often coincide with self-incompatibility which, alone, would ensure outcrossing (see Lloyd & Webb (1986) and Webb & Lloyd (1986) for reviews and references to the New Zealand flora).

Thomson (1881a) estimated that of 235 hermaphrodite species that he examined, 87 species (37%) were protandrous (i.e., pollen shed before the stigma matures) and 18 species (8%) were protogynous. These species are likely to be pollinator-dependent, unless the dichogamy is not complete. In some species, delayed selfing may occur as the flower ages. For example, in some species of *Myosotis* (e.g., *M.* sp. (1) aff. *australis*, Fig. 2C), the stigma remains receptive throughout anthesis; the flowers are initially herkogamous but later, due to the shifts in the relative positions of anthers and stigma, the herkogamy breaks down and "delayed selfing" (Lloyd 1979; Lloyd & Schoen 1992) occurs (Robertson & Lloyd 1991). Similarly, the flowers of *Clianthus puniceus* and *C. puniceus* var. *maximus* have a stigmatic cuticle that must be ruptured before pollination can occur. In *C. puniceus* var. *maximus*, this normally only occurs during visits by honeyeaters, but in *C. puniceus* the cuticle ruptures spontaneously just prior to senescence, and autonomous selfing results (Heenan 1998). *Solanum laciniatum* also has a delayed self-fertilisation system involving both herkogamy and dichogamy. Although the protogynous flowers are highly specialised for buzz pollinators, in the final days of anthesis the filaments extend so that the anthers are touching the stigma and, if pollen is left over, delayed selfing occurs (L. E. Newstrom unpubl. data).

Self-incompatibility and autonomous selfing

In self-compatible species, even complete dichogamy and strong herkogamy or monoecy will not prevent geitonogamous self-pollination (movement of pollen among flowers of the same individual). Flower visitors may facilitate within-flower selfing in herkogamous species by disturbing floral parts during visitation, making it useful to differentiate facilitated selfing (occurs as a result of pollinator movements within and between flowers) from autonomous selfing (occurs automatically within a flower without the aid of a pollinator), since the former imparts pollinator-dependence (Lloyd 1979; Lloyd & Schoen 1992). Self-incompatibility blocks self-pollination at any one of several stages of the pollination-fertilisation-seed maturation pathway (de Nettancourt 1977). New Zealand is frequently cited as having low levels of self-incompatibility, as expected under Baker's Rule (Raven 1973; Godley 1979; Webb & Kelly 1993; Barrett 1996; Anderson et al. 2001; Bernadello et al. 2001; Schueller 2004). We suggest that this conclusion may be an overgeneralization for two reasons. While few cases of self-incompatibility have been described to date, it is also true that few tests have been made (Webb & Kelly

1993). Previous surveys (Godley 1979; Webb & Kelly 1993) have listed the species known to be self-incompatible without listing the negative results. To compare the flora with other regional floras requires a test of the proportion of the cosexual species of a flora that are known to be either self-compatible or incompatible. Secondly, the few tests of compatibility that have been performed have included very few trees and many herbs. Self-incompatibility is much more commonly associated with trees than with herbs and with longer-lived plants rather than short-lived species (Stebbins 1970; Jain 1976; Arroyo & Squeo 1990; Jaimes & Ramirez 1999; Morales & Galetto 2003), suggesting that critical comparisons with elsewhere cannot yet be undertaken.

Autonomously selfing species must of course be self-compatible, but the latter does not automatically imply the former. Dichogamy and herkogamy will often be sufficiently strong to preclude autonomous selfing (Lloyd & Schoen 1992). Autonomous selfing is often regarded as a reproductive assurance mechanism that allows seed set in the face of unpredictable and variable pollinator service and is expected in conditions that are harsh for pollinators (Darwin 1876; Jain 1976; Lloyd 1980; Schoen et al. 1996). Several studies on small-stature New Zealand herbs of forests and alpine situations have revealed high rates of autonomous selfing (e.g., *Cardamine*, Pritchard (1957); *Epilobium*, Brockie (1959) and Raven & Raven (1976); *Parahebe*, Garnock-Jones (1976)), though in other cases, self-compatibility does not lead to autonomous selfing, for example in alpine *Ranunculus* (Fisher 1965). In the next section, we summarise all known available research that has quantified the potential for autonomous selfing, self-compatibility, and/or the degree of pollen limitation in populations of indigenous hermaphrodite species.

A survey of the breeding systems of New Zealand hermaphroditic plants

Dataset and breeding system indices

We included all available studies that presented results on seed or fruit set for at least two of the following treatments: *emasculation* and pollinator exclusion (to check for apomixis, i.e., reproduction by seeds formed without sexual fusion); *pollinator-exclusion* alone (to check for autonomous selfing); *hand self-* or *cross-pollination* (to check for self-compatibility); and *untreated* flowers (to measure natural pollination rates). We excluded studies that measured only one of these treatments, and excluded anecdotal evidence of, for example, the ability of lone plants to set seed; this does not distinguish between pollinator-mediated selfing and autonomous selfing (Lloyd & Schoen 1992). Similarly, we did not include studies that inferred autonomous selfing simply from high seed set in glasshouses, since insects could possibly visit flowers.

From these data, we calculated three indices of breeding system (Bawa 1974; Ruiz & Arroyo 1978; Larson & Barrett 2000). The self-compatibility index (SCI) is the hand-pollinated self/cross ratio for seed production, the autonomous selfing index (ASI) is the pollinator-excluded/cross ratio (or bag/open ratio for small highly self-compatible species), and the pollination limitation index (PLI) is the open-pollinated/cross ratio (truncated at 0, Larson & Barrett (2000)).

Fig. 2 Diversity of blossoms in *Myosotis* (Boraginaceae) in the New Zealand flora (tube flowers on the left; dish, bowl, and funnel flowers on the right). **A**, Naturalised exotic *Myosotis sylvatica* (9 mm diam.) is a typical European species with a short narrow tube and wide rim (rotate corolla), and conspicuous corolla scales at the mouth of the tube, pollinated by honeybees and bumblebees; **B**, Indigenous *M. monroi* (6 mm diam.) has strongly exserted filaments and styles with nearly synchronous flower development within each cyme resulting in a brush inflorescence; **C**, Indigenous *M.* sp. (1) aff. *australis* (5 mm diam.): as the flower ages in this species, the lengthening corolla tube lifts the anthers from a position below the level of the stigma to one that is adjacent to and eventually above the stigma. This results in "delayed selfing" if outcrossing does not occur during this initial phase; **D**, Indigenous *M. laeta* (8 mm diam.) has bowl-shaped flowers with an open tube and moderately exserted filaments and style. In the Red Hills, Marlborough, indigenous short-tongued solitary bees like this one are important pollinators; **E**, Indigenous *M. spathulata* has small flowers (2.5 mm diam.) in which the anthers dehisce shortly after opening, depositing pollen directly on the stigma, causing the flower to autonomously self; **F**, Indigenous *M. goyenii* (10 mm diam.) has a relatively wide corolla tube allowing relatively easy access to the nectar; **G**, Indigenous *M. colensoi* (8 mm diam.) shows a strongly exserted style that prevents any chance of autonomous selfing and a relatively long corolla tube (c. 7 mm), which restricts nectar access to long-tongued insects. At Castle Hill it is pollinated mainly by a tachinid fly, *Protohystricia huttoni*, which has a tongue of approximately the same length as the corolla tube; **H**, Indigenous *M. macrantha* (8 mm diam.) has a long tube and exserted style and at Mt Cook appears to be mainly pollinated at dusk by the noctuid moth *Aletia cuneata.* (Photos Alastair Robertson)

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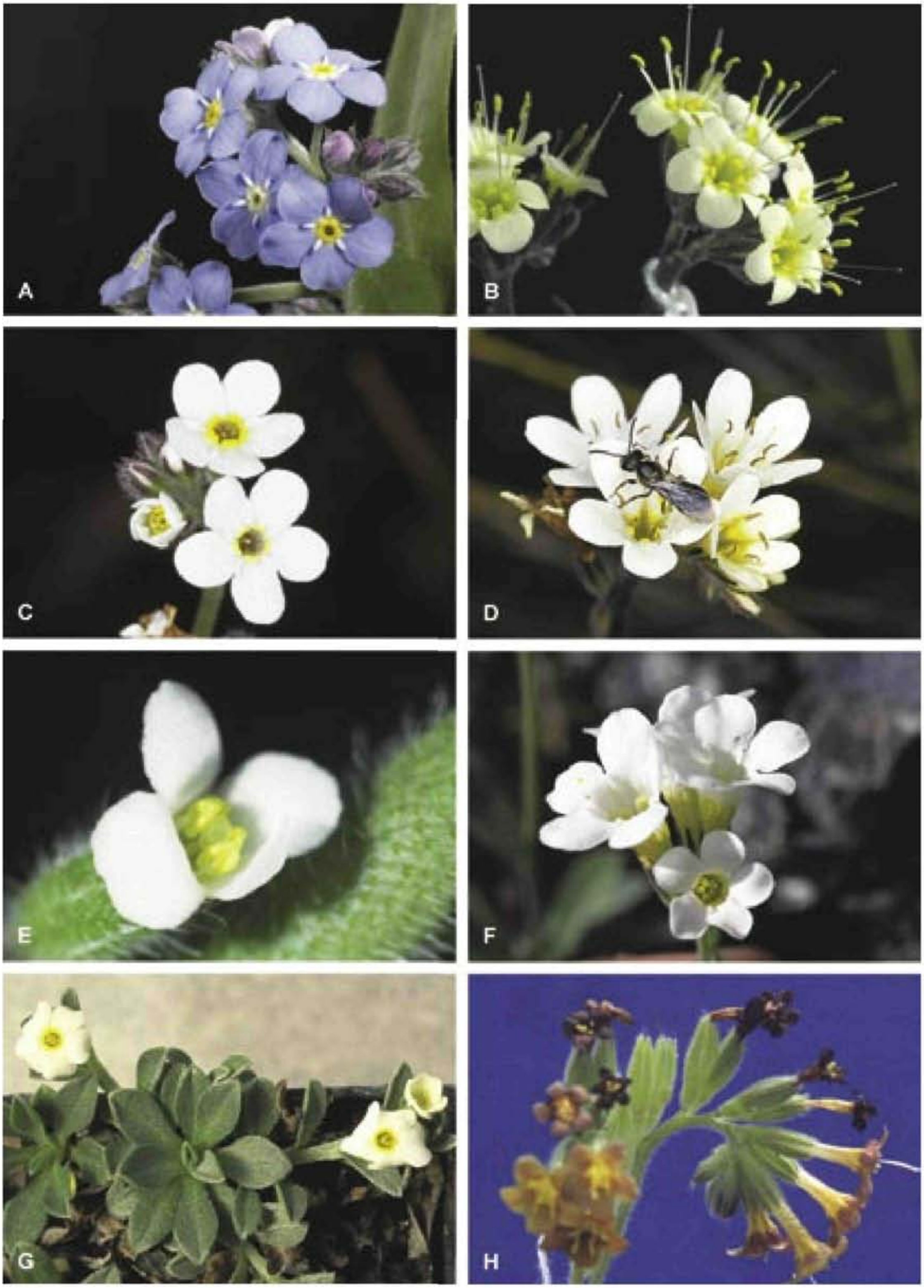
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There are a couple of potential interpretation problems with these simple indices of breeding system that should be noted. The SCI as defined here effectively measures the degree of self-sterility. Genetic incompatibility is one possible cause of such sterility, but it is also possible that early-acting inbreeding depression where selfed seeds are more prone to abortion could also produce the same effect (Seavey & Bawa 1986). However, a high rate of self-sterility, whether caused through self incompatibility or inbreeding depression, has the same net effect on the breeding system—a need for outcross pollen for successful reproduction; hence we believe it to be a useful measure of dependence on vectors that bring outcross pollen. The PLI is measured by comparing the likelihood of seed maturing from manually produced cross-pollinated flowers and naturally pollinated flowers. The difference between the two is considered the degree of pollen limitation (Bierzychudek 1981; Burd 1994). However, high PLI values may occur if resources are diverted towards hand-pollinated and outcrossed flowers which may act as a sink drawing resources away from other naturally pollinated flowers either in the current season or in future years (Janzen et al. 1980; Bawa & Webb 1984; Ashman et al. 2004). In extreme cases, heavy fruit crops caused by artificially high rates of pollination may cause the premature death of plants that otherwise may have produced as many or more seeds spread over several seasons of normal pollination conditions. Hence, a high score for PLI may not necessarily indicate a pollination problem without further evidence; it does indicate candidate populations for further investigations.

We classified each population as *apomictic* where high seed set occurs in bagged emasculated flowers, *autonomously selfing* where ASI > 0.5, self-compatible where SCI > 0.80, *partially compatible* where 0.20 < SCI < 0.80, and *self-incompatible* where SCI < 0.20 (Bawa 1974; Ruiz & Arroyo 1978). The degree of pollen limitation was classified as high where PLI > 0.75, medium where 0.25 < PLI < 0.75, and low where PLI < 0.25. We preferred to use these indices rather than testing the significance of differences between treatments, for three reasons. First, they enable the inclusion of New Zealand studies that did not test mean differences and allow comparison with other international studies; second, these indices directly measure the effect size; and, finally, we do not want to overemphasise statistical rather than biological effects. For example, the difference between two treatments that yielded 70% and 75% fruit set, respectively, may be statistically significant if sample sizes are large enough, but is not likely to be biologically important.

Data from 43 species and 50 populations are included. There is a bias towards herbs (27 species), with relative few woody plants (5 tree species, 7 shrubs, and 4 woody vines and mistletoes). Moreover, there is strong taxonomic bias in the dataset with 26 genera represented and some genera, e.g., *Myosotis*, over-represented (8 species). For these reasons, the conclusions reached from this survey must be regarded as preliminary until we have data from more species that better represent the flora as a whole or, alternatively, are conducted at a community scale, to represent the breeding system of coexisting species within habitats.

Many studies in Table 1 did not include all of the five treatments needed to investigate fully the breeding system of the species (emasculated, pollinator-excluded, hand-selfed, hand-crossed, and untreated). In particular, agamospermy (the production of seed from asexual means) has rarely been tested but could be ruled out in most cases when one of the other treatments resulted in low seed set. Other studies did not test for autonomous selfing, so the potential remains unknown for some self-compatible species. Conversely, in a few cases, self-compatibility was confirmed by demonstrating high rates of autonomous selfing. Often, the studies were conducted with cultivated plants and in most of these cases natural levels of seed production were not measured, since the plants were not in natural conditions. Self-compatibility status was established for most populations (44 out of 50) and at least once for all 43 species, though hand self- and cross-pollinations were performed on only 38 populations, with self-compatibility confirmed from high rates of autonomous selfing in the remainder.

The New Zealand flora

Strong self-incompatibility (SCI < 0.2) was found in 10 populations (21.3% of those tested) and 9 species (20.9%) (Table 1). Partial compatibility occurred in a further seven populations (14.9%), with self-compatibility in the remainder (63.9%). Self-compatibility was not randomly distributed with respect to life form (Table 2), with eight of the self-incompatible populations being trees or shrubs, and self-incompatibility or partial compatibility occurring in 80% and 88% of the tree and shrub species, respectively. In contrast, full self-compatibility occurred in 78% of the herbaceous species tested. SCI ranged between 0.00 and 1.29, and averaged 0.64 overall (Table 2), but was higher on average in herbs than in the trees

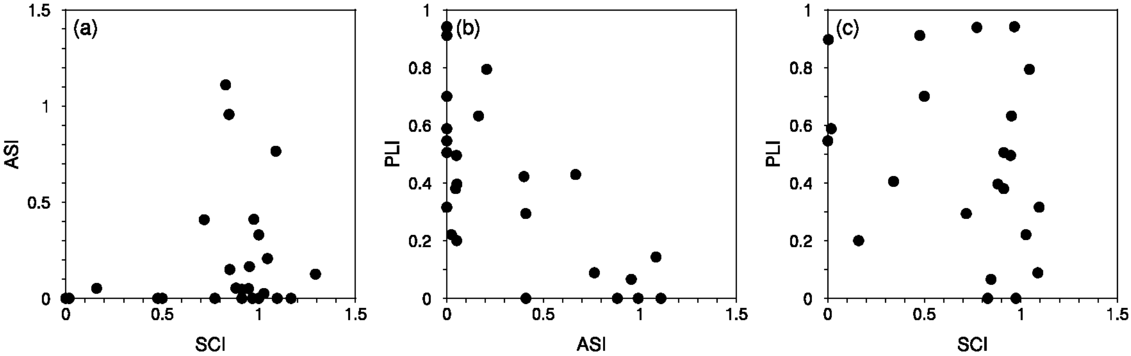

Fig. 3 Relationships between the three breeding system indices self-compatibility (SCI), autonomous selfing (ASI), and pollen limitation (PLI) of populations studied in Table 1.

or shrubs. The vines and mistletoes tested were mostly fully self-compatible, and this group also had a high average SCI (0.84).

Ten populations were found to have high rates of autonomous selfing (29% of the self-compatible or partially self-compatible populations), though none of the three self-compatible trees and shrubs was found to autonomously self. The autonomous selfing index (ASI) ranged from 0.00 to 1.11 and was very low for the trees and shrubs, and moderate overall (0.36). The ASI and SCI indices were not correlated ($r = 0.18$, d.f. = 23, $P < 0.05$) for the 25 populations for which both indices could be calculated (Fig. 3). Not surprisingly, the ASI scores were very low for populations with low SCI values, but high SCI values did not always lead to high ASI; some populations had high SCI and very low rates of autonomous selfing, presumably because of strong dichogamy or herkogamy.

The pollen limitation index (PLI) also varied widely from 0.00 to 0.94, and many populations were strongly pollen limited. Of the populations where pollen limitation was measured, 8 populations showed a high rate of pollen limitation, 13 medium, and 12 low. The few trees included in the survey were generally more pollen limited than vines, mistletoes, and herbs (Table 2), but all groups contained a wide range of PLI, and the most pollen-limited populations were orchids. Self-compatible populations tended to be much less pollen limited than the partially compatible and self-incompatible populations. A simple two-factor linear regression (GLM with Gaussian distribution) showed that PLI was negatively correlated with autonomous selfing but was unrelated to the SCI scores (Fig. 3; Table 3). Thus, fully self-compatible populations were frequently strongly pollen limited, and vice-versa.

Geographical comparisons

A number of other geographical community surveys are available for comparison with our New Zealand data (Table 4). Other surveys have shown a strong relationship between life form and self-incompatibility (Arroyo & Squeo 1990; Jaimes & Ramirez 1999; Morales & Galetto 2003) and interfloral comparisons are most realistically undertaken within life form, rather than across all species. Only 7% of New Zealand herbs measured were self-incompatible, but 42% of woody plants. Globally, herbs average 25% self-incompatibility and range from 4% to 43% (Table 4), while woody plants average 70% and range from 14% to 84%. The New Zealand figures, thus, are towards the lower half of the range in both cases, but are certainly not the lowest. Two other small oceanic islands, Juan Fernandez (Bernadello et al. 2001) and the Galapagos Islands (McMullen 1987), have lower proportions of self-incompatible taxa than New Zealand. Continental floras generally have much higher rates of self-incompatibility, particularly in the woody plants of lowland forests, but there are exceptions. Only about 4% of the monocot herbs in cloud forest in Venezuela are self-incompatible (Ramirez & Seres 1994), while a study in a very similar location (Sobrevila & Arroyo 1982) that included other types of herbs as well as woody plants showed much higher rates of incompatibility. Similarly, the Venezuelan lowland palm swamps studied by Ramirez & Brito (1990) also showed low overall incompatibility. Families and other taxonomic groupings vary widely in their propensity for

Table 1 Experimental tests of breeding systems in animal-pollinated (or autogamous) members of the New Zealand flora. The sexual system for each species is classified as hermaphrodite (H), andromonecious (Am), gynomonoecious (Gm), or gynodioecious (Gd). The breeding system of each population is classified as apomictic (AP), autonomously selfing (AS), self-compatible (SC), partially self-compatible (PC), or self-incompatible (SI), and the degree of pollen limitation scored as high (H), medium (M), or low (L) on the basis of three indices of seed or fruit set. The self-compatibility index (SCI) is the self/cross ratio, the autonomous selfing index (ASI) is bagged/cross, and the pollen limitation index (PLI) open/cross. Seed production may have been scored at the level of fruit set (FS), seed set (SS) or both, enabling seeds per flower to be calculated (FS × SS).

