POLLINATION IN NEW ZEALAND

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ABSTRACT: Pollination by animals is a crucial ecosystem service. It underpins New Zealand's agriculture-dependent economy yet has hitherto received little attention from a commercial perspective except where pollination clearly limits crop yield. In part this has been because background pollination by feral honey bees (*Apis mellifera*) and other unmanaged non-*Apis* pollinators has been adequate. However, as pollinators decline throughout the world, the consequences for food production and national economies have led to increasing research on how to prevent further declines and restore pollination services. In New Zealand, managed honey bees are the most important pollinators of most commercial crops including pasture legumes, but introduced bumble bees can be more important in some crops and are increasingly being used as managed colonies. In addition, New Zealand has several other introduced bees and a range of solitary native bees, some of which offer prospects for development as managed colonies. Diverse other insects and some vertebrates also contribute to background pollination in both natural and agricultural ecosystems. However, New Zealand's dependence on managed honey bees makes it vulnerable to four major threats facing these bees: diseases, pesticides, a limited genetic base for breeding varroa-resistant bees, and declining floral resources. To address the fourth threat, a preliminary list of bee forage plants has been developed and published online. This lists species suitable for planting to provide abundant nectar and high-quality pollen during critical seasons. Providing high-quality nutrition will help bee colonies resist diseases, pests and exposure to pesticides and improve pollinator security in New Zealand.

Key words: bee forage plants, bumble bees, floral resources, honey bees, pollination systems, pollinator decline, threats.

INTRODUCTION TO POLLINATION SYSTEMS

Pollination as an ecosystem service

Recent changes in worldwide pollinator services have given rise to a growing concern that these services can no longer be taken for granted and need to be actively managed and protected to ensure sustainable ecosystems in productive and natural landscapes (Dias et al. 1999; Millennium Ecosystem Assessment 2005a, b; NRC 2007). These changes in pollinator services have profoundly important implications for New Zealand's economy and environment. Ecosystem services are sometimes obvious, such as food and water, but services like pollination are obscure because they involve subtle movements that most people do not observe readily. Pollination is a 'mobile agent' ecosystem service in the class of 'provisioning' services (Kremen et al. 2007).

The benefits directly or indirectly provided to people by ecosystem services support survival and quality of life (Millennium Ecosystem Assessment 2005a, b). Pollination is a beneficial ecosystem service in several ways: it contributes to the production of food and other goods for humans and their domesticated animals; it underpins reproduction in wild plants that in turn provide key ecosystem services; and it provides food for wild organisms that also deliver other services (Kremen et al. 2007). Pollination is also essential for human livelihoods, and is one of the most important and critical ecosystem services that sustain both human-managed and natural terrestrial ecosystems (NRC 2007). Animal-mediated pollination is a critical ecosystem service in the New Zealand economy because many important agricultural products depend on it (e.g. kiwifruit, apples, and avocados). In addition, livestock production benefits from pollination for clover regeneration, which provides nitrogen fixation. Pollination is essential for seed production of forage and many other domestic and export crops worldwide (Klein et al. 2007).

Pollination as a process

Pollination is necessary for sexual reproduction in plants (NRC 2007). It is defined as the delivery of viable pollen from the male parts of a flower to the receptive female parts, and includes a three-step sequence: the removal of pollen from anthers, the transport of pollen by a vector such as an insect or wind, and the deposition of pollen on the receptive flower (Osborne and Williams 1996). After pollination, the pollen grains germinate on the stigmatic surface of female flower parts and grow via pollen tubes down the style to the ovules where fertilisation (fusion of the sperm nuclei from the pollen with the egg nucleus in the ovary) takes place (Osborne and Williams 1996). Successful fertilisation produces an embryo, and eventually seeds and fruits.

The agents that transfer pollen are diverse. In most plants, pollination is achieved by invertebrate animals, primarily insects; however, some vertebrates also pollinate plants (Proctor et al. 1996). In addition, abiotic agents can transfer pollen, for example wind in grasses and cereals or water in aquatic plants (Proctor et al. 1996). Pollination by animals, especially insects, is of most concern because these pollinators are declining in many countries. Multiple factors lie at the root of these declines, including biodiversity and habitat loss (NRC 2007; Pettis and Delaplane 2010; USDA 2012). These growing threats may be contributing to a serious decline in all pollinators (Allen-Wardell et al. 1998; Biesmeijer et al. 2006; Gallai et al. 2009; Garibaldi et al. 2009; Potts et al. 2010; Tylianakis 2013) and have prompted many initiatives, notably the São Paulo Declaration on Pollinators (Dias et al. 1999), which led to the formation of five major groups working on the International Pollinator Initiative (FAO 2009).

A central response to threats to these mobile agent ecosystem services is to improve the habitat and nutritional resources of the threatened service-providing organisms; thus, in an example of 'ecological engineering', plants that support natural predators of pests were deliberately established in vineyards in New Zealand (Sandhu 2007). Pollination is another ecosystem service that can be improved by ecologically engineered interventions. For example, planting nutritious floral resources to provide pollen and nectar, the natural diet of major bee pollinators, can help sustain bee populations throughout the year. Bee nutrition is accepted as one of the important factors promoting bee health and preventing the large-scale losses of honey bee colonies that

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are a major concern overseas (USDA 2012); it also governs unmanaged wild bee populations (Roulston and Goodell 2011). Moreover, improving pollinator habitat greatly benefits all ecosystem services by improving overall biodiversity, and this in turn generates other ecosystem services, including pest reduction, soil protection, and other secondary benefits (reviewed by Wratten et al. 2012).

This chapter focuses on how to conceptualise pollinator services in order to evaluate their importance in natural and agricultural ecosystems. This will enable priorities to be placed on the most urgent and pressing issues for pollinator security in New Zealand. After describing the major pollinator groups in natural and agricultural ecosystems, the chapter discusses some important trends in their conservation and sustainability of use, focusing on the agricultural and horticultural pollination systems that need interventions for pollinator security in New Zealand.

EVALUATING POLLINATORS

Managed and unmanaged pollinators

To protect or restore pollination services, 'managed' and 'unmanaged' pollinators must be distinguished. This is crucial because they differ in terms of their availability 'on demand' and what kinds of opportunities and methods are available. In temperate countries, the primary method for increasing crop yields has been the introduction of commercially managed bees, particularly the European honey bee, *Apis mellifera* (Apoidea, Hymenoptera) (Figure 1A), which has been domesticated for millennia (Berenbaum 2007; NRC 2007). In addition, bumble bees (*Bombus* spp., Apoidea, Hymenoptera) (Figure 1B), certain solitary bees, and even flies (Diptera) have also been commercially managed as pollinators for crops (NRC 2007; Ssymank et al. 2008). Domestication of honey bees has now reached the point that they depend on human intervention for their survival because they must be treated to eliminate infestations of the parasitic varroa mite (*Varroa destructor*) (Goodwin and Taylor 2007; vanEngelsdorp and Meixner 2010); Australia is now the only continent free of varroa (Leech 2012). Domestication of other managed bees or flies has resulted in various levels of dependency on humans, from fully intensive husbandry to partial management based on different techniques for each type of pollinator (NRC 2007). Further domestication of these alternatives is another avenue of research to help restore the abundance and diversity of pollinators.

In contrast, unmanaged pollinators provide 'free' ecosystem services that have always been available in both productive and natural ecosystems. These services are derived from nature and have traditionally required no human intervention other than encouraging supportive habitats for their populations. Some authors would restrict the term 'ecosystem services' to only unmanaged pollinators but this is a narrow perspective when considering pollinator services as a whole. In agriculture, unmanaged pollinator services are called 'background pollination'. For many minor crops background pollination has traditionally been sufficient, but this is changing due to general pollinator declines, especially post-varroa. Moreover, the quantity and quality of free, reliable pollination depends on the species composition of background assemblages of pollinators, and these vary greatly from one region to the next and throughout different seasons.