Plant	Family	Sexual system	Site/year	Breeding system	Pollen limitation	Level of assessment	SCI	SCI	PLI	Reference
Trees										
Cordyline australis	Agavaceae	H	Garden plants	SI	H	FS × SS	0.00	-	0.90	Beever & Parkes 1996
Cordyline kaspar	Agavaceae	H	Garden plants	SI	-	FS	0.01	-	-	Beever 1981
Cordyline pumilio	Agavaceae	H	Garden plants	SI	-	FS × SS	0.01	-	-	Beever 1983
Metrosideros excelsa	Myrtaceae	H	Auckland	PC[a]	M	FS × SS	0.34	-	0.40	Schmidt-Adam et al. 1999
Vitex lucens	Verbenaceae	H	Auckland	SC	-	FS	1.29	0.13	-	Barrell et al. 1997
Shrubs										
Carmichaelia williamsii	Fabaceae	H	Glasshouse	PC[a]	-	FS	0.77	-	-	Heenan & de Lange 1999
Corokia cotoneaster	Cornaceae	H	Bealey Spur 1982	SI	M	FS	0.02	0.00	0.59	Webb 1994
Discaria toumatou	Rhamnaceae	H	Cass 1977	SI	M	FS	0.00	0.00	0.55	Primack 1979
			Bruce Stream 1983	SI	-	FS	0.00	-	-	Webb 1985
Leptospermum scoparium	Myrtaceae	Am	Cass		L	FS	-	-	0.00	Primack & Lloyd 1980
Pentachondra pumila	Epacridaceae	H	Glasshouse	SI	-	FS × SS	0.04	-	-	Godley 1966
Pseudowintera colorata	Winteraceae	H	Garden plants	SI	-	FS	0.00	-	-	Godley & Smith 1981
			Port Hills	-	H	FS × SS	-	-	0.78	Lloyd & Wells 1992
Rhabdothamnus solandri	Gesneriaceae	H	Little Barrier Island	-	L	FS	-	-	0.04	Anderson et al. unpub.
			Auckland	-	H	FS	-	-	0.81	Anderson et al. unpub.
			Lady Alice Island	-	L	FS	-	-	0.13	Molloy 2004
			Whangarei	SC	M	FS	0.95	0.16	0.63	Molloy 2004
Vines and mistletoes										
Alepis flavida	Loranthaceae	H	Craigieburn 1993	AS	L	FS	0.83	1.11	0.00	Ladley et al. 1997
			Craigieburn 1997	AS	L	FS	-	1.08	0.14	Ladley et al. 1997
Fuchsia perscandens	Onagraceae	Gd	Buckley's Bay 1999	-	M	FS × SS	-	-	0.74	Montgomery et al. 2001
			Buckley's Bay 2000	AS	M	FS	-	0.67	0.43	Montgomery et al. 2001
			The Torrs	SC	M	FS	-	0.40	0.42	Montgomery et al. 2001
Peraxilla colensoi	Loranthaceae	H	Wakefield	SC	L	FS	0.97	0.41	0.00	Robertson et al. 1999
Peraxilla tetrapetala	Loranthaceae	H	Craigieburn 1993	PC	M	FS	0.72	0.41	0.29	Robertson et al. 1999

			Craigieburn 1995	SC	H	FS	1.04	0.21	0.79	Robertson et al. 1999
Herbs										
Earina aestivalis	Orchidaceae	H	Manawatu	PC	H	FS	0.48	0.00	0.91	Lehnebach & Robertson 2004
Earina autumnalis	Orchidaceae	H	Manawatu	SC	M	FS	0.91	0.00	0.50	Lehnebach & Robertson 2004
Earina mucronata	Orchidaceae	H	Manawatu	SC	H	FS	0.97	0.00	0.94	Lehnebach & Robertson 2004
Gastrodia cunninghamii	Orchidaceae	H	Manawatu	AP[b, c]	L	FS	0.00	0.91	0.00	Lehnebach 2002
Gentianella saxosa	Gentianaceae	H	Glasshouse	SC	-	FS × SS	1.00	0.00	-	Webb & Littleton 1987
Gentianella serotina	Gentianaceae	H	Glasshouse	SC	-	FS × SS	1.17	0.00	-	Webb & Littleton 1987
Leptinella atrata	Asteraceae	Gm	Glasshouse	SC	-	SS	0.97	-	-	Lloyd 1972
Leptinella minor	Asteraceae	Gm	Glasshouse	SC	-	SS	0.78	-	-	Lloyd 1972
Leptinella pectinata	Asteraceae	Gm	Glasshouse	PC	-	SS	0.40	-	-	Lloyd 1972
Mimulus repens	Scrophulariaceae	H	Glasshouse	SC	-	FS	0.85	0.15	-	Böcher & Philipp 1985
Myosotis brockiei	Boraginaceae	H	North-West Nelson	SC	M	SS	0.88	0.05	0.40	Brandon 2001
Myosotis colensoi	Boraginaceae	H	Castle Hill	SC[c]	-	SS	-	0.00	-	Robertson & Lloyd 1991
Myosotis forsteri	Boraginaceae	H	Central Otago	AF[c]	-	SS	-	0.87	-	Robertson & Lloyd 1991
			North-West Nelson	AS	L	SS	-	0.99	0.00	Brandon 2001
Myosotis laeta	Boraginaceae	H	Marlborough	SC	L	SS	1.03	0.02	0.22	Brandon 2001
Myosotis macrantha	Boraginaceae	H	North-West Nelson	SC	M	SS	0.91	0.05	0.38	Brandon 2001
Myosotis monroi	Boraginaceae	H	North-West Nelson	SC	M	SS	0.95	0.05	0.50	Brandon 2001
Myosotis sp. (2) aff. *australis*	Boraginaceae	H	Lyttelton Harbour	AF[c]	-	SS	-	0.89	-	Robertson & Lloyd 1991
Myosotis spathulata	Boraginaceae	H	Banks Peninsula	AF[c]	-	SS	-	1.01	-	Robertson & Lloyd 1991
Ourisia macrocarpa	Scrophulariaceae	H	Arthur's Pass	SC	-	FS	1.00	0.33	-	Schlessman 1986
Phormium tenax	Agavaceae	H	Tiri Tiri Matangi I.	SI	-	FS	0.05	-	-	Craig & Stewart 1988
Pleurophyllum criniferum	Asteraceae	H	Campbell Island	AS	L	SS	1.09	0.76	0.09	Nicholls 2000
Pleurophyllum speciosum	Asteraceae	Gm	Campbell Island	SI	L	SS	0.16	0.05	0.20	Nicholls 2000
Pterostylis alobula	Orchidaceae	H	Manawatu	PC	H	FS	0.77	0.00	0.94	Lehnebach 2002
Pterostylis patens	Orchidaceae	H	Manawatu	SC	M	FS	1.10	0.00	0.32	Lehnebach 2002
Thelymitra longifolia	Orchidaceae	H	Manawatu	AS	L	FS	0.85	0.96	0.07	Lehnebach 2002
Wahlenbergia albomarginata	Campanulaceae	H	Cass	SC[a]	-	FS	1.00	-	-	Lloyd & Yates 1982
Winika cunninghamii	Orchidaceae	H	Manawatu	PC	H	FS	0.50	0.00	0.70	Lehnebach & Robertson 2004

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[a] rate of autonomous selfing not measured.

[b] the results for this species are hard to explain, very high fruit set was found in emasculated plants and in open-pollinated plants, but hand-pollination with either hand-cross- or self-pollen yielded very little fruit hence the very high figures for ASI. For this reason, this species was not included in the analysis presented in Fig. 3 and Table 3, and despite the SCI score of 0.00, the species is regarded here as apomictic.

[c] autonomous selfing index calculated by bagged/open ratio.

self-incompatibility. Some families, e.g., Asteraceae, Rhamnaceae, Iridaceae, Solanaceae, are renowned for high rates of incompatibility (Kress & Beach 1994; Bianchi et al. 2000), while other families have generally lower values. This complicates comparisons among diverse floras. In New Zealand, very few members of some families have been tested where we might expect to find self-incompatibility, such as in the Asteraceae.

With so few New Zealand species tested for self-incompatibility and the bias that exists in families and life forms of the species that have been tested, it would be unwise at this stage to conclude that self-incompatibility in the flora is particularly low. Much more testing is required, particularly amongst the woody flora.

New Zealand's partially compatible and self-compatible species have low rates of autonomous selfing in comparison with the 10 geographical surveys that measured autonomous selfing (Table 4). Only the Venezuelan palm swamp (Ramirez & Brito 1990) and the Juan Fernandez Islands survey (Bernadello et al. 2001) showed lower rates of autonomous selfing. These three floras all have relatively low rates of incompatibility, and several of the floras that have high rates of self-incompatibility have very high rates of autonomous selfing in the self-compatible species, suggesting that other outbreeding mechanisms such as dichogamy and herkogamy tend to evolve in floras that have low numbers of incompatible species. The two exceptions to this general rule are the Galapagos Islands (McMullen 1987) and the monocots of the Venezuelan cloud forest (Ramirez & Seres 1994) where, in both cases, self-incompatibility levels are low while autonomously selfing rates are high, suggesting that pollinator dependence is low in these floras.

Reproductive assurance

There is little evidence to support the general notion that the New Zealand flora contains a large set of species that maintain self-compatibility to provide reproductive assurance as might be expected if pollinator service was unreliable. Despite having a relatively low level of self-incompatibility, there are relatively few species that regularly autonomously self in comparison with other floras (though again these conclusions are based on a relatively small set of data). Reproductive assurance will normally only be provided by autonomous selfing rather than through facilitated selfing (Lloyd & Schoen 1992). Nevertheless, there is clearly an element in the flora, particularly amongst the short-lived and small-stature herbs, that engages in autonomous selfing, e.g., *Epilobium* (Raven & Raven 1976), *Parahebe* (Garnock-Jones 1976), *Myosotis* (Robertson & Lloyd 1991), though in none of these genera is this uniformly the case; all contain pollinator-dependent species as well as regular selfers.

Mixed mating and inbreeding depression

The majority of the species in this survey are likely to experience mixed mating as a result of their breeding system. Partially and fully self-compatible species that are not autonomously selfing are almost always going to be fertilised by a mixture of self and outcross pollen since they have no barrier to geitonogamous or within-flower pollinator-facilitated

Table 2 Association between life form and breeding system for the populations of hermaphrodite species studied in Table 1. We present the average scores for each of the three indices of breeding system used for each life form (SCI, self-compatibility; ASI, autonomous selfing; PLI, pollen limitation) along with the number and percentage of populations falling into breeding system types within these life forms.

	Trees	Shrubs	Vines & mistletoes	Herbs	Total
Mean index					
SCI	0.33	0.25	0.84	0.81	0.64
ASI	0.13	0.05	0.68	0.32	0.36
PLI	0.65	0.44	0.35	0.41	0.42
No. of populations					
Apomictic or autonomously selfing	0 (0%)	0 (0%)	3 (43%)	7 (25%)	10 (21.3%)
Self-compatible (SCI > 0.8)	1 (20%)	1 (14%)	3 (43%)	15 (54%)	17 (42.6%)
Partially self-compatible (0.8 > SCI > 0.2)	1 (20%)	1 (14%)	1 (14%)	4 (14%)	7 (14.9%)
Self-incompatible (SCI < 0.2)	3 (60%)	5 (71%)	0 (0%)	2 (7%)	10 (21.3%)
Total	5	7	7	28	47

selfing (Crawford 1984; Geber 1985; Robertson 1992). Globally, studies of genetic markers show mixed mating in c. 30% of populations studied (Vogler & Kalisz 2001) despite theoretical predictions that mating strategies should be bimodal with two alternative successful strategies of either predominant outcrossing or predominant selfing. Theory suggests that mixed mating should make plants prone to inbreeding depression that reduces the fitness of the offspring resulting from selfing, while in regular selfers the genetic load that produces inbreeding depression should be purged by regular inbreeding (Lande & Schemske 1985; Charlesworth & Charlesworth 1987).

Table 3 GLM (with Gaussian distribution) of the effect of self-compatibility (SCI) and autonomous selfing (ASI) on pollen limitation index (PLI) for the populations in Table 1 where all three parameters had been scored.

	d.f.	Deviance	*F*	*P*
SCI	1	0.057	0.96	0.341
ASI	1	0.714	11.92	0.003
Residual	17	1.017		

There have been only two studies on New Zealand plants that have used markers to estimate selfing rates in natural populations. Barrell et al. (1997) used microsatellites and paternity analysis to show high rates of autogamy amongst the seedlings from one adult tree of *Vitex lucens*, a species that has been shown to be self-compatible (Table 1). Schmidt-Adam et al. (2000) used multilocus allozyme analysis to show

Table 4 **Percentage** of self-incompatibility (SCI < 0.2) (% SI) and autonomously selfing (ASI > 0.5) (% AS), self-compatible or partially compatible species in surveys of hermaphroditic herbs and woody plants in different regional floras. *n*, number of species/populations tested.

	Herbaceous		Woody		Overall			
Flora	% SI	*n*	% SI	*n*	% SI	*n*	% AS	Reference
Oceanic islands								
New Zealand	7	28	42	19	21	47	21	This study
Juan Fernandez Islands	0	4	14	14	11	18	19	Bernadello et al. 2001
Galapagos Islands					2[a]	51	63	McMullen 1987
Temperate								
Alpine meadow, Chile	27	116	71	7	29	123	74	Arroyo & Squeo 1990
Subalpine meadow, Canada	36	42			36	42		Pojar 1974
Boreal forest, Canada	27	11			27	11	38	Barrett & Helenurm 1987
Sphagnum bog, Canada	22	32			22	32		Pojar 1974
Saltmarsh, Canada	24	17			24	17		Pojar 1974
Sclerophyll montane scrub, Chile	31	32	80	5	38	37	59	Arroyo & Uslar 1993
Chaco woodland, Argentina			83	6	83	6		Bianchi et al. 2000
Chaco woodland, Argentina	33	12	54	13	44	25	67	Morales & Galetto 2003
Tropical								
Lowland rainforest, Costa Rica	34[b]	38	84	19	51	57		Kress & Beach 1994
Semideciduous forest, Costa Rica			79	34	79	34		Bawa 1974
Deciduous forest, Venezuela	21[c]	24	84	25	53	49	60	Jaimes & Ramirez 1999
Montane cloud forest, Venezuela	43	14	38	13	41	27	44	Sobrevila & Arroyo 1982
Montane cloud forest, Venezuela	4[d]	23			4	23	46	Ramirez & Seres 1994
Palm swamp, Venezuela	14	21	40	5	19	26	0	Ramirez & Brito 1990
Deciduous forest, Mexico			76	33	76	33		Bullock 1985
Savanna, Brazil			83	30	83	30		Oliveira & Gibbs 2000
Overall	25	414	70	264	43	678	53	

[a] does not indicate life form for each species, so we present just the overall mean.

[b] compares canopy (which we have assumed are trees) with lower stratum (which we have assigned to herbs, but may contain both woody and non-woody species).

[c] this study distinguishes between SI and SC on the basis on whether seed production differs significantly in the self- versus cross-pollinations rather than using SCI categories.

[d] includes only monocots.

that outcrossing rates averaged around 40–50% in five populations of pohutukawa (*Metrosideros excelsa*). Two lines of evidence suggested that inbreeding depression filters and eliminates the selfed offspring before they mature in these trees: Wright's Fixation index (a measure of homozygosity that is correlated with inbreeding) was consistently higher for progeny than for maternal parents, and seedling growth rates of potted plants were significantly less for selfed seed than for outcrossed.

Inbreeding depression and self-incompatibility both result in the elimination of selfed progeny by screening the incoming genotypes brought by pollen vectors and are, thus, logically related. Conventional sporophytic and gametophytic self-incompatibility act by screening and blocking self pollen grains as they germinate on the stigma or as the pollen tubes grow down the style. Late-acting self-incompatibility occurs after the tube enters the ovary and before fertilisation (this is what happens in *Pseudowintera colorata* (Lloyd & Wells 1992)) but the attrition may also happen post-fertilisation by aborting selfed embryos or fruits and, thus, late-acting self-incompatibility grades into inbreeding depression (Wiens et al. 1987). The fate of selfed seed may depend on the context of competing seeds on other flowers and in some plants mixed-mating progeny may be screened by cryptic self-incompatibility (Bateman 1956). This is well illustrated by the New Zealand flax *Phormium tenax*. Craig & Stewart (1988) showed that self-pollinated pods on Tiri Tiri Matangi Island (NE of Auckland) were aborted much more commonly than those that were crossed. However, Becerra & Lloyd (1992) conducted hand-pollination experiments and showed that if selfed and crossed flowers were segregated on different flowering stalks, selfed pods were likely to be retained, but as the proximity of competing outcrossed pods was increased, self pods were much more prone to abortion. This kind of system allows flexibility and can span a range of mating types from fully selfing if no outcross pollen is deposited, to fully outcrossing if sufficient outcross pollen is available within inflorescences.

A similar picture of mixed mating and inbreeding depression has been suggested to maintain gynodioecy in several species of *Hebe*. Delph & Lloyd (1996) reported inbreeding depression in progeny from hermaphrodite *Hebe subalpina* leading to weak seedlings compared with those derived from outcrossing. Geitonogamous selfing in the hermaphrodites is highly likely, and the effect of inbreeding on the progeny from these plants is suggested to confer an advantage to the obligately outcrossed seeds derived from females. Robertson et al. (unpubl. data) have also found very high levels of inbreeding depression in the gynodioecious *Fuchsia excorticata*.

Pollen and seed limitation

Moderate to high pollen limitation of seed production has been found in 21 of the 33 populations examined in Table 1. In some cases, seed production from open pollination was less than 10% of that achieved by hand-pollination, suggesting that pollinators frequently fail to supply adequate pollination service. For some plants, this may not be unexpected; for instance, orchids regularly have very low capsule set but compensate by producing thousands of tiny seeds per capsule (Nilsson 1992). Low fruit-to-flower ratios may be a normal part of several alternative plant strategies to maximise male fitness from the excess flowers; to allow a bet-hedging strategy that maximises fruit set when pollinator service is unreliable; or to allow selective abortion of low-quality fruit (Sutherland 1986; Zimmerman & Pyke 1988; Primack & Hall 1990; Burd 1994). However, it is recognised that pollination failure frequently exceeds the capacity of plants to compensate for the loss of potential seed (Wilcock & Neiland 2002).

In New Zealand, strong pollen limitation has been found in populations of several bird-pollinated species (Robertson et al. 1999; Kelly et al. 2000, 2004; Montgomery et al. 2001, 2003; Molloy 2004). Recent work has attempted to identify the ecological correlates of pollen limitation within and between populations in these species. In New Zealand, mainland-offshore island comparisons of fruit and seed production in these species are expected to show better service on the islands compared with the mainland because of the loss of honeyeaters over much of the New Zealand mainland. In *Rhabdothamnus solandri*, two recent studies that compared mainland to island showed high levels of pollen limitation on the mainland and none on the Lady Alice or Little Barrier islands where honeyeaters numbers remain high (Molloy 2004; Anderson et al. unpubl. data; see Table 1).

Studies on the bird-pollinated mistletoe *Peraxilla tetrapetala* have shown repeated pollen limitation at several sites on the New Zealand mainland (Robertson et al. 1999; Kelly et al. 2004). Within sites, however, the levels of pollen limitation appear to be less severe on the edges of forest patches than in the interior (Kelly et al. 2000). Hand-pollinations confirm that interior plants are limited by pollen supply and not by the resources needed to mature the fruit. Moreover, observations of the plants showed that visitation rates to plants by birds are greater on edge plants than in interior plants (Montgomery et al. 2003). It appears, therefore, that these plants may be tolerant of some degree of forest fragmentation and take advantage of the increased edginess that it creates.

Brandon (2001) has shown that at a very local scale, the density of conspecific flower shoots strongly influences the seed production of several pollen-limited *Myosotis* spp., presumably due to some change in the nature of the plant–pollinator interactions. Here, even a modest loss of reproductive individuals from the population could lead to a reduction in population viability. Should the plant density decrease, seed supply will diminish at an accelerating rate because of the combined effects of the loss of plants and the reduced seed set of the plants that remain.

A potential difficulty in the interpretation of these kinds of pollen-limitation studies is in understanding the demographic consequences and whether there is evidence of seed limitation (Crawley 1990; Bond 1994). It is possible that although seed production is reduced by pollen supply, sufficient remains to perpetuate the population, and that reduction in seed output simply reduces the amount of density-dependent thinning that occurs post establishment. Seed-sowing experiments where natural local seed production is augmented by extra seed can help establish the case for seed-limitation (Turnbull et al. 2000). Molloy (2004) conducted seed-sowing experiments with *Rhabdothamnus* on the mainland in plots monitored for 18 months, and documented increased seedling densities where extra seeds were sown. Ladley et al. (unpubl. data) have also shown that where *P. tetrapetala* seeds were sown in clumps and at varying distances apart, the chance of seedling establishment and growth was unaffected by proximity of neighbours (a requirement to show seed limitation), and success may even be enhanced by being part of a dense clump as the viscin that allows the seed to adhere to the branch is more effective when in small groups rather than as isolated individual seeds.

It seems likely that in most of these cases, limited pollen supply leads to a reduction in seed supply and in turn compromises the regenerative potential of the population. The challenge in these cases is to restore mutualism services through management of the ecosystem to maintain pollination systems (Kelly et al. 2005).

PLANT–POLLINATOR INTERACTIONS

The role of pollination in governing plant mating patterns and the various pollination requirements that different breeding systems impose on plants link the evolution of pollination and mating systems (Lloyd & Barrett 1996) and influence conservation and restoration efforts. Recent research on pollination systems has focused on how the mechanics of pollen dispersal (based on floral biology, proximate ecological factors, and plant sexual systems) combine to influence the realised mating patterns in plant populations (Lloyd & Barrett 1996). However, as we have seen, there are insufficient mating system data to understand how these aspects combine in New Zealand plants. The pollination systems of most New Zealand plants are also too poorly known, which hampers our ability to identify species that are vulnerable to pollination disruption. However, some progress may be possible by inferring the likely effectiveness of candidate pollinators from pollination syndromes and blossom classes.

Syndrome concept

In the absence of field data, the syndrome concept is often used to predict the nature of pollination systems but current debate about the validity of the syndrome concept indicates that it may not be relevant for New Zealand. Armbruster et al. (2000) and Fenster et al. (2004) defined a pollination syndrome as a suite of floral traits and rewards that are associated with the attraction of specific types of pollinators. They specify that a syndrome's "origin and/or maintenance reflects selective pressures imposed by certain groups of similar visitors (past or present)" (Armbruster et al. 2000). The hypothesis that generalisation predominates in New Zealand suggests that syndromes are not strong here and that New Zealand plants can often effectively utilise a large proportion of the local flower visiting assemblage (Thomson 1927; Heine 1937; Dugdale 1975; Godley 1979; Lloyd 1985; Webb & Kelly 1993). This implies that there is little precision or exclusiveness on the part of either plants or pollinators, with few morphological or advertising differences in co-occurring flowers. It also implies that different flower visitors vary little in their effectiveness and therefore impose little selection on plants to exclude ineffective visitors which can give rise to distinctive syndromes.

However, pollination syndromes in New Zealand have not been examined. The classical syndromes reflect the history of pollination studies that originated primarily in the Northern Hemisphere, where most of the detailed investigations have taken place.