Free pollination services from unmanaged pollinators are delivered by both native and non-native pollinators. Native pollinators make significant contributions to agriculture in many countries, particularly those with a high diversity of large hairy bees (Fontaine et al. 2006; Winfree et al. 2007, 2008; Kremen 2008; Klein et al. 2012; Garibaldi et al. 2013). On the other hand, unmanaged non-native species are derived from stock either deliberately imported for agriculture or that arrived by accident (Donovan 2007). Imported pollinators often escape to live freely in the wild, thus becoming part of unmanaged pollinator assemblages; when these domesticated species naturalise to form self-sustaining populations they are called 'feral'. All eight species of managed non-native bees introduced to New Zealand for agriculture have escaped and naturalised to various degrees (Donovan 2007). In the past, feral honey bees and bumble bees have contributed greatly to background pollination in agriculture and probably benefited natural ecosystems because they also service native plants (Newstrom and Robertson 2005). However, their true effects remain contentious. If these non-native escapees compete with native pollinators for floral resources, they could adversely affect native pollinator abundance and diversity, although Donovan (1980, 2007) states that after over 170 years of contact, native bees have enjoyed considerable competitive success in their interactions with feral honey bees and bumble bees; however, this conclusion relates to natural co-existence with unmanaged feral bees, not with managed domesticated bees, because manipulation of commercially managed bee densities can shift the balance. Elsewhere, competition from introduced bee pollinators is considered a problem in regions like Australia (honey bees) and Tasmania (bumble bees) (reviewed by Goulson 2003). In New Zealand, however, the issue is largely theoretical because feral honey bee colonies have been decimated by the varroa mite, which arrived in Auckland in early 2000 and spread rapidly throughout the North Island (Donovan 2007; Goodwin and Taylor 2007) and, after 2006, throughout the South Island.

Accidentally introduced non-native pollinators are often inadvertently assisted by humans, and are often referred to as 'adventive' (Donovan 2007). These pollinators can also naturalise to become part of background pollination available to crops and native plants. Whatever their origin or method of introduction, the value of unmanaged non-native pollinators can be significant in agricultural and natural ecosystems (NRC 2007). The value of any pollinator to a target flower in either system depends on biological factors such as life history and species-specific traits (e.g. their behaviour and fit to the morphology of the flower) and ecological factors such as habitat, including forage and nest site availability.

Pollinator importance

When evaluating the worth or importance of any pollinator species – managed or unmanaged; native or non-native – two components are assessed: first, the effectiveness of the pollinator in transferring a sufficient quantity of high-quality pollen to a given flower (in a single visit), and second, the abundance of the pollinator (population density) and its rate of visiting the target flower (Herrera 1987, 1989; Ne'eman et al. 2010). Thus, the most abundant pollinator may not be the most effective and the most effective may not be the most abundant (Schemske 1983). This means the overall importance of a pollinator species at a given time and place must reflect the total amount of pollen transferred to target flowers. For this reason, pollinator importance is defined as effectiveness multiplied by abundance, the latter including visit rate (Ne'eman et al. 2010). Recognising the distinction between effectiveness and abundance is critical when evaluating