Many authors have documented strong associations between floral and pollinator traits for the syndromes (e.g., Baker & Hurd 1968; Faegri & van der Pijl 1979; Proctor et al. 1996). These syndromes are often organised into tables of associated traits, e.g., the "harmonic relationships" (Table 5). However, for the Southern Hemisphere and parts of the tropics, new plant–pollinator interactions are still being discovered, e.g., pollen carried on bird's tongues (Pauw 1998) and feet (Johnson & Brown 2004), by cockroaches (Nagamitsu & Inoue 1997), and by lizards (Olesen & Valido 2003). New syndromes are being described such as thrips pollination (Proctor et al. 1996) and small beetle pollination (Armstrong & Irvine 1989). In addition, examples of unusual pollinators such as long-tongued flies (see Barth 1985) have shown high levels of specialisation in South Africa (Johnson & Steiner 1995; Goldblatt & Manning 1999).

Since the most obvious syndromes are the most highly specialised, the syndrome concept is inextricably interwoven with our understanding of specialisation (reviewed by Johnson & Steiner (2000), Olesen (2000), and Armbruster (unpubl.)). Authors differ in what they mean by a specialist pollination system (Wilson & Thomson 1996; Armbruster et al. 2000; Johnson & Steiner 2000) so comparing plant populations, species, communities, or floras is difficult. Because the issues are both semantics and scale, concepts of syndromes and specialisation, like the species concept, are not easily defined or utilised by biologists. Such concepts always have inherent cognitive/linguistic issues because organising the diverse products of evolution (organisms or interactions) into categories based on multiple criteria inevitably leads to incongruence especially when high-resolution data at broad spatial or temporal scales are obtained. The problem is exacerbated when these categories are used as fundamental units for inferring evolutionary history (Hey et al. 2003).

The syndrome concept has recently been criticised as a typological oversimplification (e.g., Ollerton 1996, 1998; Waser et al. 1996; Waser 2001). Authors have frequently challenged the paradigm that diversity in floral forms reflects the diversity of natural selection by specific groups of pollinators (see discussions in Armbruster et al. (2000) and Wilson & Thomson (1996)). Ollerton (1996) presented the paradox "that the evolution of floral diversity seems to be based upon specialised relationships with pollinators, yet (with some obvious exceptions) the majority of angiosperms appear to be promiscuously pollinated by a range of taxa". Pollinator spectra for many plant species range across orders of insects (beetles, flies, bees, butterflies, and moths), classes of animals (insects, birds, mammals) (Herrera 1996; Ollerton 1996, 1998; Waser et al. 1996; Waser 1998, 2001), and pollination agents (wind, animal) (Culley et al. 2002). Field studies of spatio-temporal variation often show that some classical pollination syndromes may not be so specialised (e.g., Herrera 1987, 1988, 1989, 1996). It is argued that generalised pollination systems are much more common than specialised systems and that selection should favour generalisation whenever pollinator populations are variable (see Herrera 1996; Waser et al. 1996; Ollerton 1998; Waser 1998, 2001; Johnson & Steiner 2000; Kay & Schemske 2004).

Despite these criticisms, many authors maintain that the syndrome concept is still useful (e.g., Armbruster et al. 2000; Johnson & Steiner 2000; Thomson et al. 2000; Pellmyr 2002; Fenster et al. 2004). At the very least, it forms the basis for testable

Table 5 Blossom classes associated with classical pollination syndromes, adapted from Faegri & van der Pijl (1979, fig. 4, p. 97). Each pollinator group represents a syndrome that is associated with certain blossom classes (dish/bowl, bell/beaker, brush, gullet, flag, and tube) visited by that pollinator. Bees visit all types of blossoms but bats and other groups are more restricted. Lizards and large non-flying animals were not included in the original classical syndromes.

	Dish/bowl	Bell/beaker	Brush	Gullet	Flag	Tube
Beetles	●					
Wasps	●	●				
Flies	●	●				
Bats	●	●	●			
Bees		●	●	●	●	●
Moths			●	●		●
Butterflies			●	●	●	●
Birds			●	●	●	●

predictions (Pellmyr 2002) that can be formalised into "systematic rules" (Thomson et al. 2000) and these show strong associations in many cases (e.g., Wilson et al. 2004). Discussions of the concept have shown that unrealistic expectations of how it is to be used have contributed to the debate but also the conceptual framework needs modification and updating. For example, Armbruster et al. (2000) and Fenster et al. (2004) advocate distinguishing between *evolutionary specialisation* and *ecological specialisation* to alleviate some of the confusion. They use a simple operational definition of specialisation: "successful pollination by a relatively small proportion or sub-set of the available flower-visiting fauna". Evolutionary specialisation is the *process* of evolving toward greater specialisation in response to selection generated by pollinators; ecological specialisation is the *state* of being specialised, i.e., having only a few similar species of pollinators in contemporary time.

They also advocate that syndromes be defined by functional groups rather than by taxonomic groups. One of the strongest objections to the syndrome concept, which is partly defined at the level of insect orders, is that insects from many different orders commonly visit the same plant species (Herrera 1996; Ollerton 1996; Waser et al. 1996). Indeed, Faegri & van der Pijl (1979) noted little difference between pollination by a bee fly and similar-sized bees and there is striking similarity among long tongued flies, bees, and moths (see Barth 1985, fig. 30). Armbruster et al. (2000) and Fenster et al. (2004), therefore, proposed basing syndromes on functional groups of pollinators with similar size, morphology, and behaviour and similarity of selective pressure exserted on flowers. These functional groups can be described at several different scales. For example, Frankie et al. (1983, 2004) have distinguished between large and small bee syndromes in the tropical dry forest of Costa Rica and Vinson et al. (2004) described several functional groups of bees. Organising data by functional groups facilitates comparisons of pollination systems at the community level (e.g., Frankie et al. 2004). Community comparisons which have often been based on taxonomic diversity (number of plant species matched to number of pollinator species as used in connectance indices or food webs) could incorporate functional groups to add more meaningful structure to the analyses (see Jordano 1987; Memmot 1999; Dicks et al. 2002; Memmot & Waser 2002; Olesen & Jordano 2002; Kay & Schemske 2004).

These two proposed modifications of the syndrome concept (i.e., differentiating evolutionary from ecological specialisation and defining syndromes by functional groups) do not entirely resolve the problem. There are still difficulties in using the term specialisation. It is well recognised that specialisation and generalisation are opposing endpoints on a continuum (Johnson & Steiner 2000), from extreme specialisation (e.g., fig species exclusively serviced by only one fig wasp species) to extreme generalisation (e.g., sturdy brush inflorescences pollinated by mammals, birds, and insects). Communicating intermediate levels of specialisation for pollination, however, remains an unresolved problem for two reasons.

The first is semantic. Determining intermediate levels of specialisation from the plant's perspective requires differentiating effective pollinators from floral visitors (Armbruster et al. 2000; Fenster et al. 2004). Specialisation is achieved by several different mechanisms involving the type or timing of rewards, signals, attractants, or deterrents (reviewed by Armbruster (unpubl.)). Moreover, pollinator importance depends not only on effectiveness in transferring a large amount of high quality pollen but also on the abundance and visiting rate of pollinators (Herrera 1987, 1989). The most abundant pollinator may not be the most effective and the most effective pollinator may not be the strongest selective agent influencing key floral traits (e.g., Schemske 1983; Armbruster unpubl.).

Furthermore, when effectiveness is measured in terms of the amount of pollen picked up and deposited or wasted (according to the principles of pollen presentation theory) it is clear that the composition of the pollinator assemblage profoundly influences effectiveness ranking (Thomson 2003). A pollinator may be an important mutualist in one milieu, but in another milieu it may be a relative parasite (e.g., if it wastes pollen that could have been transferred by a more effective pollinator) (Thomson 2003). In addition, pollinator choices are context sensitive because they are influenced by competing floral resources and pollinators that are available in the community. In modified habitats, disrupted plant–pollinator relationships could be difficult to interpret with respect to specialisation.

The second reason that specialisation is difficult to communicate is the issue of scale. A system for referring to intermediate levels of specialisation at different scales is still lacking (Dupont & Skov 2004). Although specialisation can be scaled to class, order, family, genus, or species, the term is generally used without explicit reference to scale and often no distinction between plant and pollinator perspectives. The asymmetry of specialisation between plants and pollinators is well known; for instance, bees that specialise on Asteraceae genera or species occur in North America, but these same plant taxa are not necessarily specialised to any particular pollinator (Schemske 1983). Thus, reporting specialisation at mixed scales and perspectives to compare populations, species, communities, or floras has produced confusing results.

These semantic and scale issues in understanding specialisation highlight the need for sufficient field observations and experiments (Pellmyr 2002). Full community analyses are recommended (Jordano 1987; Waser et al. 1996; Armbruster et al. 2000), such as the extensive surveys by Momose et al. (1998) and Frankie et al. (2004). Most importantly, incomplete data on visitors (diurnal and nocturnal), inadequate assessment of pollinator effectiveness, or insufficient temporal and spatial replication can lead to wrong conclusions about specialisation and, hence, pollinator syndromes (Herrera 1996; Waser et al. 1996; Momose et al. 1998). Even with sufficient data, however, the validity of the syndrome concept cannot be fully clarified until communication issues for specialisation are resolved. Thus, the syndrome concept, as it is currently defined and used, appears to be a reliable predictor of pollinators primarily for highly specialised systems, which are obvious. In the case of intermediate levels of specialisation, or systems with high levels of spatial and temporal variability, we need a simpler, more concrete, and context-independent method for predicting plant–pollinator interactions, such as the blossom class concept.

Blossom class concept

Blossom classes

The blossom class concept has received less attention but it is a basic part of the syndrome concept and much used by floral biologists (Weberling 1989; Endress 1994). A blossom refers to an inflorescence, a flower, or a part of a flower that acts as the fundamental functional unit in pollination (Faegri & van der Pijl 1979). Blossom classes are immensely important in understanding the evolutionary ecology of pollination because they differentiate floral units in terms of the pollinator's approach and access to rewards, thus providing a strong predictive tool (D. G. Lloyd pers. comm.). The blossom class indicates the morphological shape and physical features of both the flower and inflorescence but does not include floral traits such as colour, scent, or other attractants or deterrents that are part of the syndrome concept.

If the syndrome concept has any predictive value, the inclusion of these additional floral traits should improve predictions based on blossom class alone. However, some floral traits such as colour and scent are not always reliable predictors (Proctor et al. 1996; Momose et al. 1998; Raguso 2001; Pellmyr 2002; Fenster et al. 2004) because their influence on floral preferences is context dependent. Pollinators can be trained to change their preferences in response to reward levels. For example, if an alien pollinator lacks its chief blossom in a new area, it will forage and train to whatever plant species it can detect and use, regardless of colour, scent, or time of day. Similarly, plant species will survive service by inferior pollinators so long as sufficient pollen is successfully transferred, regardless of the precision of the transfer process. This means that predictions in modified habitats with absent indigenous or added exotic pollinators and plants require community-level analyses at several sites.

Blossom class alone can provide a simple logic for making predictions about pollinator exclusion (see Faegri & van der Pijl 1979; Weberling 1989; Proctor et al. 1996). The fit or match of the visitor (potential pollinator) to the shape and size of the blossom is readily observed and context independent. Precision mechanisms such as herkogamy, dichogamy, and heterostyly (Barrett 2002), or floral traits such as colour, scent, visual or olfactory nectar guides, and timing of rewards, etc., do increase the effectiveness of pollination and perhaps drive evolutionary changes but they do not physically exclude visitors or inefficient pollinators. The key question is do we need these additional floral traits of the syndrome concept to improve first-level predictions based on blossom class alone? For example, if a completely accessible blossom has a restricted subset of visitors, can we ask the question: do other floral traits (e.g., those governing detection or attraction) better explain the specialisation (given all suitable pollinators are present)? Or is the apparent specialisation an artefact of missing pollinators due to habitat modification? This two-tiered approach, firstly using blossom class to predict exclusions and then using syndrome traits to analyse detection and attraction in a community context, contrasts with a one-tiered approach using multivariate analyses of all floral traits simultaneously (Ollerton & Watts 2000).

To analyse this question, we have constructed a matrix of blossom classes associated with functional groups. The associations are based on physical exclusion of floral visitors or pollinators according to three criteria:

1. Access to rewards (or exclusion)
2. Available landing facilities (e.g., perches)
3. Protection of ovules (e.g., damage by beaks)

We have listed a sequence of blossoms classes relevant to the New Zealand flora by combining information from Faegri & van der Pijl (1979), Weberling (1989), Endress (1994), Brown & Hopkins (1995), Proctor et al. (1996), Momose et al. (1998), Bernadello et al. (2001), and Ramirez (2003). The blossom classes are grouped into three main series: open-, directed-, and closed-access (Endress 1994). Blossom classes that are most important for New Zealand are listed here in order of most to least accessible within each of the three access series.

Open-access

1. Aggregation of brush or tubular flowers with strongly exserted anthers (e.g., Fig. 4A,B)
2. Aggregation of dish/bowl/"knob" flowers or inconspicuous flowers (e.g., Fig. 4C)
3. Aggregation of short tubular florets in a capitula (e.g., Fig. 4D)
4. Brush/fluffy cup flowers (not illustrated but see single flowers of Fig. 4B)
5. Dish/bowl/"knob" flowers (e.g., Fig. 4E,F,I, 6A)
6. Inconspicuous flowers (shape ignored because too small) (e.g., Fig. 4G,H)

Directed-access

1. Bell/funnel flowers (wide tubes) (e.g., Fig. 5A)
2. Gullet/lip flowers (e.g., Fig. 5B)
3. Medium to large tubular flowers (e.g., Fig. 5C, D, F) including some flag flowers (e.g., Fig. 5E)
4. Trumpet/salverform narrow-tubed flowers (e.g., Fig. 2H)
5. Spurred flowers (not illustrated)

Closed-access

1. Trap flowers (e.g., closed-access orchid in Fig. 6B cf. open-access orchid in Fig. 6A)
2. Complex flowers (e.g., flag (Fig. 6C), personate, or G*revillea*-type)
3. Pollen flowers with poricidal anthers (e.g., Fig. 6E–H)
4. Explosive bud flowers (e.g., mistletoe species) (e.g., Fig. 6D)
5. Syconia (figs with florets enclosed inside) (not illustrated but see Gardner & Early (1996)).

The matrix associating these blossom classes with functional groups of floral visitors or pollinators is illustrated in Table 6. This matrix does not predict contemporary pollinator frequency, effectiveness, or importance; nor does it necessarily distinguish pollinators from visitors. In other words, a cell in the matrix may not portray the most highly adapted pairing possible but it does illustrate that an interaction can occur.

In the open-access blossom classes, we consider aggregated flowers to be the most accessible blossoms because they provide broad landing facilities that permit more visitor and pollinator groups than would a single flower of the same type. They also provide accessible nectar or pollen rewards that are more efficient to extract compared with single flowers sparsely located on the plant. For example, sturdy aggregated brush blossoms, common in the Southern Hemisphere, are accessible to (and withstand damage from) diverse floral visitors from a range of sizes such as insects, birds, bats, lizards, and non-flying mammals. These brush blossoms are the most generalised of all blossom types.

In the open-access group, several blossom classes are distinctive, especially in the Southern Hemisphere. We have distinguished "fluffy cup" flowers (Brown & Hopkins 1995), which are a type of brush flower because the protruding fringe of stamens is the attractant rather than petals. These are often aggregated into a brush inflorescence. However, the term brush inflorescence has also been used for aggregated small tubular flowers with prominent exserted anthers such as in *Hebe* (Fig. 7A) and in *Myosotis* (Fig. 2B). We include "knob" blossoms (Brown & Hopkins 1995) in the dish/bowl category because this type of flower (e.g., *Schefflera*, Araliaceae) may be significant for perching bird pollination in the Southern Hemisphere (see below). We also include the "inconspicuous" blossom class to refer to single flowers too small (< 3 mm) for shape to be important (Faegri & van der Pijl 1979; Bernadello et al. 2001). However, clustered inconspicuous flowers (the "tiny clusters" type of Brown & Hopkins (1995)) are placed in the aggregated dish/bowl/"knob" blossom class because their combination into a dense inflorescence contributes to their visual detection, landing facilities, and reward access.

In the directed- and closed-access group, we follow Endress (1994) and Proctor et al. (1996) by considering "spurred flowers" with elongate nectar spurs and "pollen flowers" with poricidal anthers

(Fig. 6E–H) to be distinct blossom classes. In the complex flower category, we have grouped closed flowers with (1) flag (e.g., pea flowers with standard, wings, and keel, Fig. 6C), (2) personate (e.g., snapdragons), and (3) *Grevillea* types of construction, but there are other types. These flowers require manipulation and usually some strength on the part of the pollinators to open the flower to access the reward. Trap blossoms are an extremely diverse group worldwide but we focus only on those that are common in New Zealand such as some orchids that are at least partially closed (Fig. 6B; see discussion below). "Explosive bud" flowers are an unusual blossom class that requires pollinators to open the bud (Fig. 6D; see mistletoes below). The "bursting open" blossom class reported by Momose et al. (1998) probably belongs in this explosive bud category.

Underpinning the "blossom class – functional group" analysis is the general principle that the relative sizes of the blossom and visitor must be suitable for a good match, but this is not explicit in the matrix (see Bernadello et al. (2001) for an analysis of 152 plant species incorporating size explicitly). Size is an overriding factor because, regardless of shape, large visitors or pollinators are unlikely to visit very small flowers but small visitors or pollinators readily access large flowers, e.g., in the Costa Rican dry forest, bees tend to visit some large bat flowers but bats do not visit small bee flowers (G. W. Frankie pers. comm.). Large visitors would not prefer small flowers if the reward was energetically too expensive to extract; however, they may visit small flowers aggregated into compact inflorescences (e.g., Castro & Robertson 1997). In addition, large visitors may need to expand their range to include small flowers if visitor densities are too high (Rasch & Craig 1988; Castro & Robertson 1997; see bird pollination below). Small visitors on large flowers usually do not contact stigmas or anthers unless they specifically forage on these organs. In any case, they are unlikely to be effective pollinators because they would carry much less pollen than a well-matched large visitor. Size relationships, thus, complicate a simple analysis of blossom classes. For example, a bell flower is similar to a tubular flower but appears to be distinguished in the syndromes of Faegri & van der Pijl (1979) based on whether or not the pollinator can crawl into the flower rather than on the length-to-width ratio. The width of the opening is a critical factor in restricting access as illustrated in *Myosotis* (Fig. 2).

Predicting visitors or pollinators based on blossom class alone is further complicated because access to pollen and nectar can be at different levels, such as in tubular flowers with exserted anthers. In this type of flower, birds may contact stigma and anthers simultaneously while taking nectar; but insects, if unable to access nectar at the bottom of the tube, may forage only on the exposed pollen at the entrance to the tube. For simplicity, we arbitrarily prioritise access to nectar over pollen when both are presented. Thus, the matrix does not account for interactions based on visitors seeking only pollen while ignoring less accessible nectar.

At a coarse scale, associations between blossoms and pollinator functional groups (e.g., insect, bird, and bat) can provide insights for predicting disruptions in indigenous pollination systems when exotic pollinators are introduced. Clearly, we expect open-access blossoms to show no exclusion unless the visitor is so big that it cannot land or so ineffective that it destroys the flowers while foraging. Apart from this consideration, if any specialised visitation does occur, then syndrome traits may explain the exclusion (e.g., detection by scent or attraction

Fig. 4 Open-access blossoms in the New Zealand indigenous flora. **A**, *Weinmannia racemosa* (Cunoniaceae), brush blossom (raceme 60 mm long.) with aggregation of flowers (petals 2–3 mm long with stamens exserted). Visited by birds and insects (Photo Alastair Robertson); **B**, *Metrosideros umbellata* (Myrtaceae), aggregation of brush flowers (petals c. 5 mm long and stamens c. 2 cm long). Visited by small insects, birds, bats, and lizards (Photo Ilse Breitwieser); **C**, *Gingidia* sp. (Apiaceae), aggregated open flowers (Photo Chris Morse); **D**, *Anaphalioides bellidioides* (Asteraceae), a capitula of disc and ray florets (Photo Chris Morse); **E**, *Pseudowintera colorata* (Winteraceae), open dish flower, primitive features with stigma sessile on carpel, (petals 4–5 mm long). Visited by diverse small insects, stigma exudate taken by flies and beetles (Photo John Lovis); **F**, *Corokia macrocarpa* (Cornaceae), open dish flowers (up to 1 cm in diam.) (Photo Chris Morse); **G**, *Ascarina lucida* (Chloranthaceae), minute inconspicuous flower with no petals. Shape is not important in flowers this small, visitors unknown (Photo John Lovis); **H**, Close-up of *Ascarina lucida*. Arrow points to sessile ovary with broad sessile stigma, to the right is the sessile cylindrical 2-celled anther (c. 2.5 mm long). (Photo John Lovis); **I**, *Donatia novae-zelandiae* (Donatiaceae), small flowers embedded in matted cushion of leaves. Flower 10 mm diam. with petals 2–3 mm long. Visited by flies, mainly tachinids (Photo John Lovis).

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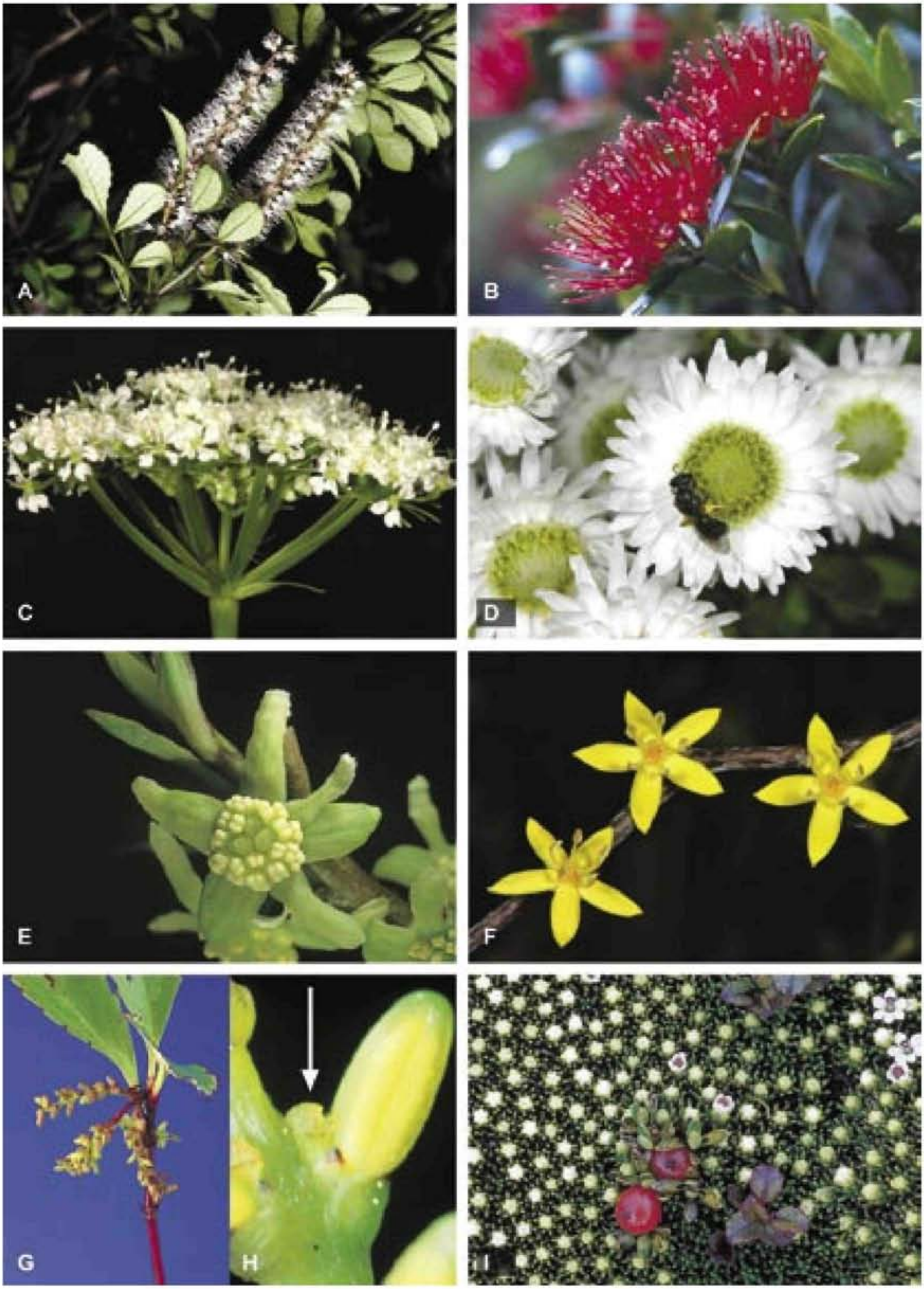
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by speciality rewards). Lindsey & Bell (1985) and Webb (1994) called this type of restricted visitation to an open-access blossom, *cryptic specialisation.*

In directed-access blossoms, exclusion is most noticeably related to body size and tongue length. For example, large visitors can gain access to deep nectar resources only if their tongues are long enough. Directed-access blossoms are vulnerable to nectar robbery (e.g., birds or insects piercing flowers at the base of the tube), which is an important feature in understanding the potential effects of exotic pollinators on indigenous flowers.

In closed-access blossoms, entry is restricted to only a few visitor or pollinator groups based on physical exclusion alone, unless some form of cryptic specialisation is also operating. Closed-access blossoms show the clearest associations between plant and pollinator and are not likely to change among regions or over time, e.g., large bees to exotic flag flowers, fig wasps to fig syconia. Some of these may be considered *absolute specialisations* and would be vulnerable in the absence of their pollinators. However, such blossom classes are uncommon in the indigenous flora of New Zealand, but they do occur in the naturalised and weedy flora (see invasive mutualisms below).

PLANT–POLLINATOR ASSOCIATIONS IN NEW ZEALAND

Blossoms classes in New Zealand

This "blossom class–functional group" matrix (Table 6) is preliminary and should be viewed as a first approximation only but it does build on the blossom class analyses by Godley (1979) and Lloyd (1985) for New Zealand pollination systems. The New Zealand indigenous flora has a low diversity of blossom classes and they are not evenly represented. The majority of indigenous plants have open-access blossoms (mainly dish flowers) or directed-access blossoms (mainly tubular flowers) (Lloyd 1985). Aggregation into compact inflorescences is extremely common (Lloyd 1985). Some directed-access blossoms (e.g., particularly gullet, lip, and salverform) are less frequent, spurred flowers are rare, and closed-access blossoms uncommon. Several books illustrating New Zealand flowers confirm these trends (e.g., Salmon 1963, 1991; Eagle 1978; Moore & Irwin 1978; Webb et al. 1990; Mark & Adams 1995).

On the other hand, Lloyd (1985) found that the few genera with directed- or closed-access blossoms typically had low species diversity suggesting little radiation involving pollinator selection. He cited examples of New Zealand species shared with Australia that have relatively complex zygomorphic flowers, and which are represented by only one or a few species with restricted distributions: *Mimulus* (Scrophulariaceae), *Utricularia* (Lentibulariaceae), *Chiloglottis* and *Cryptostylis* (both Orchidaceae). Of the 15 largest genera in New Zealand, only one has a complex zygomorphic flower, *Carmichaelia* (Fabaceae), with flag blossoms (Lloyd 1985). Another large genus, *Myosotis* (Boraginaceae), is also unusual because it has considerable diversity in blossom classes including salverform flowers, which are very uncommon (Fig. 2, and see below). Examples of the very few genera with spurred flowers are *Utricularia* and *Viola* (Violaceae). Interestingly, the largest animal-pollinated genus in the monocotyledons, *Pterostylis* (Orchidaceae, Fig. 6B), has a closed-access trap blossom (Lloyd 1985). Compared with other monocotyledon families, Orchidaceae is well known for specialisation of highly complex flowers leading to frequent speciation (e.g., Gravendeel et al. 2004).

The New Zealand genera that do have high species diversity tend to have open-access blossoms, or, if directed-access, then simple tubular shapes. Of the plant groups derived from Australia that have successfully radiated here, most have dish or tubular flowers, mainly actinomorphic or weakly

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Fig. 5 Directed-access blossoms in the New Zealand indigenous flora. **A**, *Wahlenbergia mathewsii* (Campanulaceae), bell flower. Flowers 2–3 cm diam. with corolla tube 8 mm long. Visited by small bees, flies and other insects (Photo Robert Uschold); **B**, *Vitex lucens* (Verbenaceae), gullet flower. Corolla 2-lipped c. 2.5–3.5 cm long. Visited primarily by birds (Photo Linda Newstrom); **C**, *Dysoxylum spectabile* (Meliaceae), short tubular (10 mm or more long) waxy flower. Visited by honeyeaters, silvereyes, and moths (Photo Robert Uschold); **D**, *Alseuosmia macrophylla* (Alseuosmiaceae) has long (35 mm), red-coloured tubes with copious nectar but also has a strong scent so may be pollinated by both insects and birds (Photo Alastair Robertson); **E**, *Sophora microphylla* (Fabaceae), polypetalous tubular flower (up to 4.5 cm long) with flag construction, showing pollination by tui, the most effective and frequent visitor when present (Photo Robert Uschold); **F**, *Phormium tenax* (Agavaceae) tubular flower (50 mm long) with copious nectar, visited by honeyeaters, diverse insects, and lizards (Photo Ilse Breitwieser). ➤


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zygomorphic, for example: *Hebe* (Plantaginaceae (Scrophulariaceae)), *Epilobium* (Onagraceae), and *Leptinella* (Asteraceae) (Lloyd 1985). Radiation in the second most species rich genus, *Hebe* (89 spp.), and the related *Parahebe* and *Chionohebe* (Garnock-Jones 1976; Godley 1979; Lloyd 1985) has occurred in both flower shape (shallow dish flowers in *Parahebe* compared with short tubular flowers in *Hebe* (Fig. 7A)) and in inflorescence architecture. Lloyd (1985) also cited several genera that show "respecialisation" in New Zealand (e.g., *Fuchsia* (Onagraceae), *Ranunculus* (Ranunculaceae)). Few of these modifications within a genus are dramatic shifts from one blossom class to another which is often found in some North American genera such as *Phlox* (Polemoniaceae) (Grant & Grant 1965) or *Penstemon* (Scrophulariaceae) (Wilson et al. 2004) and South African genera such as *Disa* (Orchidaceae) (Johnson et al. 1998).

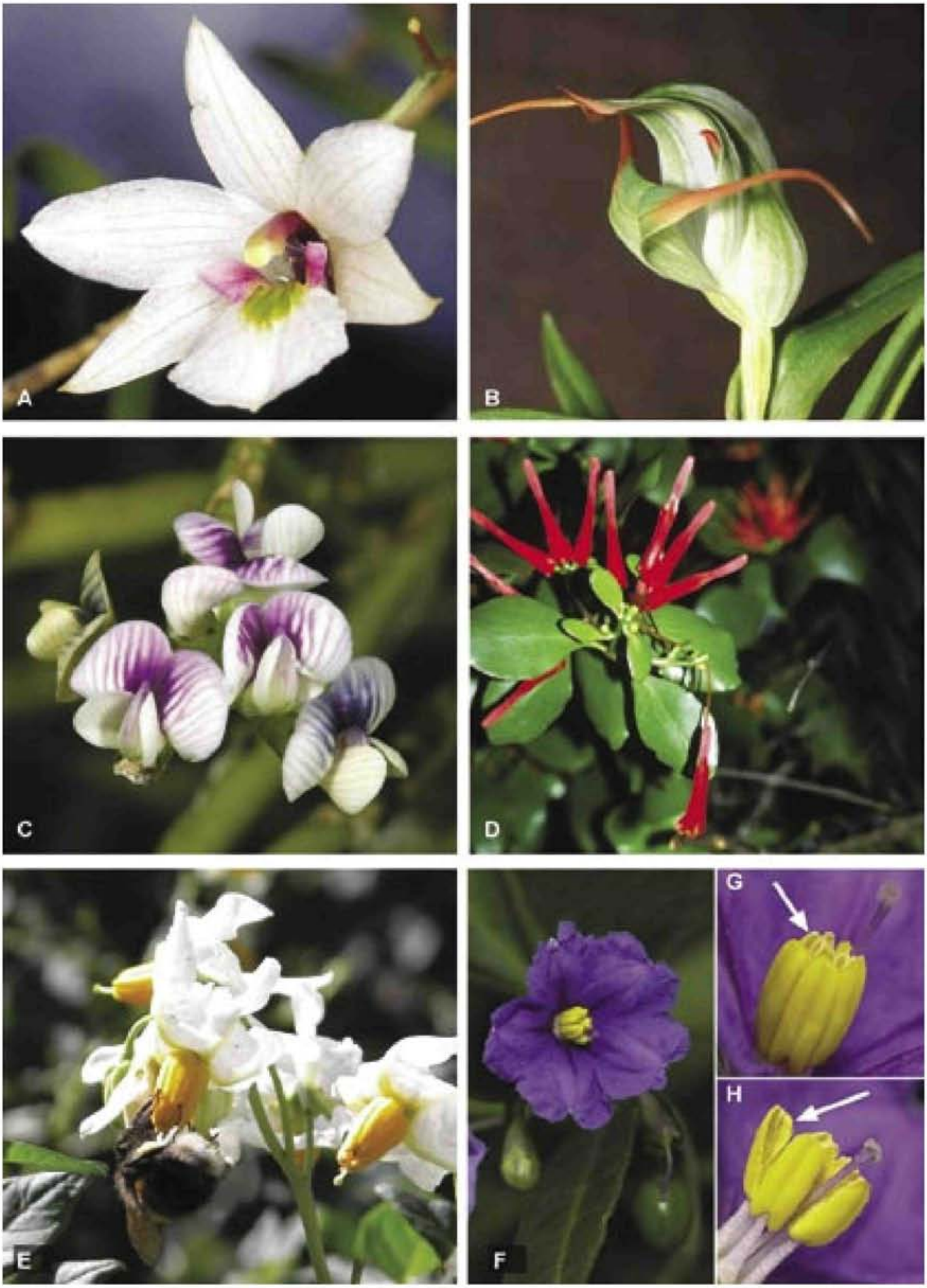
The opposite evolutionary trend, despecialisation, toward a more generalised blossom, may be more frequent in New Zealand compared with elsewhere. Lloyd (1985) described several examples: *Melicytus* (Violaceae) (Powlesland 1984), *Myosotis* (Boraginaceae) (Robertson 1989), and Scrophulariaceae in general. Recently, Wagstaff & Wege (2002) presented another New Zealand example in *Oreostylidum* (Stylidiaceae). On the island of Madagascar, Armbruster & Baldwin (1998) observed an example of despecialisation in *Dalechampia* (Euphorbiaceae), but otherwise this trend has not been well investigated. Other examples of despecialisation may occur in several New Zealand genera showing subtle shifts towards simpler floral shapes, for example, gullet blossoms evolving towards tube shapes in *Ourisia* and *Euphrasia* (both Scrophulariaceae) and bell blossoms evolving towards dish shapes in *Wahlenbergia* (Campanulaceae) (Lloyd 1985).

Compared with the indigenous flora, the naturalised exotic flora in New Zealand has a higher diversity in blossom classes with greater representation of directed- and closed-access blossoms, particularly those with strong zygomorphic shapes, e.g., *Echium* (Boraginaceae), *Lupinus* and *Trifolium* (both Fabaceae), and some examples of strongly spurred flowers (e.g., *Impatiens* (Balsaminaceae) (Webb et al. 1988; Roy et al. 2004). However, most weedy naturalised floras of the world also have abundant open-access blossoms such as capitula in Asteraceae and aggregated dish blossoms in Apiaceae, which are found in cosmopolitan weeds of New Zealand (Roy et al. 2004). No statistics on the frequency of blossom classes are available to make comparisons between the indigenous and exotic floras but it is obvious that indigenous flowers are less diverse in blossom classes.

Insect pollination

New Zealand plants rely on a higher proportion of unspecialised and imprecise indigenous insect pollinators than do plants in most other parts of the world (Lloyd 1985). Regions with similarly depauperate and unspecialised pollinator fauna are found in other high latitude areas, especially oceanic islands (e.g., Elberling & Olesen 1999; Hingston & McQuillan 2000; Bernadello et al. 2001). Insect pollinators in

Fig. 6 Closed-access and other blossoms in the New Zealand indigenous and exotic flora. **A**, Indigenous open-access flower of *Winika cunninghamii* (Orchidaceae) (20 mm wide) presents freely accessible nectar and pollinia on a simple column, with the petals and sepals forming a simple dish shape. A wide variety of insects are attracted to these flowers (Photo Alastair Robertson); **B**, Indigenous closed-access flower of *Pterostylis patens* (Orchidaceae) (18 mm wide) traps fungus gnats in the lower part of the flower by a sensitive trigger mechanism that causes the labellum to close against the back of the flower, forcing the fly to crawl past the stigma first and then the pollinia as it squeezes out of the trap. Highly specialised with deceipt pollination (no reward) (Photo Alastair Robertson); **C**, Indigenous closed-access flowers of *Carmichaelia* sp. (Fabaceae), with flag flower pollinated mainly by indigenous bees (Photo Robert Uschold); **D**, Indigenous closed-access *Peraxilla tetrapetala* (Loranthaceae), mistletoe with explosive bud (27 mm long) dependent on birds or indigenous bees to open the bud for pollination. Lower half of photo shows a dangling overmature bud with the unopened corolla falling off (Photo Jenny Ladley); **E**, Exotic closed-access flowers of *Solanum tuberosum* (Solanaceae), buzz-pollinated flower (2–4 cm diam.) with poricidal anthers. Photo shows *Bombus* sp. buzz-extracting pollen by vibrating its thoracic muscles to shake the pollen out through the pore at the tip of the anthers. In New Zealand, probably only bumblebees are able to buzz pollinate the flowers (Photo Robert Uschold); **F**, Indigenous closed-access flower of *Solanum laciniatum* (Solanaceae), buzz-pollinated flower (4–5 cm diam.) with poricidal anthers (Photo Matt Walters); **G**, Early stage anthers of *Solanum laciniatum* with small pores to dispense pollen. Stigma receptive for one day before anther pores start opening. Arrow points to anther pore (Photo Matt Walters); **H**, Late-stage anthers of *Solanum laciniatum* splitting longitudinally to expose the leftover pollen. Small indigenous bees, syrphids, tachinids, and other small flies scavenge pollen Arrow points to anther split (Photo Matt Walters). ➤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New Zealand include all orders usually involved in pollination, but important families are missing and some are extremely low in diversity or abundance compared with other areas of similar size (Godley 1979; Lloyd 1985).

The most significant disparity is the complete lack of large social bees, both long- and short-tongued. Indigenous bees (e.g., Fig. 7C) are not large (with the biggest about the size of worker honeybees); usually solitary (a few have some social structure) and all short-tongued. Bees are the most important pollinators worldwide because they depend on pollen and nectar for their brood, unlike most other insect groups. A recent treatment by Donovan (unpubl.) lists only 40 species of bees in New Zealand: 32 indigenous and 8 naturalised. The most primitive bee family, the Colletidae (all solitary bees), is well represented with 18 endemic species of *Leioproctus*, 6 endemic and 2 adventive species of *Hylaeus*, and 1 species each of *Hyleoides* and *Euryglossina* (both adventive). The Halictidae, a more advanced family with some species demonstrating a type of social structure, is represented by three species of endemic and one indigenous *Lasioglossum* as well as one *Nomia* species imported for agriculture. Two solitary bee species of *Osmia* and *Megachile* were also imported for agriculture and belong to a more advanced family, Megachilidae. The most important agricultural introductions are the large social bees, bumblebees, *Bombus* (four species, three long tongued) (Macfarlane & Gurr 1995), and honeybees, *Apis mellifera* (Fig. 7A), both in the Apidae, the most advanced bee family (Donovan 1980, 1990, unpubl.).

Another important disparity is the low diversity of butterflies: fewer than 30 named indigenous and exotic species occur (Parkinson & Patrick 2000). Adult butterflies feed on nectar in the daytime. Of the c. 13 indigenous butterflies, at least c. 11 are endemic to New Zealand (e.g., red admiral, *Vanessa gonerilla*, (Nymphalidae) (Fig. 7D) and two are shared with Australia (Gibbs 1980). Some exotic butterflies (c. 7 spp.) are transient visitors from Australia and do not breed here (Gibbs 1980; Dugdale 1988; Parkinson & Patrick 2000). New Zealand has a much lower ratio of butterflies to moths than found in Australia (Armstrong 1979). No specialised butterfly pollination system has been reported (Lloyd 1985) but this has not been fully investigated.

The diversity of moths is much higher; over 1800 species (Dugdale 1988; Parkinson & Patrick 2000). Adult moths feed on nectar mainly at dusk or night, although some feed in the day. In addition, adults of the primitive moth family Micropterigidae have modified maxillary palpi that are adapted to feed on fern spores and pollen, and may be pollen scavengers resulting in accidental pollination in some New Zealand species (J. Dugdale pers. comm.). Little research on moth pollination has been conducted in New Zealand but limited data are available. Apart from the observations of Thomson (1927) and Heine (1937), Godley (1979) observed nocturnal noctuid moths on *Pittosporum* (Pittosporaceae); Primack (1978, 1983) found diurnal, crepuscular, and nocturnal moth pollination in his montane and subalpine survey; Robertson (1989) found crepuscular noctuid moths on *Myosotis macrantha* (Fig. 2H) at a site near Mt Cook; L. E. Newstrom & R. Uschold (unpubl. data) found moth visitation on *Olearia* species in Hinewai Reserve, Banks Peninsula (Fig. 7E), and R. J. Toft & L. E. Newstrom (unpubl. data) observed abundant nocturnal moth visitation on *Leptospermum scoparium* and *Kunzea ericoides* (both Myrtaceae) in Nelson. Resident hawkmoths (Sphingidae) are absent except for one exotic species, *Agrius convolvuli*, primarily found in the North Island with larva feeding on Convolvulaceae (e.g., *Calystegia soldanella*) (J. Dugdale pers. comm.). No

Fig. 7 Examples of insect pollination in New Zealand. **A**, Naturalised exotic honeybee, *Apis mellifera* (Apidae), c. 17 mm long, foraging on indigenous *Hebe* sp. (Plantaginaceae (Scrophulariaceae)) in Landcare Research garden at Lincoln, May 2004 (Photo Robert Uschold); **B**, Indigenous bristle fly, *Perrissina albiceps* (Tachinidae), c. 11 mm long, feeding on nectar from indigenous manuka, *Leptospermum scoparium* (Myrtaceae), Grampians hill, Nelson, November 2004. Flowers up to 12 mm or more diam. (Photo Richard Toft); **C**, Indigenous bee (male), *Leioproctus* sp. (Colletidae), foraging on indigenous *Carpodetus serratus* (Escallioniaceae), Grampians hill, Nelson, November 2004. Flowers 5–6 mm diam. (Photo Richard Toft); **D**, Indigenous red admiral butterfly, *Vanessa gonerilla* (Nymphalidae), c. 20 mm long, feeding on nectar from naturalised exotic *Achillea millefolium* (Asteraceae) during the day at Hinewai Reserve, Banks Peninsula, April 2004 (Photo Robert Uschold); **E**, Indigenous looper moth, tentatively *Cleora scriptaria* (Geometridae), c. 18 mm long, feeding on nectar from indigenous *Olearia paniculata* (Asteraceae) after dark at 6.30 p.m. at Hinewai Reserve, Banks Peninsula, April 2004 (Photo Robert Uschold); **F**, Indigenous chafer beetle, *Odontria striata* (Scarabaeidae), c. 14 mm long, feeding on nectar from indigenous *Olearia avicenniifolia* (Asteraceae) after dark at 6.30 p.m. at Hinewai Reserve, Banks Peninsula, April 2004 (Photo Robert Uschold).