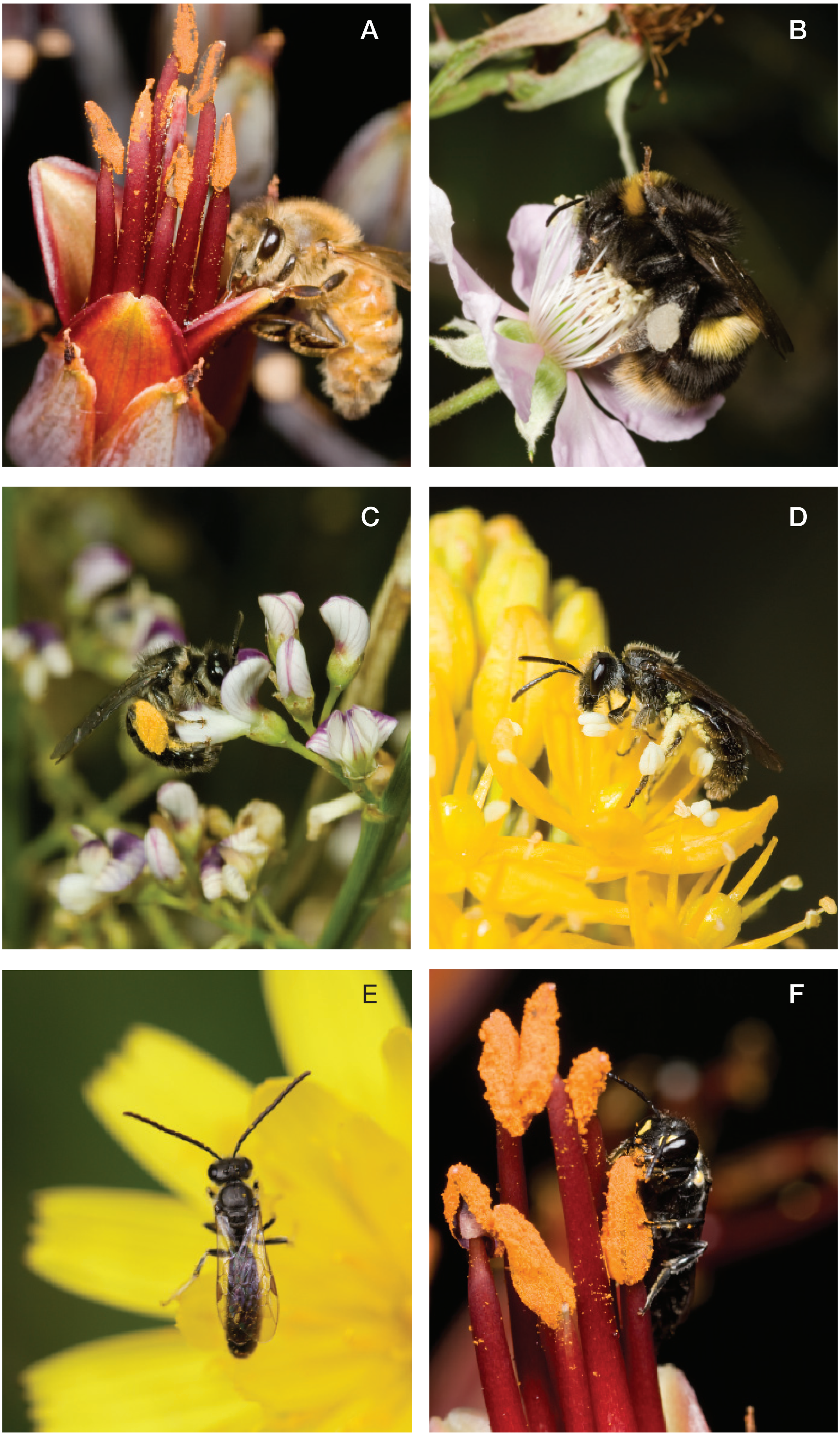

FIGURE 1 Bee pollinators in New Zealand: **A**) Introduced honey bee (*Apis mellifera*) on New Zealand flax (*Phormium tenax*); **B**) Introduced bumble bee (*Bombus* sp.) on blackberry (*Rubus fruticosa*); **C**) Native bee (*Leioproctus* sp.) on New Zealand broom (*Carmichaelia* sp.); **D**) Native bee (*Leioproctus* sp.) on Maori onion (*Bulbinella* sp.); **E**) Native bee (*Lasioglossum* sp.) on introduced daisy; **F**) Native bee (*Hylaeus* sp.) on New Zealand Flax (*Phormium tenax*). Photos A,B,E,F by Neil Fitzgerald; D by Chris Morse; C by Sascha Koch. Copyright Landcare Research.

pollinators for both agricultural and natural ecosystems because a less effective pollinator can be important simply because of its population size.

The context in which a pollinator performs its service is also important. In this respect, two factors are particularly important in determining the relative importance of a pollinator to a plant: the availability of other pollinators that service the same flower (Thomson et al. 2000), and the availability of other flowering species. Pollinators have a range of floral preferences and different reactions to competing pollinators; in addition, they have a range of nest site requirements. In short, the community context of competing flowers and pollinators is basic to evaluating pollinator importance. A pollinator's relative importance is highly context dependent in both time and space, and it changes in different situations (Kremen et al. 2007).

Finally, a critical factor for evaluating managed pollinators in crop and pasture situations, but not in natural ecosystems, is how easily the pollinators can be transported. Many large-scale crops flower for only a few weeks of the year, presenting an extremely high demand for pollinators for a very brief period (McGregor 1976; Free 1993). Moving pollinators in and out of these crops is a special case when evaluating importance. The efficacy of permanent versus mobile managed pollinators for agriculture depends upon the type of crop, the farm operations, pest and weed issues, and climatic and landscape factors. Ecosystem services from unmanaged pollinators may be ostensibly free, but in large-scale intensive agriculture, populations of these pollinators may be too small to produce high yields. Nevertheless, a mixture of diverse, managed and unmanaged pollinators can have a synergistic effect in some crops, as demonstrated in California almonds (Brittain et al. 2013), implying that utilising both managed and unmanaged pollinators may have a distinct advantage.