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confirmed observations of adult hawkmoth nectar feeding have been made. Some authors reported this hawkmoth to be associated with the introduction of sweet potato (*Ipomoea batatus*, Convolvulaceae) by Maori (Miller 1971; Gibbs 1980; Parkinson & Patrick 2000; Crowe 2002) but whether this refers to the larval or adult feeding stage is unclear. Data on pollination by adult moths is fragmentary but moth pollination is expected to be important for some indigenous plant species and could include specialised relationships based on scent.

The abundance and diversity of Diptera is very high in New Zealand (c. 2000 spp.; Crowe 2002; Macfarlane 2005) but no recent treatment is available. Many dipteran families are significant pollinators worldwide, ranging from opportunistic nectar

Table 6 Preliminary "blossom class – functional group" matrix showing associations based on access to rewards, landing facilities, and protection of the ovary. Blossom classes are ordered from most to least accessible in three series: open, directed, and closed and refer to early stages of flowering only. Floral visitor and pollinator groups are in a series of potential functional groups that have similar behaviours. Hummingbirds are not present in New Zealand. Symbols: ● association with good pollination potential; ○ association with ineffective pollination potential; ☼ association found in New Zealand but unusual worldwide; blank: little to no visitation or pollination expected.

	Open access to center and rewards (depends on limitations by size)						Direct access to centre or other rewards				Closed or partially closed, access restricted				
Functional groups of visitors and pollinators	Brush inflorescence	Aggregation of dish/ bowls	Aggregation of tubes in capitula	Brush/ fluffy cup flowers	Dish/bowl/"knob" flowers	Inconspicuous flowers < 3 mm	Bell/funnel flowers	Gullet/ tube flowers	Trumpet/ salverform flowers	Spurred flowers	Trap flowers (orchid)	Complex flowers (e.g., flag)	Poricidal anthers, pollen only	Expolsive closed buds (mistletoe)	Syconium (figs)
Insects															
Fig wasps															●
Chewing mouthparts (thrips, weevils, beetles)	○	●	●	●	●	●	○	○	○		○				
Short sucking mouthparts (flies, bees)	○	●	●	●	●	●	○	○			●	●		☼	
Long tongues (flies, bees, moths,	●	○	●	○	○	○	●	●	●	●		●	●	○	
Hovering with long tongue (hawkmoths)	●						●	●	●	●					
Birds															
Hovering hummingbirds	●			●			●	●							
Perching birds	●	☼		●			●	●						☼	
Bats															
Bats	●	●		●			●								
Non-flying vertebrates															
Lizards	●	●													
Mammals (e.g., possums, rodents)	●	●		●	●										

and pollen consumers to specialised nectar feeders with long tongues (Proctor et al. 1996; Kearns 2001). Examples of important families in New Zealand are bristle flies (Tachinidae) (Fig. 7B) and hoverflies (Syrphidae). Pollen feeding by hoverflies has been observed by Holloway (1976) and Hickman et al. (1995) in New Zealand. Other important pollinators are horse flies (Tabanidae), which in New Zealand are nectar feeders rather than biters/bloodsuckers (J. Dugdale pers. comm). Diverse groups of flies such as the Bibionidae and Calliphoridae are also common on New Zealand flowers (Primack 1983; L. E. Newstrom, R. J. Toft, & J. Reese unpubl. data) but their relative effectiveness has not been explored. Thomson (1927) and Heine (1937) interpreted the floral features as adaptations to flies rather than to the bees and butterflies that dominate in Europe and North America. However, it has been suggested that most dipterans do not transfer abundant or high quality pollen because they tend to carry small pollen loads and lack constancy to flowers (Proctor et al. 1996; Kearns 2001). Unlike bees, flies do not depend on nectar or pollen as resources for their brood. However, tachinid flies are capable of carrying large pollen loads and show some flower constancy, e.g., *Protohystricia huttoni* that visits *Myosotis colensoi* (Fig. 2G; Robertson 1989, 1992). Several dipteran groups in New Zealand, such as the horse flies (Tabanidae), the Tachinidae (Tachininae, Goniinae), and some Calliphoridae carry pollen on the gena (the chin or cheeks of a fly), which bear conspicuous bristles and could transfer significant amounts of pollen (J. Dugdale pers. comm.).

Evidence for beetle pollination has been demonstrated by several authors (e.g., Thomson 1927; Heine 1937; Godley 1979; Primack 1983; Webb 1994; Wilton 1997), but no studies have focused on their effectiveness; their contribution to pollination has largely been ignored. Since beetles are less mobile, they may not have such an important role as bees, flies, and moths. However, on some plant species, for example mat-forming alpine Asteraceae, they are abundant (Wilton 1997; R. McKenzie unpubl. data; L. E. Newstrom & C. Morse unpubl. data). Nocturnal beetle pollination has been found in *Olearia paniculata* (Asteraceae) (Fig. 7F; L. E. Newstrom & R. Uschold unpubl. data).

The role of very small insects is also poorly known but some cases have been documented. For example, extremely small insect pollinators such as indigenous thrips (Norton 1980, 1984) carry few pollen grains, but their populations can rapidly expand into the millions (D. Teulon pers. comm.). Godley (1979) also listed weevils as pollinators but the effectiveness of such small insects has not been investigated. Armstrong & Irvine (1989) have described "microcantharophily", a small-beetle pollination syndrome, in the rainforest of Queensland, Australia. They suggested that this type of pollination differs significantly from large-beetle pollination (cf. Proctor et al. 1996) and will be found in small, inconspicuous flowers with few exposed floral parts and little to no post-opening movement. Further study of minute blossoms could reveal specialisation to small insects because rewards are likely to be too insignificant for larger insects.

Community analyses are the best approach to determine the relative roles of the different groups of insect pollinators. In New Zealand, the only community study has been conducted by Primack (1983) in the montane and subalpine habitats in the South Island where Diptera were 50–80% of the total flower visitors. Fly pollination can be especially important during cold rainy weather when other insects, such as bees, are inactive (Primack 1978, 1983; Lloyd 1985; L. E. Newstrom & R. Uschold unpubl. data). Since New Zealand is characterised by intermittent inclement weather year round, the relative contribution of different pollinating groups is expected to vary hourly, daily, and weekly (Primack 1983; Lloyd 1985; L. E. Newstrom pers. obs.). This has the potential to increase selection for generalised pollination systems (Waser et al. 1996). On a seasonal basis strong trends are found with indigenous and exotic bees mostly inactive or less active in winter. The pollinator fauna also changes with altitude (Primack 1978), as demonstrated in *Hebe* spp. with fewer bees and more flies and butterflies visiting plants at higher altitudes (Delph 1988).

Open-access blossoms visited by insects

Open-access blossoms are well adapted for most pollinating insects, although very shallow flowers are not best suited for long-tongued insects. Historically, fly pollination in New Zealand has been associated with the preponderance of small, white or pale dish/bowl flowers (Heine 1937; Godley 1979; Lloyd 1985), but these types of flowers are also associated with the small-bee syndrome (Frankie et al. 1983, 2004) which includes visits from diverse dipterans and lepidopterans (but they are often not as effective as the bees). For example, many indigenous plant species are visited by a wide diversity of both indigenous and exotic flies, bees, moths, butterflies, and even birds, such as the large dish flowers of *Hoheria* and aggregated short tubular flowers of *Hebe* (Fig.

7A; Godley 1979; Primack 1983; Lloyd 1985; Delph & Lively 1992; Butz Huryn 1995; Castro & Robertson 1997; L. E. Newstrom & R. Uschold unpubl. data). However, some indigenous plant species do not attract exotic social bees, e.g., *Olearia* spp. and other Asteraceae (Primack 1983; L. E. Newstrom & R. Uschold unpubl. data). Some indigenous species attract flies and beetles more than indigenous bees (e.g., the primitive flowers of *Pseudowintera colorata* (Fig. 4E; Lloyd & Yates 1982; Wells 1988). In New Zealand, indigenous flies and bees visit many exotic plant species with open-access blossoms (e.g., Donovan 1980, 1990, unpubl.; Primack 1983; Donovan & Macfarlane 1984).

These results correspond to the high degree of generalisation expected for open-access blossoms. Are there examples of open-access blossoms with restricted visitation showing specialisation? If pollinator effectiveness is taken into account then some flowers may be more specialised than they appear at first. Webb (1994) suggested cryptic specialisation for *Corokia cotoneaster* (Cornaceae), which is pollinated by indigenous bees that were more effective than other insect visitors such as diverse flies. An intriguing potential example of cryptic specialisation, perhaps mediated by floral scent, was observed by Wilton (1997) in selected Asteraceae species but more data are needed to confirm this. Other potential examples of cryptic specialisation may be related to amount of reward. For example, Primack (1983) observed only flies (Tachinidae and Muscidae) visiting the inconspicuous blossoms of *Donatia novae-zelandiiae* (Donatiaceae), which has small, white flowers (petals 2–3 mm long; Allan 1961; Fig. 4I).

Directed-access blossoms visited by insects

Directed-access blossoms in indigenous plant species are relatively generalised. Discussion of the large directed-access blossoms adapted for bird pollination (but shared with insects) is deferred to the section on bird pollination below. An example of a medium-sized directed-access blossom with single bell/funnel flowers is the indigenous *Wahlenbergia albomarginata* (Campanulaceae), which is primarily adapted for insects. This species was visited by a wide array of indigenous bees, flies (including tachinids and syrphids), day-flying moths, and butterflies (Primack 1983). At the Landcare Research garden, *W. mathewsii* was also visited by diverse bees, flies, and other insects but not by honeybees or bumblebees in spite of their abundance in the garden (L. E. Newstrom & R. Uschold unpubl. data). However, Butz Huryn (1995) reported that *Wahlenbergia* spp. is visited by honeybees, based on data from pollen loads taken by Pearson & Braiden (1990). Other indigenous species with directed-access blossoms visited by diverse indigenous insects including bees, flies, and butterflies (and sometimes honeybees) are *Mimulus repens* (Böcher & Philipp 1985) and *Ourisia macrocarpa* (Schlessman 1986), both species in Scrophulariaceae.

Primack (1983) reported the potential for specialisation in at least three examples of indigenous directed-access blossoms. First, *Mazus radicans* (Scrophulariaceae) was visited only by small indigenous bees even though the blue and purple zygomorphic flowers appeared to be suited to bumblebees that were present on other exotic plant species at the site. Second, at the montane site, the fragrant flowers of *Dracophyllum acerosum* and *D. uniflorum* (Epacridaceae) were visited only by numerous and diverse moths at night and were not visited during the day. In contrast, at the subalpine site, *D. pronum*, with a shorter corolla, was visited by flies, bees, and moths. (The bird-pollinated *Dracophyllum* species, referred to by Godley (1979), is probably the large-flowered forest species and not the small-flowered subalpine and alpine species discussed here.) Third, only the day-flying moth *Dasyuris aceps* visited *Pratia macrodon* (Campanulaceae (Lobeliaceae)) at the subalpine site (Primack 1983). In contrast, *Pratia angulata* was visited by a wide diversity of insects including small bees, flies (syrphids mainly), day-flying moths, and butterflies at the montane and subalpine sites. The contrast in apparent specialisation and generalisation in different species of *Dracophyllum* and *Pratia* requires further research to confirm and explain the patterns. Lloyd (1985) noted that the trend from gullet to a more simple tube blossom in *Pratia* had the potential for despecialisation.

Among exotic plant species, many with directed-access blossoms in Primack's (1983) survey showed restricted visitation. Indigenous bees did not visit *Echium vulgare* (Boraginaceae), *Digitalis purpurea* (Scrophulariaceae), *Marrubium vulgare* (Lamiaceae), or *Prunella vulgaris* (Lamiaceae). These exotic plant species, with gullet or lip flowers, were mainly visited by *Bombus* spp., sometimes *Apis mellifera*, and a few syrphids. However, Donovan (unpubl.) has recorded indigenous bees visiting these same species at other sites. Primack (1983) also reported that indigenous bees did not visit red clover, *Trifolium pratense* (Fabaceae), or white clover, *T. repens*, which have aggregated tubular flowers based on the flag construction. These species were both visited mainly by *Bombus* spp., but also a few syrphid flies and butterflies. Species of *Bombus* were originally introduced to New Zealand to improve seed set in red clover pastures because the short-tongued honeybees and indigenous bees were ineffective (Donovan 1980, unpubl.). For many exotic plant species introduced bees may be more effective, but indigenous bees have been observed visiting numerous exotic species (Donovan unpubl.). The niche overlap in floral resources between indigenous and exotic bees on both indigenous and exotic plants appears to be wide. Variation in floral preferences, however, would depend on plant and pollinator population densities and diversity at the community level.

Myosotis (Boraginaceae)

Myosotis, the 10th most species rich angiosperm genus (c. 40 spp.) in New Zealand (Wilton & Breitwieser 2000), portrays an unusually high diversity of blossom classes (Fig. 2). Recent molecular work on the genus indicates rapid and recent speciation in New Zealand after arrival in the Tertiary (Winkworth et al. 1999, 2002b). In comparison with elsewhere, New Zealand species are characterised by low molecular diversity but considerable morphological and floral diversity (Winkworth et al. 1999). Splits-graph analysis of ITS and *mat*K sequence data show a distinct New Zealand clade (which includes some South American and Australian species) with very short internal branch length embedded in a more diverse tree that includes representatives of European, North American, and African species. The northern hemisphere species contain more sequence divergence but are rather conservative in flower morphology and plant form with the typical pale blue flowers similar to *M. sylvaticus* (Fig. 2A). At least one northern species, *Myosotis scorpioides*, is self-incompatible (Varopoulos 1979) while all the New Zealand species tested to date are all fully self-compatible (see Table 1).

Within the New Zealand *Myosotis*, diverse trends in floral morphology are evident, ranging from short tubes with flat spreading rims (rotate corolla) (Fig. 2C) to long narrow tubes with flat rims (salverform corolla) (Fig. 2H), as well as variations with wider, more funnel-form tubular and bowl-shaped flowers (Fig. 2B,D,F). Some species have retained the rotate corolla and narrow tubes present in their northern hemisphere counterparts (Fig. 2A) but vary the ratio of style and anther placements, which, combined with the elongation of the tube and, with it, the epipetalous anthers, allows for variation in the likelihood and timing of autonomous selfing. In some, selfing is automatic as soon as the anthers dehisce (Fig. 2E), while in others, selfing is delayed until the anthers finally reach the stigma (Fig. 2C), or is prevented by the long style which is never overtopped (Fig. 2G) (Robertson & Lloyd 1991).

The variation in tube length and width also alters access to nectar and, in some cases, appears to result in an unusual degree of reliance on one or a small number of insect species. Populations of several *Myosotis* species have been observed to receive effective flower visits from a very restricted but diverse set of pollinators (Robertson 1989). The long corolla tube of *M. colensoi* (Fig. 2G) restricts access to nectar which appeared to be collected exclusively by a long-tongued fly, *Protohystricia huttoni* (Tachinidae, Diptera), at Castle Hill, Canterbury (Robertson 1989). *M. macrantha* (Fig. 2H), which has chocolate-brown, pendulous, long funnel-shaped tubes with a trumpet-like opening (salverform corolla), was visited only at dusk by the moth *Aletia cuneata* (Noctuidae, Lepidoptera) at Mt Cook (Robertson 1989). *M. goyenii* (Fig. 2F), with similar flowers but a wider funnel and larger opening, was only visited in the late afternoon by *Helle longirostris* (Acroceridae, Diptera) in Canterbury (Robertson 1989).

Other New Zealand *Myosotis* show a trend towards floral despecialisation (Lloyd 1985), losing the concealed nectar, inserted anthers, and rotate or salverform corolla as they move towards bowl-shaped flowers, such as *M. laeta* (Fig. 2D), and towards shorter corolla tubes with exserted anthers and aggregated flowers forming a short brush-like inflorescence, such as *M. monroi* (Fig. 2B) (Robertson 1989). Short-tongued bees seem to be the most important pollinators for these species (Brandon 2001). No flower visitors have been recorded from *M. spathulata* (Fig. 2E) which produces no nectar and autonomously selfs.

Closed-access blossoms visited by insects

The few indigenous species with closed-access blossoms that are adapted for insects tend to show rather specialised pollination systems. However, in some species the flowers ultimately develop more open access at later stages of anthesis providing the opportunity for generalised pollination to take place eventually. Examples of indigenous genera (*Pterostylis*, *Carmichaelia*, and *Solanum*) and several exotic species in Fabaceae, *Solanum*, and figs demonstrate the diversity of mechanisms in insect-pollinated closed-access blossoms.

Pterostylis and other Orchidaceae

The New Zealand orchids exhibit a diversity of floral strategies including widespread autogamy and both generalised and specialised pollination systems (Thomson 1879b, 1927; Molloy 1990; Lehnebach 2002; Lehnebach & Robertson 2004). Molloy (1990) estimated that as many as half of the New Zealand orchid flora may be autonomous selfers. On the other hand, some species have well-developed strategies for attracting visitors and several are now known to be partially self-incompatible (see Table 1; Lehnebach & Robertson 2004).

In New Zealand four species of epiphytic orchid (Lehnebach & Robertson 2004) are unusual in having despecialised open-access blossoms that present large quantities of unconcealed nectar taken by a wide variety of insect visitors including bees, members of seven families of dipterans, beetles, ants, and wasps, as well as exotic honeybees and bumblebees (e.g., *Winika cunninghamii* (Fig. 6A)). Epiphytic orchids elsewhere, largely restricted to the tropics, usually have concealed rewards and generally form specialised relationships with a narrow set of flower visitors (Tremblay 1992; Neiland & Wilcock 1998). In contrast to these four epiphytic orchids with generalised pollination, the New Zealand terrestrial greenhood orchids (*Pterostylis* spp., Fig. 6B) show specialised pollination. They appear to use sexual deception to entice male fungus gnats (Culicidae, Mycetophilidae, Phoridae, and Keroplatidae) to visit the trap blossoms (Cheeseman 1873; Jones & Clements 2002; Lehnebach 2002). *Pterostylis*, as mentioned above, is the largest animal-pollinated genus in the monocotyledons of New Zealand, which may be related to its specialised pollination system.

As is typical of orchids worldwide, all the New Zealand species examined so far that do not autonomously self have been moderately to strongly pollen limited (Table 1). However, Lehnebach (2002) made the observation that efficiency of the pollen transfer process differs in the epiphytic orchids and the greenhoods. In the epiphytes, between 30% and 90% of the flowers had pollinia removed but generally less than 10% of flowers had pollen deposited on the stigmas, while in the much more specialised greenhood orchids, pollen depositions were as common or more common than removals (more depositions than removal can occur when pollinia break up, as a single pollinia can deposit pollen on more than one stigma).

Carmichaelia (Fabaceae) and other flag blossoms

Many flag flowers are closed-access blossoms because they restrict entry to only those insects, usually bees, strong enough to pry open the flowers or trip explosive mechanisms (Faegri & van der Pijl 1979; Proctor et al. 1996). Lloyd (1985) predicted that flag blossoms of indigenous species of *Carmichaelia* (Fabaceae) would be specialised (Fig. 6C). These flowers are small and match the size and capabilities of indigenous bees such as *Leioproctus* (Heine 1937; Donovan 1980, unpubl.), which are highly attracted (B. Donovan pers. comm.). In Primack's (1983) survey, *C. arborea* and *C. odorata* were visited by *Leioproctus* spp. and unidentified tachinids, syrphids, and other large flies. It is not known if some tachinid flies, which are larger than some indigenous bees, are able to open these flag flowers; they may only scavenge. Indigenous *Leioproctus* species have been observed to easily depress the keel to gain entry to several *Carmichaelia* species (B. Donovan pers. comm.; L. E. Newstrom pers. obs.). Honeybees and bumblebees also visit some species of *Carmichaelia* (Butz Huryn 1995; Donovan unpubl.; L. E. Newstrom & J. Lammerding unpubl. data) but they are often relatively large for the flower. Moths and butterflies also visit but are nectar robbers as they do not open the flower to contact stigma or anthers (L. E. Newstrom pers. obs.). One species, *C. williamsii*, is not in the insect-pollinated group as it has a large tubular blossom and is adapted for bird pollination, as described by Heenan & de Lange (1999).

Indigenous bees are too small and not adept at handling large exotic flag flowers which often have explosive mechanisms (e.g., *Lupinus polyphyllus* and *Cytisus scoparius* (both Fabaceae)), but they do attempt to open them and are usually stunned in the process (B. Donovan pers. comm.). In New Zealand, efficient and successful flower opening is restricted to large exotic social bees (honeybees and bumblebees). Primack (1983) reported flower visitors to be virtually absent from *L. polyphyllus*, yet he did list some visitation by *Bombus* spp. and *Leioproctus* spp. He observed only *Lasioglossum sordidum* visiting broom, *C. scoparius*, although elsewhere bumblebees and honeybees favour these flowers (Parker & Haubensak 2002). In New Zealand, bumblebees are the fastest and most adept at tripping broom flowers but honeybees are able to trip them more slowly (L. E. Newstrom pers. obs.). The specialisation of these blossoms for large social bees plays a significant role in weed invasions (Hanley & Goulson 2003; see below).

Solanum (Solanaceae)

All *Solanum* species share a floral morphology that requires specialised insect pollination. The flowers generally have no nectar (Symon 1979), and this excludes several pollinators (e.g., butterflies, most moths, birds). All *Solanum* flowers further restrict access, at least initially, because the anthers have a very small pore for dispensing pollen and require buzz pollination for effective removal of pollen. Therefore, *Solanum* flowers are considered closed-access blossoms in spite of the open dish shape (Endress 1994). King & Buchmann (2003) showed that species of *Bombus* and *Xylocopa* were able to vibrate *Solanum* anthers at the right frequency to extract pollen but *Apis mellifera* and the dronefly, *Eristalis tenax* (Syrphidae), were not. This does not mean that the latter are not able to transfer pollen; rather, they are inefficient compared with the former.

Two indigenous *Solanum* species stand out in the New Zealand flora because of their brightly coloured large flowers. *Solanum laciniatum* (blue petals) (Fig. 6F) and *S. aviculare* (pink petals) both belong to section Archaeosolanum restricted to Australia, New Zealand, and New Guinea (Symon 1979). Their large fleshy fruits suggest they arrived by bird dispersal from Australia where several large bee species most likely buzz pollinate the flowers (e.g., *Amegilla*, Armstrong 1979; C. Gross pers. comm.). The plants' arrival in New Zealand was pre-European (Allan 1961) but no indigenous bees are able to buzz pollinate (B. Donovan pers. comm.). However, more information on syrphids is needed (P. Johns pers. comm.; Proctor et al. 1996, p. 70) and the horse fly *Scaptia* (Tabanidae) is large, hovering, and buzzy (J. Dugdale pers. comm.). If these flies are ruled out, then information available indicates that, in New Zealand, the only buzz pollinators may be *Bombus* spp., which were not introduced until 1885 (Donovan 1980). They are highly attracted to yellow anthers against blue backgrounds and have frequently been observed buzzing *S. laciniatum* flowers (L. E. Newstrom pers. obs.).

Less effective non-buzzing insects also visit buzz-pollinated species because they are able to scavenge spilled pollen from flower parts. On *S. laciniatum*, diverse flies and indigenous bees (e.g., *Lasioglossum*) scavenge pollen in early-stage flowers (day 1 to 2) when anthers still have very small pores (Fig. 6G) (L. E. Newstrom unpubl. data). In late-stage flowers (day 3 to 7), diverse pollinators ultimately have access to more abundant pollen because anthers gradually split open longitudinally exposing the remaining pollen (Fig. 6H). Since the anther-splitting trait occurs in all species of Archaeosolanum, the transition from a closed-access blossom to a more open-access condition did not evolve in New Zealand and is not an example of despecialisation. In addition, *S. laciniatum* is self-compatible (L. E. Newstrom unpubl. data) and has a delayed autonomous selfing mechanism as mentioned above, so reproduction is assured in the absence of its specialised buzz pollinator, which could explain the colonisation of this species before the introduction of *Bombus*.

A third species, *S. americanum*, presumed to be indigenous, belongs to the section Solanum (Webb et al. 1988), but anthers have not been examined. The numerous naturalised exotic species of *Solanum* in New Zealand appear to belong to sections of the genus usually lacking the anther-splitting trait. Limited data show that naturalised exotic *S. tuberosum* (Section Petota) was visited exclusively by *Bombus* spp. (Fig. 4E) in the Landcare Research garden (L. E. Newstrom & R. Uschold unpubl. data). Aside from *Solanum*, specialised buzz pollination may also occur in members of the Ericaceae, a family noted for poricidal anthers. Primack (1983) observed *Bombus* spp. visiting flowers of indigenous *Gaultheria crassa* (Ericaceae) but he also saw other visitors such as unidentified flies and small bees.

Ficus (Moraceae)

Fig species (*Ficus* spp., Moraceae) have the most highly specialised pollination system in the world because the flowers are enclosed inside the fig (called a syconium) and only certain species of wasps (Aagonidae) have access. They must enter the syconium through a small opening (the ostiole) that differs in size, shape, and surrounding scales and matches the size and shape of different wasp species, which means that in most cases the association is species specific (Ramirez 1970). Of 40 fig species indigenous to Australia (Chew 1989), 5 have been cultivated in New Zealand but only 2 are known to have their appropriate fig wasp pollinator present (Gardner & Early 1996). At least 25 years ago, the fig wasp *Pleistodontes imperialis*, which is specific to the Port Jackson fig, *Ficus rubiginosa*, arrived in New Zealand, but the arrival of the fig wasp *P. froggatti*, specific to the Morton Bay fig, *F. macrophylla*, in New Zealand is very recent (Gardner & Early 1996). These two fig species have both naturalised. The pollinators of the other three introduced figs have not been found; however, 50% of *F. obliqua* figs on a solitary tree contained unsuitable female *P. imperialis* stuck in the ostiole. This suggests that the fig wasps that have arrived in New Zealand so far are species specific.

Bird pollination

Godley (1979) listed eight indigenous bird pollinators in New Zealand, including the self-introduced silvereye, *Zosterops lateralis* (Zosteropidae). Like bee pollinators, the low diversity of bird pollinators has been contrasted with the much higher diversity in Australia (Ford 1979; Lloyd 1985). However, many other regions of the world also have low bird pollinator diversity; e.g., only three species of long-billed nectar-feeding birds were major pollinators in the tropical lowland dipterocarp forest in Sarawak (Momose et al. 1998) and bird pollinators are absent in Europe (Ford 1979). Bird pollination in New Zealand has been reviewed recently by Anderson (1997), Castro & Robertson (1997), and Kelly et al. (unpubl.). The latter authors added three more indigenous flower-visiting bird species and five exotic birds to the list for New Zealand. They emphasised the lack of data on pollinator status of some of these species; nectar robbers (flower piercers) and non-nectar feeders may have been included in the list. Based on published data on frequency of bird visits to flowers, they showed the majority of flower visits (89%) were by indigenous tui, *Prosthemadera novaezelandiae* (Fig. 5D), indigenous bellbird, *Anthornis melanura* (both Meliphagidae), and silvereye.

The role of bird pollinators varies with season, habitat, and region. At the community level throughout the entire year the proportion of bird-pollinated plant species in many countries is much lower than that of insect-pollinated species. For example, bird-pollinated species in a Costa Rican tropical dry forest was 2% of all species surveyed, a nearby cloud forest around 10% (Frankie et al. 2004), and lowland tropical rain forest 15% (Kress & Beach 1994). In Sarawak, a tropical lowland dipterocarp rain forest had 7% (Momose et al. 1998). These estimates cannot be compared with New Zealand because year-round community studies including birds have not been conducted. However, the relative importance of bird pollination can also be estimated by the number of bird-pollinated plant species in the entire flora. Lloyd (1985) suggested that only 1% of the indigenous New Zealand flora is adapted for bird pollination compared with around 15% in the Australian flora. Previous counts by Godley (1979) and Craig et al. (1981) show 1.5% (30/1896 spp.) of the indigenous flora is visited by birds but not all of these have bird-adapted blossoms. The current list of 51 bird-visited indigenous species represents nearly 3% but also includes species not well adapted for bird pollination (Tables 7 and 8 and references therein).

Guild-level studies have shown that, in winter, birds play a dominant role in certain habitats in New Zealand. For example, Anderson (1997, 2003) investigated nine selected bird-visited species in coastal broadleaf forest at three sites in the North Island. These canopy trees had more frequent visits by birds than by insects and exclusion experiments showed more effective pollination by birds than by insects for most of the nine species. In temperate Australia, many specifically bird-pollinated plants flower in winter (Ford 1979). A similar pattern in New Zealand is likely to be widespread in some habitats since indigenous bees and many other pollinating insects are not active in winter.

In the New Zealand winter, though, the number of indigenous species in flower is low: around 5% (39 spp.) flower in July compared with a summer peak of 83% (600 spp.) in December (Fig. 8; n = 729 spp. from Allan (1961), Moore & Edgar (1976), and Webb et al. (1988)). In communities where birds remain an important component, such as the canopy trees of the northern broadleaf forests, bird pollination is dominant in winter at least, but summarising over all habitats and seasons insect pollination dominates in New Zealand. These bird-dominated communities were probably more widespread in the past and contrast with the year-round bee-dominated pollination of canopy trees in the neotropical forests (Stiles 1978; Frankie et al. 1983) and the year-round fly-dominated pollination in the montane and subalpine communities of New Zealand (Primack 1983).

In New Zealand the diversity of blossom classes in bird-visited species is highly unusual. Birds have classically been associated with only four major blossom classes: in the open-access series, mainly brush flowers and inflorescences; and in the directed-access series, mainly tubular, gullet, and flag flowers (see Table 5). Of the reported bird-visited species in New Zealand, approximately 28 have open-access blossoms including brush and dish/bowl/"knob" flowers, 20 have directed-access blossoms including bell, tubular, gullet, and tubular flag, and 2 have closed-access blossom with explosive buds (Tables 7 and 8).

Brush and tubular blossoms are considered to be bird adapted but dish/bowl/"knob" blossoms are not. They are considered entomophilous rather than ornithophilous (Faegri & van der Pijl 1979; Proctor et al. 1996). In addition, explosive bud blossoms are highly unusual. Such a wide range of bird-visited

Table 7 Indigenous plant species regularly visited by birds in New Zealand. The C&R score indicates how many of 3 nectar-feeding birds (tui, bellbird, and stitchbird) visited on Kapiti Island (Castro & Robertson 1997). Score of 9 indicates all 3 regularly visited; 6, only bellbird and stitchbird; 3, only bellbird; n/a, plant species not present. Market indicates identified honey sold in NZ; surplus indicates species provides more honey than needed for honeybee colony maintenance (Butz Huryn 1995). Pollination system and size of flowers from Castro & Robertson (1997). Inflor., inflorescence.

	Family	Flower size	Kapiti Island C&R score	Used for honey	Blossom class Godley (1979)	Blossom class this paper	Reference
Ornithophilous							
Metrosideros excelsa	Myrtaceae	large	9	market	brush	brush inflor.	Godley 1979
Metrosideros fulgens	Myrtaceae	large	9	market	brush	brush inflor.	Godley 1979
Metrosideros robusta	Myrtaceae	large	9	market	brush	brush inflor.	Godley 1979
Metrosideros umbellata	Myrtaceae	large	n/a	market	brush	brush inflor.	Godley 1979
Knightia excelsa	Proteaceae	large	9	market	brush	brush inflor.	Godley 1979
Vitex lucens	Verbenaceae	large	9	surplus	tube	gullet	Godley 1979
Alseuosmia macrophylla	Alseuosmiaceae	small	n/a	surplus	tube	tube	Godley 1979
Phormium tenax	Agavaceae	large	9		tube	tube	Godley 1979
Fuchsia excorticata	Onagraceae	large	9		tube	tube	Godley 1979
Rhabdothamnus solandri	Gesneriaceae	large	n/a		tube	tube	Godley 1979
Sophora spp.	Papilionaceae	large	3	surplus	tube	flag/tube	Godley 1979
Clianthus spp.	Papilionaceae	large	n/a		flag	flag/tube	Godley 1979
Alepis flavida	Loranthaceae	medium	n/a			explosive bud	Ladley et al. 1997
Peraxilla spp.	Loranthaceae	large	n/a		tube	explosive bud	Ladley et al. 1997
Entomophilous							
Weinmannia racemosa	Cunoniaceae	minute	9	market	brush	brush inflor.	Godley 1979
Dracophyllum spp.	Epacridaceae	small	n/a		tube	tube	Godley 1979
Dysoxylum spectabile	Meliaceae	medium	9	surplus	tube	short tube	Godley 1979
Pittosporum crassifolium	Pittosporaceae	medium	9		tube	short tube	Godley 1979
Pittosporum eugenioides	Pittosporaceae	small	9			short tube	Castro & Robertson 1997
Pittosporum tenuifolium	Pittosporaceae	small	9			short tube	Castro & Robertson 1997
Pittosporum umbellatum	Pittosporaceae	medium	9		tube	short tube	Godley 1979
Pittosporum cornifolium	Pittosporaceae	medium	6			short tube	Castro & Robertson 1997
Elaeocarpus dentatus	Elaeocarpaceae	medium	9	surplus		bell	Craig et al. 1981
Myoporum laetum	Myoporaceae	medium	6			bell	Castro & Robertson 1997
Geniostoma rupestre	Loganiaceae	small	9	surplus		"knob"	Castro & Robertson 1997
Pseudopanax arboreus	Araliaceae	small	9	surplus	open	"knob"	Godley 1979
Griselinia littoralis	Cornaceae	minute	6	surplus		dish	Castro & Robertson 1997
Cordyline spp.	Agavaceae	medium	n/a	surplus		dish	Craig et al. 1981

blossoms with a high proportion of open-access dish blossoms are inconsistent with the classical bird pollination syndrome. Do birds in New Zealand forage widely due to a scarcity of bird-adapted flowers or are they naturally associated with (and well adapted to) a wider range of blossoms than was previously thought? Since the preponderance of research on bird pollination has historically focused on hummingbirds, perching bird syndromes are not well characterised (Brown & Hopkins 1995; see references cited therein); thus, the associated blossom classes of perching birds may be underestimated.

Table 8 Indigenous plant species visited by birds on Kapiti Island (Castro & Robertson 1997). The C&R Score indicates how many of tui, bellbird, and stitchbird visited. A score of 3 generally means that only stitchbird or bellbird visited regularly (see Castro & Robertson 1997 for which species) and a score of 2 or 1 indicates only occasional visitation by any bird species but usually not tui. Other abbreviations and sources are the same as in Table 7.

	Family	Flower size	Kapiti Island C&R score	Used for honey	Blossom class Godley (1979)	Blossom class this paper	Reference
Entomophilous							
Aristotelia serrata	Elaeocarpaceae	small	3			bell/dish	Castro & Robertson 1997
Metrosideros perforata	Myrtaceae	medium	3	market	brush	brush inflor.	Godley 1979
Laurelia novae-zelandiae	Monimiaceae	small	3			dish	Castro & Robertson 1997
Rubus cissoides	Rosaceae	small	3			dish	Castro & Robertson 1997
Ripogonum scandens	Smilacaceae	medium	3			dish	Castro & Robertson 1997
Kunzea ericoides	Myrtaceae	small	3			dish	Castro & Robertson 1997
Rhopalostylis sapida	Arecaceae	medium	3			aggregated dish	Castro & Robertson 1997
Syzygium maire	Myrtaceae	medium	3			brush inflor.	Castro & Robertson 1997
Corynocarpus laevigatus	Corynocarpaceae	minute	2		cup	bowl/bell	Godley 1979
Myrsine salicina	Myrsinaceae	minute	2			bowl/bell	Castro & Robertson 1997
Beilschmiedia tawa	Lauraceae	minute	2			dish	Craig et al. 1981
Hoheria populnea	Malvaceae	medium	2	surplus		dish	Castro & Robertson 1997
Melicytus ramiflorus	Violaceae	small	2			dish	Godley 1979
Pseudopanax crassifolius	Araliaceae	small	2		open	dish/"knob"?	Godley 1979
Shefflera digitata	Araliaceae	small	2		open	dish/"knob"?	Godley 1979
Passiflora tetranda	Passifloraceae	medium	2			dish/"knob"?	Castro & Robertson 1997
Myrsine australis	Myrsinaceae	minute	1			dish	Castro & Robertson 1997
Earina autumnalis	Orchidaceae	medium	1			irregular	Castro & Robertson 1997
Astelia spp.	Liliaceae	minute	1	surplus		dish	Castro & Robertson 1997
Nestegis lanceolata	Oleaceae	minute	0		apetalous	inconspicuous	Godley 1979
Toronia toru	Proteaceae	small	0		open	dish	Godley 1979
Hebe spp.	Plantaginaceae	minute	0		tube	brush inflor.	Godley 1979
Cyathodes spp.	Epacridaceae	minute	0		tube	short tube	Godley 1979

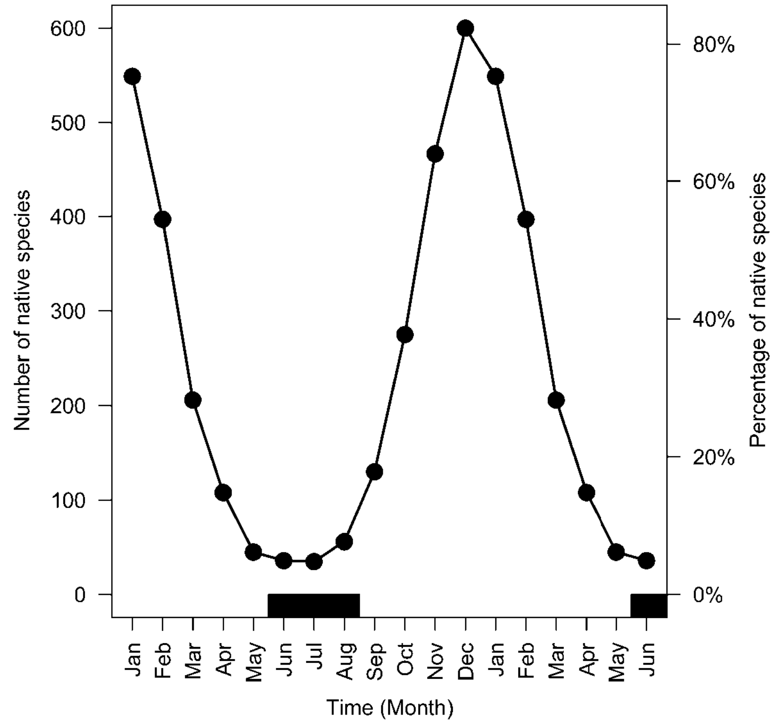

Fig. 8 Number of indigenous species in the New Zealand flora that flower in each month. Dark bar indicates winter months of June, July, August. Flowering peak of 82% (600 species) in December (mid summer) compared with 5% (39 species) in July (mid winter). Data based on a sample of 729 species with data out of 1896 indigenous species (38% coverage) from Allan (1961), Moore & Edgar (1976), and Webb et al. (1988).

Open-access blossoms visited by birds

Dish/bowl/"knob" flowers and inflorescences

In New Zealand, perching birds visit numerous species with open-access blossoms (Tables 7 and 8) but many of these, especially those with dish/bowl/"knob" flowers, have been considered entomophilous (Anderson 1997, 2003; Castro & Robertson 1997; Webb et al. 1999). However, these types of flowers are also frequently visited by perching birds in Australasia (Armstrong 1979; Ford 1979; Brown & Hopkins 1995). The simplest explanation is that when floral resources are scarce, the marginal value for visiting less rich, relatively unsuitable blossoms is enhanced (Rasch & Craig 1988; O'Donnell & Dilks 1994; Castro & Robertson 1997). For example, the largest nectar-feeding bird in New Zealand, tui, do not usually forage on small nectar-poor flowers and are known to aggressively monopolise the largest, richest flowers in a community, driving smaller birds to small flowers (e.g., Rasch & Craig 1988; Anderson 1997; Castro & Robertson 1997). Similar dominance hierarchies are found in Australia (Ford 1979).

Castro & Robertson (1997) demonstrated a dominance hierarchy in a survey of nectar-feeding birds on Kapiti Island (off the west coast of North Island) which is predator-free and has high bird densities compared with the mainland. Their analysis of floral preferences by tui, bellbird, and stitchbird, *Notiomystis cincta* (Meliphagidae), showed that many small-flowered species had sufficient nectar to support bird-foraging activity (Tables 7 and 8). However, only the smaller birds, bellbird and stitchbird, regularly visited dish blossoms of eight species with small- to medium-flowers listed in Table 8. In contrast, none of the three honeyeaters regularly visited 15 of the entomophilous species but they did make occasional visits to many of them (Table 8).

In a remarkable exception to this pattern, all three honeyeaters, including the large tui, regularly visited the small, shallow dish flowers of *Pseudopanax arboreus* (Araliaceae) and *Geniostoma rupestre* (Loganiaceae) (Table 7). These blossoms are undoubtedly entomophilous but bird visits to *P. arboreus* are so frequently reported they must be rewarding, even for tui (Godley 1979; Rasch & Craig 1988; O'Donnell & Dilks 1994; Anderson 1997, 2003; Castro & Robertson 1997). Castro & Robertson (1997) showed that cumulative nectar for the entire blossom (i.e., one inflorescence) in these species was equivalent to other ornithophilous single flowers. They proposed the term "lollipop" pollination because of the way in which the birds lap up the copious sticky nectar. Brown & Hopkins (1995) used the term "knob" flower for similar flowers of *Schefflera stahliana* and *S. actinophylla* (Araliaceae) in their community study of bird pollination in a New Guinea tropical rainforest. The adaptations for perching bird pollination in the New Guinea blossoms are similar to *P. arboreus*: compact inflorescences, protrusion of anthers, copious nectar, and reduction or absence of petals facilitating birds lapping up nectar.

How well matched are the birds for the morphology of these types of flowers? Unlike hummingbirds, perching-bird bill morphology did not correlate with flower morphology in the study by Brown & Hopkins (1995). Accessibility of nectar based on flower shape was not a predictor of bird pollinator species because the range of blossom classes visited by perching birds differs dramatically from those visited by hovering hummingbirds. Since perching birds are agile and acrobatic, capable of foraging from many different positions, Brown & Hopkins (1995) suggested that the key predictors will be body mass and perch size but these were not measured in their study. If so, then for perching birds, landing facilities rather than nectar access (i.e., flower shape) may be the most important factor to predict associations with blossoms.

Why perching birds visit such small, seemingly entomophilous, blossoms has two explanations depending on the size of the reward and morphology of the flowers. The flower visitation records of Castro & Robertson (1997) and other work by Rasch & Craig (1988) show that dominance hierarchies and the marginal value theorem explain some visits to small dish/bowl blossoms that are not favoured by any birds or only by smaller birds (Table 8), but it does not explain the regular visits to "knob" flowers (Table 7) by large birds. These flowers may be adapted for nectar lapping by perching birds as an integral part of a type of "lollipop" pollination.

Brush flowers and inflorescences

Association with brush flowers and inflorescences (e.g., Fig. 4B) has been an important component of the classical bird pollination syndrome as well as bee, bat, and non-flying mammal syndromes (Table 5; Faegri & van der Pijl 1979; Proctor et al. 1996). As previously discussed, these are the most highly generalised blossoms if they have sturdy landing platforms. In brush flowers, stamens are the attractive display (petals are absent) forming shapes such as "fluffy cups" (Brown & Hopkins 1995) or "shaving brushes" (Proctor et al. 1996). In contrast, brush inflorescences include diverse flower types, e.g., aggregations of brush flowers (*Metrosideros*, Fig. 4B) or of short tubular flowers with protruding anthers (e.g., *Hebe* spp. (Fig. 7A) and *Myosotis monroi* (Fig. 2G). Brush inflorescences composed of short tubular flowers are often entomophilous depending on landing platform stability and are not equivalent to brush inflorescences with sturdy brush flowers adapted for larger pollinators.

In New Zealand, there are at least eight bird-visited species with brush inflorescences (Tables 7 and 8) (O'Donnell & Dilks 1994; Castro & Robertson 1997). Of these, five are considered ornithophilous but two species with more delicate inflorescences and small flowers have been considered entomophilous: *Weinmannia racemosa* (Cunoniaceae) (Fig. 4A) and *Metrosideros perforata* (Myrtaceae) (Castro & Robertson 1997; Webb et al. 1999). *Hebe* spp. (counted as one instance in the list) are primarily entomophilous and only occasionally visited by birds (Godley 1979; Castro & Robertson 1997). In the Kapiti Island survey, all of the species with brush blossoms including *W. racemosa* but excluding *M. perforata* and *Hebe* spp. were regularly visited by all three honeyeaters (Tables 7 and 8). In brush inflorescences the level of generalisation can be very high, for example, *Metrosideros excelsa* is visited by many orders of insects as well as birds (Schmidt-Adam et al. 2000), bats (Arkins et al. 1999), and lizards (Whitaker 1987). Schmidt-Adam et al. (2000) showed that although birds carry large pollen loads, insects can be as effective as birds if they are very abundant. This illustrates that pollinator importance is a function of both the amount of pollen transferred per visit and the frequency and rate of visitation. It also suggests that *M. excelsa* may be considered a keystone species since it supports a diversity of pollinators.

Directed-access blossoms visited by birds

Most of the 16 taxa with directed-access blossoms that are regularly visited by birds in New Zealand (Table 7) have simple tubular flowers with the exception of *Vitex lucens* (Fig. 5B) and *Rhabdothamnus* *solandri* with gullet flowers, *Elaeocarpus dentatus* and *Myoporum laetum* with bell flowers, and *Carmichaelia williamsii*, *Sophora* spp. (Fig. 5E), and *Clianthus* spp. with tubular flag flowers. Similar floras, such as in Tasmania, also have bird-visited plant species associated with tubular flowers (Hingston & McQuillan 2000). In the Kapiti Island survey, all of the large directed-access blossoms had regular visitation by all three honeyeaters except *Sophora*, which was only visited by bellbirds at Kapiti Island (Castro & Robertson 1997) but is regularly visited and dominated by tui elsewhere in New Zealand (Kelly et al. unpubl.).

Interestingly, half of the 16 directed-access blossoms have been considered entomophilous rather than ornithophilous (Table 7). These species have small-to-medium tubular flowers and many are also visited by moths (e.g., *Pittosporum* spp., *Dracophyllum* spp. (Godley 1979; Primack 1983)). Moth and bird syndromes have certain similarities (Proctor et al. 1996) and cluster closely in a multivariate analysis of floral traits (Ollerton & Watts 2000). For example, birds by day and moths at night share access to the winter-flowering *Dysoxylum spectabile* (Meliaceae) (Fig. 5C) Whangarei, North Island (L. E. Newstrom & R. Uschold unpubl. data). The short white tubes with included anthers, sweet scent at night, and small amounts of nectar (2–5 µl; L. E. Newstrom & R. Uschold unpubl. data) are adapted to moths. However, this dioecious species (Braggins et al. 1999) also has features adapted to birds because the sturdy waxy flowers protect the ovules from damage by bird beaks. Because the hanging inflorescences are delicate, the landing facilities are better adapted to bellbird than the larger tui, which are only able to access flowers from branches (Anderson 1997).

An example of a large directed-access blossom that birds do not share with moths is the gullet flowers of *Vitex lucens* (Verbenaceae). The flowers have many features associated with bird pollination: red colour, exserted anthers, no scent, copious nectar (>150 µl/flower; L. E. Newstrom & R. Uschold unpubl. data) with high energy return (26 calories/flower; Anderson 1997). In Raumanga Park, Whangarei, abundant silvereye visited *V. lucens* but moths did not (L. E. Newstrom & R. Uschold unpubl. data). Moths in the vicinity (< 50 m away) were visiting *D. spectabile* and white flowers of horticultural *Camellia* spp. but they failed to visit the large *V. lucens* tree nearby. The dull red colour of *V. lucens* and lack of scent predict that moths would not detect this flower in spite of the excellent nectar access and landing facilities. This example demonstrates the value of the syndrome concept because, in this case, floral traits from the syndrome provide a better prediction than blossom class alone.

At a coarse scale (animal class), *Vitex lucens* is predicted to be specialised for birds and is considered ornithophilous (Anderson 1997; Castro & Robertson 1997). At a finer scale, is there evidence for specialisation (e.g., differential effectiveness) among bird species in *V. lucens*? All three honeyeaters (stitchbird, bellbird, and tui) visited *V. lucens* on Kapiti Island (Castro & Robertson 1997). However, tui are not well matched because they are too large for the exserted anthers to contact their forehead (Anderson 1997). In spite of the copious nectar reward, tui did not visit the exposed tree of *V. lucens* in Raumanga Park where bellbirds were absent and silvereye were visiting but tui were elsewhere in the vicinity dominating *D. spectabile* trees (L. E. Newstrom & R. Uschold unpubl. data). The preference by tui for *D. spectabile* over *V. lucens* in this case does not match expectations based on the amount of nectar. Other site characteristics such as exposure of the tree or landing platform problems at the flower may account for this. At Tiri Tiri Matangi Island (NE of Auckland), bellbirds were the most frequent visitor to *V. lucens*, but in the absence of bellbirds at Wenderholm, near Whangarei, silvereyes were more frequent than tui (Anderson 1997; Kelly et al. unpubl.). A specialised relationship between any one bird species and *V. lucens* requires more multi-site comparisons; however, based on morphological match, bellbirds are likely to be the most effective pollinator.

Disregarding pollinator effectiveness, some bird-visited species with directed-access blossoms appear to have generalised pollination, sharing access to diverse insect visitors. For example, *Sophora microphylla* (Fabaceae) is visited by tui (Fig. 5E), bellbirds, kaka, silvereyes, chaffinches, bumblebees, honeybees, butterflies, and indigenous moths at night (Godley 1979; Clout & Hay 1989; Kelly et al. (unpubl.). In Chile, hummingbirds and large bumblebees visit this species (Godley 1979; Clout & Hay 1989). Nevertheless, the relative effectiveness of these visitors appears to show some degree of specialisation. Morphological match indicates that tui are the most effective in removing and depositing pollen because the long floral tubes (based on the flag flower construction with separated petals forming a tube) are too deep for small birds such as bellbirds and silvereyes. These small birds resort to accessing nectar at the base of the flower between the petals thus often avoiding contact with pollen and stigma (Anderson 1997). In addition, tui are usually the most frequent visitors, dominating in four out of six sites at which they were present, with bellbird dominating over tui at another two sites, and silvereyes dominating when both tui and bellbird are absent (Kelly et al. unpubl.). Further evidence of an important relationship between tui and *S. microphylla* is that at Tiri Tiri Matangi Island (NE of Auckland), visitation was higher than indicated by tui background abundance and lower than indicated by bellbird background abundance (Anderson 1997). This means that in the absence of tui, bellbird or silvereye may be effective pollinators; but, in the presence of tui, they are probably parasites since they may be robbing nectar or wasting pollen that could have been better transferred by tui (see pollen presentation theory; e.g., Thomson 2003).

Nectar robbery in directed-access flowers is a critical feature to examine when considering the effect of exotic pollinators on indigenous pollination systems. For example, in *S. microphylla* the exotic hedge/house sparrow, which is even less suited for pollinating this species, pierces the base of the flower (Stidolph 1974 cited in Godley 1979). Holes made by silvereyes or sparrows gave illegitimate access to large populations of honeybees (which are unable to pierce the base) at Landcare Research garden in winter 2004 (L. E. Newstrom pers. obs.). Bumblebees also robbed nectar and may be strong enough to make their own holes. As one of the few winter-flowering species, *S. microphylla* is attractive because the energy return is high (28 calories/flower; Anderson 1997). Exotic bees could drain a significant proportion of the nectar but it is not known if indigenous birds could outcompete at the same trees. In bird-pollinated *Phormium tenax*, another tubular-flowered species, exotic insects and indigenous lizards have also been observed to rob nectar (Whitaker 1987; Craig & Stewart 1988; Donovan unpubl.; Kelly et al. unpubl.).

Closed-access blossoms visited by birds

Mistletoes (Loranthaceae)

Among the bird-pollinated flora of New Zealand, perhaps the most spectacular are the red-flowered mistletoes (*Peraxilla* spp.) because of their highly unusual closed-access blossoms. The discovery of explosive flowering in *P. colensoi* and *P. tetrapetala* (Fig. 6D), which was the first time explosive bud opening had been found in these mistletoes outside Africa (Ladley & Kelly 1995), initially suggested a highly specialised pollination system. In explosive mistletoes, nectar is already present and the pollen is shed prior to the buds being opened explosively by a twist of a bird's beak applied to the tip of the bud (Ladley et al. 1997). It appeared in these species that only tui and bellbirds regularly performed the feat, and a dependence on these two species seemed probable. However, Kelly at al. (1996) subsequently observed small indigenous short-tongued bees (*Hylaeus* and *Leioproctus*) opening buds (at the time, these authors were unaware that discovery of bee-opening in another mistletoe, *Alepis flavida*, had already been made much earlier by Godley and reported in Dugdale (1975) and Godley (1979)). The realisation that bees as well as birds opened buds, and that many insects visited the flowers once they had been opened, prompted Robertson et al. (2005) to reconsider the degree of specialisation and the idea that all pollen removal and deposition occurs in the act of bud opening by birds.

Nectar production in these plants indeed stops soon after ripe buds are opened (Ladley et al. 1997), but pollen deposition in the course of flower opening by either birds or bees was remarkably low (Robertson et al. 2005), and, instead, pollen continued to accumulate on the stigma over the next several days (see also Robertson et al. (1999)). Hand-opening buds inside a cage that excluded birds but allowed insects access, including the bud-opening bees and a range of other insects, demonstrated that, at two out of three sites, insects could substantially increase fruit set (compared with bagged control flowers) by gradually adding pollen to stigmas of opened flowers. This occurred despite the wide spatial separation between stigmas, nectar remains, and anthers and the likelihood that these visitors would fail to contact the stigmas. It was considered much more likely that birds would regularly contact the stigma in the course of searching the plants for new buds to open (Robertson et al. 2005).

Taken together, these results suggest that the most effective pollinators are the indigenous honeyeaters since they open buds, carry high pollen loads, and are much more likely to contact the stigma of open flowers. Indeed, bees may, through high rates of pollen removal, reduce the chances of pollen deposition by birds since they limit the standing crop of pollen in the system (Wilson & Thomson 1991; Thomson & Goodell 2001). However, given the reduction in avian honeyeater populations that has occurred on the New Zealand mainland, bees may now offer an alternative service that can at least partially replace that provided by the declining bird pollinators. If the bud is not opened by a specialist, it falls from the plant unopened (Fig. 6D), so the dependence on the bud-opening pollinators is absolute.

Bat pollination

New Zealand has only two species of indigenous terrestrial mammals: the short-tailed bat, *Mystacina tuberculata* (an archaic bat, which is the sole member of the endemic New Zealand family Mystacinidae), and the long-tailed bat, *Chalinolobus tuberculatus* (in the cosmopolitan Vespertilionidae) (Daniel 1976; Godley 1979; Arkins et al. 1999). Flower-visiting bat species only total about 50 worldwide and are represented by the megachiropterans (Pteropodidiae) in the Old World and the microchiropterans (Phyllostomidae) in the New World (Dobat 1985 cited in Winter & von Helversen 2001). The most highly specialised bats for nectar feeding are the long-tongued subfamily Glossophaginae with 35 species in the Neotropics (Winter & von Helversen 2001).

Mystacina, unlike *Chalinolobus*, has several adaptations for nectar feeding such as the small brush of fine hairs or papillae at the tip of its tapered tongue, although the brush is considerably less marked than in Glossophaginae bats (Daniel 1976; Arkins et al. 1999). In contrast, *Chalinolobus* is solely an aerial insectivore (Daniel 1976) and therefore not involved in pollination. Specialist flower-visiting bats generally require large nectar resources (Winter & von Helversen 2001) but *Mystacina* is not a nectar-feeding specialist; it has a broad omnivorous diet including flying and non-flying arthropods, plant parts such as flowers and fruits, as well as nectar and pollen (Arkins et al. 1999). *Mystacina* does not hibernate in winter as does *Chalinolobus* (Daniel 1976). As a winter-nectar feeder, *Mystacina* is in competition with honeyeaters when flowering and fruiting levels are low (Daniel 1976), and, as a large nocturnal feeder, it would also be in competition with lizards (Whitaker 1987).

Bat pollination in New Zealand is unusual because *Mystacina* is capable of "gleaning"; i.e., foraging on surfaces on the ground or tree trunks, a feeding habit documented in some other bats (Arkins et al. 1999 and references cited therein). *Mystacina* has evolved behavioural and morphological adaptations associated with "gleaning", such as the ability to use its folded wings as a second pair of limbs for manoeuvring on a surface (Daniel 1979, 1990). The absence of mammalian predators in New Zealand has allowed *Mystacina* to develop a unique mutualism on the ground with the rare, dioecious, obligate root parasite *Dactylanthus taylorii* (the sole New Zealand member of Balanophoraceae) in the North Island (Ecroyd 1996). Intensive investigation including video footage showed that *Mystacina* is not only a pollinator but also the most frequent. However, possums (*Trichosurus vulpecula*), ship rats (*Rattus rattus*), Pacific rats (*Rattus exulans*), and, less often, mice (*Mus musculus*), and various birds and insects, particularly wasps and flies, also visited (Ecroyd 1996). This species is now endangered partly because of habitat destruction (Wilson & Given 1989) but also because introduced mammals, especially the Pacific rat and possum, destroy the flowers (Ecroyd 1996).

A few other plant species may be bat pollinated. Pollen analyses from fresh guano and stomach contents of *Mystacina* at Omahuta Kauri Sanctuary in the North Island and on Stewart Island (Daniel 1976) showed high percentages of pollen from *Metrosideros* spp. (Myrtaceae) and *Knightia excelsa* (Proteaceae), which both have abundant nectar. Less pollen was found from *Collospermum hastatum* (Liliaceae) and a trace from *Freycinetia baueriana* (Pandanaceae) although *Mystacina* take fruits from both these species (Arkins et al. 1999). The association with bat pollination of these latter species has not been demonstrated, but *F. baueriana* is adapted for bat pollination (Cox 1984; Lord 1991). On Little Barrier Island (east of Auckland), pollen loads taken from bat fur and guano showed three indigenous plant species most commonly visited for pollen: *Metrosideros* spp., *Knightia excelsa*, and *Collospermum* spp. (Arkins et al. 1999). Further evidence associating *Mystacina* with pollination of *M. excelsa* consists of recordings of bat echolocation "passes". *Mystacina* averaged 175 passes per night on flowering trees compared with only 25 on non-flowering trees, indicating that these bats are actively foraging in *M. excelsa.*

Godley's (1979) analysis of the four bat-visited blossoms (*Metrosideros* spp., *Knightia excelsa*, *Collospermum* spp., and *Freycinetia* spp.) showed three important features: "the pollen is exposed; the nectar, if present, is not hidden but easily available to a tongue that can protrude 5 mm; and the flowers are aggregated in large or prominent inflorescences". These four taxa all have open-access aggregated brush or dish blossoms. *D. taylorii* has similar features. The only potential bat blossom with large directed-access flowers was suggested by Lloyd (1985 citing Cranwell 1962): *Tecomanthe speciosa* (the sole New Zealand member of Bignoniaceae). This species, with large cream-coloured tubular flowers (4 cm long) and short peduncles, is considered an endangered endemic of tropical origin and occurs only in the Three Kings Islands, off the north tip of the North Island (Allan 1961; Wilson & Given 1989). Although it appears to be adapted for bat pollination, no bats have ever been found on the islands and the plants have not been known to reproduce sexually in the wild (Wilson & Given 1989).

Otherwise, no classically specialised bat blossoms are found in New Zealand, i.e., large, dull, white or pale flowers with copious nectar that are not easily detected by other animals and hang down from long peduncles thus excluding non-flying animals (Faegri & van der Pijl 1979; Proctor et al. 1996; Winter & von Helversen 2001). The New Zealand bat-visited blossoms discussed above tend to have easy access to non-flying mammals. For example, Lord (1991) found that possums browse on *F. baueriana* and pollination still takes place in the absence of *Mystacina*. The disadvantage of generalisation is illustrated in *D. taylorii*. The scent of the flowers attracts possums, but they destroy the flowers thus endangering the plant species (Ecroyd 1996). Resistance to such damage may be a feature of some of the other bat-pollinated flowers, particularly the brush inflorescences, but this has not been investigated.

Lizard pollination

A lizard pollination syndrome has never been described. Indeed, many doubt that lizards are able to transfer pollen. Whitaker (1987) documented that at least for *Metrosideros excelsa* (Myrtaceae) two gecko species (*Hoplodactylus duvauceli* and *H. pacificus*) probably achieve pollination in New Zealand. Their pollen deposition rate is unknown but they do contact the stigma, carry pollen for up to 12 hours at least 50 m, and may facilitate outcrossing amongst plants (Whitaker 1987). Similarly, Eifler (1995) observed *H. duvauceli* and *H. maculatus* feeding on nectar from *M. excelsa* and *Phormium tenax* (Agavaceae) (Fig. 5F).

Whitaker (1987) recommended that other brush inflorescence blossoms be investigated such as *Knightia excelsa* (Proteaceae) or *Weinmannia racemosa* (Cunoniaceae), which are both also bird-pollinated. However, he doubted that lizards are effective pollinators for other classes of blossoms. For example, although geckos can force petals apart to reach nectar in the robust tubular flowers of *P. tenax*, he thought the blossoms did not have the best morphology for pollen transfer compared with brush flowers of *M. excelsa*. Eifler (1995), however, observed geckos pressing their heads into the corolla on *P. tenax*. Gecko species also take nectar from *Myoporum laetum* (Myoporaceae) and *Hebe bollonsii* (Plantaginaceae (Scrophulariaceae)), but these flowers do not have suitable morphology for pollen transfer (Whitaker 1987) and seem too fragile to withstand damage from such relatively large animals.

Whitaker's (1987) proposal of lizard pollination was one of the earliest reports on this phenomenon (NyHagen et al. 2001). Since then, a number of new studies reviewed in Traveset & Sáez (1997) and NyHagen et al. (2001) provide experimental evidence that lizards may be effective pollinators, particularly on islands. On Cabrera Island (in the Balearic Islands), lizards played a predominant role in the pollination of the shrub *Euphorbia dendroides* (Euphorbiaceae) because, at one site, they were more frequent in the cold season than insects (Traveset & Sáez 1997). Nonetheless, in their study, no evidence was found for pollinator-mediated selection on plant traits related to fitness. Although lizards may be pollinators, any adaptations of the plants or the pollinators have yet to be demonstrated and hence no syndrome can be described. The floral traits that match the requirements for lizard pollination are similar to those for other large non-flying animals: accessible nectar that can be lapped up, stigma and anthers exposed beyond the corolla and adapted for imprecise pollen transfer, sturdy landing platforms, and, most importantly, protection from damage to the ovaries.

In New Zealand, lizard-visited blossoms discovered so far have generalised pollination systems with open access blossoms that birds, bats, and insects also visit. Pollination and dispersal by lizards is most common on islands, which could be explained by the high densities of lizards and low predation risk on islands compared with mainland situations (Olesen & Valido 2003). In New Zealand, lizards have been shown to play a role in frugivory (Wotton 2002); their contribution to pollination merits further investigation.

EFFECTS OF EXOTIC POLLINATORS AND PLANTS ON INDIGENOUS POLLINATION

In the past, Thomson (1927) and Heine (1937) have both stated that land conversion in New Zealand may have already depleted indigenous flower visitors and, coupled with the introduction of exotic plants and animals, the interpretation of indigenous pollination systems would be difficult and complicated. It is beyond the scope of this review to address the potential for disruption of indigenous pollination systems due to the loss of indigenous pollinators or plants: little information exists for insect pollination, bird pollination has been reviewed by Kelly et al. (2004), and some bat pollination issues have been discussed by Ecroyd (1996). This section focuses on the potential effects of the addition of exotic pollinator and plant species, which have both become extremely widespread and ecologically important in New Zealand. In the context of pollination, few exotic birds play a significant role (Kelly et al. unpubl.), but amongst the insects, the introduced social bees are of great importance. The long-term effects of introduced social bees, primarily the honeybee and bumblebee, on indigenous pollination systems in New Zealand and Australia have recently been debated (e.g., Butz Huryn 1997; Parker 1997; Morales & Aizen 2002; Parker & Haubensak 2002; Goulson 2003a).

Exotic insect pollinators are not expected to simply blend into the mix of indigenous pollinators and connect with indigenous flora by merely expanding the existing web of species interactions. Exotic social bees differ from indigenous bees in many characteristics: (1) size, e.g., bumblebees are large; (2) diurnal activity, e.g., bumblebees and honeybees forage earlier than indigenous bees; (3) seasonality, e.g., honeybees are active in some regions in winter; (4) temperature flight thresholds, e.g., bumblebees tolerate cold; (5) quantity of floral resources needed, e.g., honeybees and bumblebees require abundant pollen and nectar; and (6) population dynamics, e.g., honeybees form very large colonies and bumblebees smaller colonies but indigenous bees are primarily solitary. Exotic bees may, therefore, have unexpected effects on indigenous pollination systems. Similarly, as discussed above, exotic plant species differ from indigenous species primarily in the diversity of blossom classes, the complexity, size, and colour of flowers, and opportunities for specialisation.

Insights into the debate about the effects of exotics can be gained by systematically analysing all of the potential combinations using the blossom class analysis proposed above. The three possible combinations for the effects of exotics are: (1) exotic pollinators on exotic plants, (2) exotic pollinators on indigenous plants, and (3) indigenous pollinators on exotic plants (see summary in Table 9). Goulson (2003a) reviewed the possible negative consequences of exotic pollinators: an increase in invasions by exotic pollinators spreading exotic weeds, competition with indigenous pollinators for floral resources, and disruption of the pollination of indigenous plants. He also included competition for nests and co-introduction of natural enemies that may infect indigenous organisms, but these are not considered a problem for indigenous bees in New Zealand (Donovan 1990).

Not all effects of exotics are predicted to be negative, for example, the gain of a better pollinator can increase the fitness of an indigenous plant species or the gain of an exotic plant species may provide supplementary floral resources for indigenous pollinators. The following discussion lists examples of potential negative and positive effects of the different combinations of exotic pollinators and plants, in the context of the benefits to New Zealand's economy and biodiversity in pollination systems. Some examples are obvious or have already been demonstrated but others are speculative. This is a new area of research in need of field observations and experiments and has significance for conservation, restoration, biosecurity, biosafety, and sustainable agriculture, horticulture, and honey production (Table 9).

Exotic pollinators on exotic plants

Positive effects

The worldwide importance of pollinators for sustaining agricultural and horticultural production (Delaplane & Mayer 2000; Kevan & Imperatriz-Fonseca 2002; Goulson 2003b) particularly applies to New Zealand's economy. Both social and solitary bees have been successfully imported to meet these needs as discussed above (Donovan 1990, unpubl.). Honeybees and bumblebees are the most abundant and widespread pollinators for crops in New Zealand (e.g., for clover, kiwifruit, and seed production industry). Bumblebees were specifically introduced to New Zealand for clover seed production as mentioned above. It is well recognised that economic benefits of social bees go beyond their pollination services to exotic crop and pasture species and include nitrogen fixation by clover pastures. In addition the honeybee industry benefits from many exotic plant species (Butz Huryn 1995; Butz Huryn & Moller 1995).

Negative effects

Hanley & Goulson (2003) summarised evidence for a causative relationship between exotic bee pollinators and the spread of certain exotic weeds. In particular, the specialised relationships between honeybees and/or bumblebees and weedy Fabaceae species are of concern (e.g., *Cytisus scoparius*, *Lupinus arboreus*, *Ulex europaeus*). Butz Huryn & Moller (1995) listed the association of honeybees with these three plant species as having an unknown importance for weed problems in New Zealand because of the lack of information on their pollination. However, all three species have closed-access flag blossoms that are specialised for either honeybees or bumblebees or both. Hanley & Goulson (2003) and Goulson (2003a) cited evidence, including examples from New Zealand, that without these exotic bees reproduction in the weeds would be limited or reduced. For fabaceous species with closed-access flag blossoms, the inability of indigenous bees or other insects to open the flowers means that the weeds depend on large social bees that are capable. This relationship, incorporating a positive feedback loop between plant and pollinator, has been called an invasive mutualism in which the exotic specialist pollinators and the exotic weeds promote each other's expanded distributions (Hanley & Goulson 2003).

Another example, though minor and not a threat at this point, is the absolute dependency of figs on their specialised fig wasp pollinators. Gardner & Early (1996) recommended that planting fig trees be discontinued and naturalised trees in areas of ecological interest be removed. The trees may not be a serious threat if they are not weedy but their size and vigour, lack of possum browsing, and especially their prolific fig production (which provides food for non-indigenous frugivorous birds and possums, rats, and mice in seasons of scarcity) may result in negative effects. With their specialist pollinators available, the spread of fig species can be expected and may result in an invasive mutualism in the long term (the Morton Bay fig has recently been listed as a weed by the Auckland Regional Council).

The potential risk of invasive mutualisms can be predicted using the blossom class analysis and syndrome concept. Any blossom that fails to attract

Table 9 Potential positive and negative effects of the introduction of exotic plants and pollinators on indigenous pollination systems in New Zealand. Positive and negative effects are considered in the context of New Zealand's economy and sustainable production with reference to effects on biodiversity conservation, biosecurity, and biosafety. Examples are discussed in the text; some are obvious or have been demonstrated but others are possible or potential and have not been investigated yet.

	Exotic pollinators		Indigenous pollinators	
	Positive effect	Negative effect	Positive effect	Negative effect
Exotic plants	*Sustainable production*: increased crop and pasture seed yield and honey production, e.g., kiwifruit, *Brassica* spp., clover pasture and honey including nitrogen fixation	*Biosecurity*: invasive mutualisms (weeds and their specialist pollinators), e.g., Lupin, broom, figs. *Biosafety*: potential for exotic pollinators to carry pollen from GM crops to wild relatives	*Biodiversity*: enhanced floral resources for indigenous pollinators, e.g., solitary bees on kiwifruit, *Brassica* spp., weeds	*Biodiversity*: potential displacement of indigenous plant species if indigenous pollinators switch to exotic plant *Biosafety*: potential for native pollinators to carry pollen from GM crops to wild relatives
Indigenous plants	*Sustainable production*: increased honey production such as manuka export honey *Biodiversity*: improved pollination and seed set e.g., buzz pollination of *Solanum laciniatum*, bumblebees on *Hoheria*	*Biodiversity*: 1. displaced indigenous pollinators, e.g., bees potentially draining resources of *Sophora* or manuka 2. Damaged indigenous plants, e.g., possum *Dacytlanthus taylorii* 3. inadequate pollination or nectar robbery		

or cannot be handled by indigenous pollinators is a candidate for an invasive mutualism if the plant species has weedy tendencies in the long term and its exotic pollinators are present. Understanding this relationship can provide opportunities for weed management options especially for off-shore islands without social bees.

Exotic pollinators on indigenous plants

Positive effects

An important economic benefit of exotic insect pollinators on indigenous plants occurs in the honeybee industry. Butz Huryn (1995) documented 224 indigenous plant taxa used by honeybees. Bird-visited species, which tend to have copious nectar, are especially important. Plant species providing honeybees with nectar beyond the amount required for current colony maintenance are called "surplus producers" (Butz Huryn & Moller 1995). Many of these species have bird-visited brush blossoms (Tables 7 and 8), such as the marketed specialty honeys of *Weinmannia racemosa*, *Knightia excelsa*, and several *Metrosideros* spp. (Butz Huryn 1995; Butz Huryn & Moller 1995). Others have bird-visited tubular and bell blossoms such as *Phormium tenax*, *Sophora microphyllum* and *S. tetraptera*, and *Elaeocarpus dentatus*. The open-access "knob"-flowered *Pseudopanax arboreus* and *Geniostoma rupestre* are also surplus producers. Primarily insect-visited surplus producers are *Discaria toumatou* (Rhamnaceae) (Primack 1979; Webb 1985) and manuka, *Leptospermum scoparium* (Primack & Lloyd 1980); the latter is an increasingly important export market honey because of its medicinal value.

A benefit for biodiversity derived from exotic pollinators on indigenous plants may be the possibility of enhanced pollinator services that could improve fitness of indigenous species through increased seed set, particularly since both honeybees and bumblebees carry large pollen loads. This advantage depends on the blossom class and size of flower but could apply, for example, to large polliniferous flowers such as *Hoheria* spp. In addition, buzz-pollination in *Solanum laciniatum* and *S. aviculare* may only be effectively achieved by bumblebees, which would promote outcrossing in this species and improve pollination beyond the level that indigenous insects could achieve by scavenging spilled pollen.

Negative effects

Although exotic pollinators may increase fitness in indigenous plants, this may come at a net cost if indigenous pollinators are displaced. It is difficult to find unequivocal evidence for such displacement, not only because of the lack of field data for New Zealand but also because manipulative experiments are difficult to design (Goulson 2003a). The absence of indigenous pollinators at some sites populated by exotic pollinators may be due to disturbance or habitat loss rather than competitive displacement (Butz Huryn 1997). Nevertheless, Murphy & Robertson (2000) have at least some circumstantial evidence that honeybees are displacing indigenous insects from nectar resources in Tongariro National Park in New Zealand. Examples from other countries are cited by Goulson (2003a). The competition can be either exploitative due to draining floral resources (social bees forage earlier than indigenous bees) or interference with active aggressive interactions or deterrence at the flower. In addition, the effect of nectar robbing by honeybees, bumblebees, and introduced birds has not been assessed for indigenous plants such as *Sophora microphylla*. Finally, in some blossoms, social bees or other exotic insects may be inefficient compared with indigenous insects and reduce fitness of indigenous plants (e.g., an example in Australia demonstrated by Gross & Mackay 1998).

Indigenous pollinators on exotic plants

Positive effects

For indigenous pollinators, the main benefit of exotic plants, including crops (e.g., kiwifruit, brassica) and flower gardens, is an increase in available floral resources, particularly from nectar- and pollen-rich flowers that are accessible and attractive. Indigenous bees visit a large number of exotic plants, e.g., solitary *Lasioglossum sordidum* has been recorded from the blossoms of 56 exotic plant species (Donovan unpubl.). The level of supplementation beyond the resources available in indigenous plants is unknown.

Negative effects

It is possible that indigenous insects, particularly bees and perhaps butterflies and moths, could favour exotic over indigenous plant species if the pollen or nectar was superior or easier to extract. Would this leave some indigenous species without pollinator services in some communities or are there sufficient indigenous and exotic pollinator populations to prevent such a possibility? Little information is available on the relative preferences of indigenous insect pollinators for exotic versus indigenous plant species. Primack (1983) found exotic and indigenous pollinators sharing some exotic species but the population levels of exotic social bees were not high at the sites. Community-level analyses are needed to address this question because pollinator preferences are influenced by the available abundance and composition of floral resources and competing pollinators.

CONCLUSIONS AND FUTURE RESEARCH

Breeding systems and pollinator dependency

The floral biology of the New Zealand flora does not appear to have been overwhelmingly influenced by selection for reproductive assurance. Many plants are highly dependent on pollinators for seed production, and autonomous selfing does not appear to be particularly common in the flora. There is currently a modest set of plants that have been shown to be self-incompatible, but the proportion of the species tested that are incompatible is comparable with other floras. Sexual dimorphism and monoecy are common features of the flora and impart those species with pollinator dependence. Taken together, plants adopting these strategies represent a large proportion of the flora especially amongst the woody plants. Relatively few species have been shown to be regular autonomous selfers and the proportion of flora they represent is not especially high.

There is increasing evidence, particularly amongst the bird-pollinated plants, of strong pollen limitation sufficient perhaps to compromise the persistence of some populations in the wild. Bird and bat pollinators have declined over much of their former ranges, and may in many cases be at densities too low to efficiently pollinate some indigenous plants. The demographic consequences of these shifts in pollinator service require further investigation, but some species appear to be likely to suffer seed limitation and population decline as a result of these changes.

Pollination systems

The potential for disruption of indigenous pollination systems in New Zealand is difficult to assess without baseline field data. Nevertheless predictions can be made using the blossom class and syndrome concepts although there are limitations. New Zealand has a limited diversity of indigenous pollinators, including insects (flies, solitary short-tongued bees, moths, and butterflies) and perching birds (primarily honeyeaters). One bat and a few lizard species play a minor role. Pollination and visitation by beetles and small insects (e.g., thrips, weevils) are evident but no data are available to assess their importance although some species with inconspicuous flowers appear to be adapted for small insects. Pollination in winter, especially in canopy trees of broadleaf forests of the North Island, is distinctive because of the dominance of bird visits to trees. Otherwise, insect pollination predominates in terms of number of species visited and pollinated. Exotic social and long-tongued bees, self-introduced silvereye, and other birds that have naturalised are now important in the pollination of both indigenous and exotic plant species. Indigenous pollinators also regularly visit and may benefit from exotic plants.

A conceptual framework using a two-tiered approach for predicting pollination systems in New Zealand is proposed. The first part, the blossom class analysis, is preliminary and operates at a coarse scale to make initial predictions of floral visitors and potential pollinators. The "blossom class – functional group" matrix is based on physical match of the visitor according to access to rewards, landing facilities, and protection of the ovary. It provides a rationale for exclusion of floral visitors and estimation of potential specialisation. For example, closed-access blossoms in the indigenous flora tend to have specialised pollination (e.g., greenhood orchids, flag flowers of *Carmichaelia*, buzz-pollinated flowers of *Solanum*, and explosive mistletoes). Large directed-access blossoms tend to predominate in bird pollination, with potential for specialisation in terms of which bird species are more effective (e.g., tui on *Sophora microphylla*, bellbird on *Vitex lucens*). However, other birds and insects also visit, pollinate, and rob these flowers. Multi-site comparisons highlight that plant–pollinator relationships shift in time and space but, at the scale of animal class, it is clear that directed-access flowers such as *V. lucens*, *S. microphylla*, and *P. tenax* have floral traits adapted for birds. If we consider only the 28 species most frequently visited by birds (Table 7), then 57% (16 taxa) have directed-access tubular blossoms while 22% (6 taxa) have open-access brush blossoms, only 14% (4 taxa) have open-access dish or "knob" blossoms, and 7% (2 taxa) have closed-access explosive bud blossoms. Almost no data are available for interpreting pollinator effectiveness in insect pollination. Some evidence, however, indicates that indigenous bees may be the most effective pollinators in some open-access blossoms corresponding to the "small-bee syndrome", e.g., *Corokia cotoneaster*, but diverse other insects also visit.

On the other hand, the most generalised of all blossoms are the open-access brush inflorescences with sturdy landing facilities which are visited and pollinated by all pollinating animal classes: insect, bird, bat, lizard, and other non-flying animals. The importance of each of these depends on their effectiveness, visitation rate, and abundance; therefore, pollen presentation theory and population dynamics are needed to interpret these systems. The primary limitation of using the blossom class as a predictor is that it does not distinguish pollinators from visitors or robbers and fails to predict exclusions from an open-access flower (e.g., if a potential visitor does not detect or is not attracted (cryptic specialisation)). However, the analysis does predict highly specialised systems in closed-access blossoms which have associations that are invariant over time and space (absolute specialisation) in that if the specialised pollinator is absent, then no pollination is likely (e.g., figs, certain flag blossoms).

The second part of the conceptual framework operates at a finer scale and uses the floral traits of the syndrome concept such as those mediating detection, attraction, and deterrence. For example, pollinators may ignore open-access blossoms that have nectar rewards below the threshold for profitable foraging, although this depends on which other floral resources and pollinators are in the community. Pollinators may be excluded from some open-access blossoms based on scent or visual detection, e.g., moths not visiting *Vitex lucens*. The value of the syndrome concept derives from the predictive power of associations between floral traits (especially nectar quantity and concentrations) and pollinator traits based on behaviour and sensory capacities of the pollinator.

Within each classical pollination syndrome the blossom class analysis shows a continuum of specialisation from open-access to closed-access (longer tubes, more tightly closed complex flowers). Highly specialised closed-access blossoms are not common in the indigenous New Zealand flora. The predominance of open-access small, white or pale, dish/bowl blossoms in New Zealand are best characterised by the "small-bee syndrome", which is a generalised syndrome matching the predominance of indigenous short-tongued bees, which have not been well appreciated in the early literature. In addition, unusual associations for a few species with small open-access flowers could not be predicted by either the blossom class or syndrome concepts and this reflects our lack of knowledge about perching-bird pollination syndrome in the Southern Hemisphere. For example, "knob" flowers associated with perching birds are relatively uninvestigated and have not been included in the classical bird syndrome. Similar blossoms with convex nectar surfaces adapted for lapping up copious nectar may be important for bat and lizard pollination or other large animals in the Southern Hemisphere.

The above examples demonstrate both the value and limitations of coarse-scale blossom class and fine-scale syndrome trait analyses for interpreting and predicting plant–pollinator relationships in New Zealand. The much debated syndrome concept can be interpreted at several levels. At the most basic level, a pollination syndrome is akin to a medical syndrome because it (1) does not make perfect predictions, (2) is influenced by context, and (3) demonstrates high levels of variability among organisms and over time. When a syndrome is defined at this level (e.g., as a group of symptoms that consistently occur together as a characteristic combination (Concise Oxford Dictionary)), it is useful for predicting at least coarse-scale (animal class) plant–pollinator relationships (e.g., syndrome traits have explanatory power to address cryptic specialisations not predicted by blossom class analyses). This definition of the syndrome concept is not useful for interpreting evolutionary patterns (evolutionary specialisation) or predicting specialisation over broad temporal and spatial scales (ecological specialisation), but it does argue for a pluralistic approach to using the syndrome concept (similar to multiple definitions for the species concept).

The view that New Zealand has predominantly generalised entomophilous pollination systems is valid but must not be overstated to include the entire flora during all seasons or assume that all insect pollination systems are homogeneous and that flies conduct the majority of the pollination. There is strong evidence that community-level pollination systems are highly structured with clear differentiation among pollination syndromes in many cases. Specialisation, though uncommon, is evident and can be predicted from the blossom class. More examples of specialisation are expected in insect-pollinated plants, particularly cryptic specialisation based on scent or size of nectar reward.

Future research

As one of the most critical and essential ecosystem services, pollination in the context of plant breeding systems represents an important area for further research, particularly since so little is known about either of these aspects in our indigenous flora.

Apart from the need for investigating neglected insect pollination systems, the most important areas of research are identifying pollinator-dependent plant species and vulnerable specialist pollination systems, as well as determining the positive and negative effects of exotic pollinators and plants on indigenous pollination systems. To advance these goals, several approaches are available. Anderson et al. (2002) recommended three types of comparisons for reproductive biology: (1) members within the same clade (phylogenetic mapping studies); (2) populations of a single species over a geographical range and years; and (3) interactions at the community level over time.

Phylogenetic studies

Godley (1979) and Lloyd (1985) set the stage for pollination studies in New Zealand. Their recommendations to use the plant genus as the unit of analysis to search for patterns in floral traits among congeneric species from overseas forecast modern analyses of mapping floral traits and pollination systems onto phylogenies. These phylogenetic analyses may reveal both the evolution and loss of specialisation, e.g., despecialisation in *Myosotis* and *Oreostylidium*. As more phylogenies become available, the radiation of different groups may show that despecialisation is more prevalent than respecialisation in New Zealand. The increasing use of phylogenetic data for interpreting the evolution of reproductive systems will contribute to further progress on many of the questions on the evolution of the New Zealand flora originally raised by Godley (1979) and Lloyd (1985).

Single species and guild studies

Focal studies of single species or guilds at multiple sites over time reveal the resilience of pollination systems under different pollinator regimes. Such studies are represented by those on mistletoe and *Fuchsia* and several bird-pollinated guilds. Further work at the guild level for bird-pollinated species as well as bat- and lizard-pollinated species will demonstrate the relative roles of these larger pollinators and their vulnerability to habitat loss. The management of endangered and vulnerable species relies on knowledge of dependencies on the part of both pollinator and plant species for the long-term sustainability of conservation and restoration projects.

Community-level studies

Community-level analyses are required to investigate the potential for specialisation and the effects of exotic plants and pollinators on indigenous pollination systems. When diverse plant–pollinator communities are compared, they reveal how pollinator substitution, redundancy, and complementation can be achieved for given blossom types. Community-level studies in regions other than montane and subalpine South Island are needed to provide baseline data on the relative importance of different functional groups of pollinators, indigenous and exotic. In particular, knowledge of the extent of invasive mutualisms that depend on specialist exotic pollinators will assist their management in land-use planning, particularly for offshore islands. Our ability to assess positive and negative effects of exotic pollinators and plants in the context of New Zealand's economy and biodiversity as well as declines in both exotic and indigenous pollinators, especially insects, is hampered by an almost complete lack of quantitative data for baseline monitoring in plant communities in New Zealand.

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Appendix 1 Glossary of terms and abbreviations

Actinomorphic: radially symmetrical flower, e.g., buttercup.
Agamospermy: reproduction by seed without sexual fusion.
Andromonoecy: all plants bear both male and hermaphrodite flowers.
Anemophily: wind pollination.
Anthesis: flower opening.
Apomixis: the agamospermous production of seed without involving male gametophytes.
Autochthonous: evolved or derived from within, e.g., characters that developed following colonisation.
Autogamy: seed derived from any mode of self-pollination (autonomous and facilitated).
Autonomous selfing: autogamy that occurs within a flower, without the aid of a pollen vector.
Autonomous selfing index (ASI): the ratio of seed set following pollinator exclusion to seed set from hand-crossing.
Corolla: inner whorl of the perianth composed of free or fused petals an surrounding the sexual organs of a flower.
Dichogamy: the temporal separation of male and female phases within flowers.
Dicliny: having unisexual flowers, either male or female, on the same or different plants.
Dioecy: having male and female flowers on separate plants.
Entomophilous: pollinated by insects.
Geitonogamy: autogamy caused by flower-to-flower pollination on the same plant.
Gynomonoecy: all plants bear both female and hermaphrodite flowers.
Gynodioecy: some plants with only hermaphrodite flowers and other plants with only female flowers.
Herkogamy: the spatial separation of male and female function within flowers.
Heterostyly: plants occur as two or three morphs that differ reciprocally in the placement of anthers and stigmas in the flower tube, only between-morph pollen movements result in seed production.
Microcantharophily: syndrome of small beetles and other small insects (bugs, etc) pollinating flowers.
Monoecism: unisexual flowers of both types (male and female) on the same plant.
Ornithophilous: pollination by birds.
Partial-compatibility: seed set following self-pollination is reduced compared to cross-pollination but it is not close to zero.
Pollen limitation: the degree to which seed production is limited by the supply of compatible pollen.
Protandry: pollen matures and dehisces before the stigma is receptive.
Protogyny: stigma is receptive before the pollen matures and dehisces.
Reproductive efficiency (RE): ratio of seed set from natural pollination to seed set from hand-crossing.
Self-compatibility: ability to form seed following self-pollination.
Self-compatibility index (SCI): ratio of seed set from hand-selfing to seed set from hand-crossing.
Self-incompatibility: self-sterility.
Zygomorphic: Symmetrical in one plane only, e.g., foxglove.