Plant–pollinator partnerships and networks

Pollination is a mutually beneficial interaction: while delivering pollen to the flower, pollinating animals receive some type of food or other reward (nectar, pollen, oil, resins, etc.) (Proctor et al. 1996). An important factor to consider when evaluating the importance of pollinators at a community level is diet breadth; that is, the diversity of flowers the pollinators prefer to visit. Pollinator preferences are determined by physical characteristics (e.g. scent, colour, shape of the flower), the quality and quantity of rewards, and the energetics involved in working the flower, such as landing platforms, proximity to the next flower, and accessibility of the pollen or nectar. Pollinators with a wide diet breadth are called generalists while pollinators with a narrow diet breadth are specialists (Proctor et al. 1996). Plants and pollinators vary in how much they depend on each other; therefore, their level of specialisation versus generalisation can be analysed from either perspective. Some pollinators rely on a narrow range of flowering plants throughout their life cycle, but others, while preferring some flowers, will readily visit and gain rewards from a broad range of flowering species. Similarly, a plant that can be pollinated by a large diversity of pollinator species is said to have a generalised pollination system, while one that can be serviced by only one or few pollinator species has a specialised pollination system. Strict interdependency of a specialist pollinator with a specialist plant species is rare but does occur (Waser et al. 1996; Waser and Ollerton 2006). Generalisation and specialisation from either the pollinator or plant perspective is a significant predictor of the impact of any disturbances to plant–pollinator communities, including crop plant communities. Network analysis techniques provide promising new methods to demonstrate the interconnections of plant–pollinator partnerships at a community level (Memmott 1999; Corbett 2000; Memmott et al. 2004; Bascompte and Jordano 2007).

Analysing pollination systems

Since pollinator services are dynamic and contextual, the responses of pollinators to natural or anthropogenic changes and disturbances are frequently complex and unintuitive (Kremen and Ricketts 2000; Roubik 2001). Consequently, restoring and conserving pollinator services must be based on understanding multiple interacting factors (Kremen and Ricketts 2000). Pollination systems must be analysed in terms of two things: the participants (the providers of the services) and the processes (the biological and ecological interactions in the plant–pollinator community). A useful approach to understand how to protect pollinator services, no matter how disrupted, is to analyse the service using four major steps (Kremen 2005): (1) identify the key service providers by constructing a 'functional inventory' of pollinators; (2) measure the spatio-temporal scale over which providers and their services operate; (3) assess the key environmental factors influencing their services; and (4) determine the 'functional structure' of the plant–pollinator community by characterising what aspects of community structure influence function. This fourth step enables predictions about how different species composition, disturbances, or management regimes will change the services (Kremen 2005; Kremen and Ostfeld 2005). In crop pollination, the plant community includes the target crop itself and all surrounding plants flowering at the same time within the pollinator's foraging range when the pollinator is active. An analysis based on these four steps can produce robust predictions about the nature and security of pollinator services; it can also provide principles to elucidate best management practices to protect or restore pollinators.

This chapter focuses mainly on the first of these four steps in Kremen's (2005) scheme; namely, constructing a functional inventory of pollinators. A functional inventory aims to identify all the available pollinator groups that could render pollination services. It is particularly vital to understand which of these are most important for the agricultural and horticultural sectors on which New Zealand's economy depends. A secondary focus of this chapter is to address one of the most urgent and pressing issues threatening pollination security in the agricultural and horticultural sectors: the health of the most important managed pollinator, the honey bee. Restoring the lost food sources of the honey bee is a type of ecological engineering that can easily be put into practice and will result in multiple outcomes to safeguard New Zealand's pollinator security and hence its food security. Replacing lost floral resources is just one of several pathways to prevent the current problems challenging agricultural pollination systems overseas, namely pollinator declines and repeated large-scale losses of honey bee colonies (Williams et al. 2010).

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Towards a functional inventory of pollinators

Although New Zealand is a relatively large island in Oceania, its pollinator assemblages differ from those of continental countries. Most island ecosystems in Oceania have evolved in isolation from continental landmasses and have unique and fragile plant–pollinator partnerships that are particularly sensitive to land use intensification, habitat loss, and invasion by alien species (Pattemore and Wilcove 2011). In keeping with global patterns of pollinator decline, Pacific Island pollination systems are losing key pollinators, plants, and habitats, and are being disrupted by invasive species (Cox and Elmqvist 2000). In general, pollinators on oceanic islands are more vulnerable than those on continental land masses because they have small populations, low genetic diversity, extreme reproductive isolation, and some obligate dependencies on a very restricted pollinator fauna (Cox and Elmqvist 2000; Kremen and Ricketts 2000).

New Zealand has a distinctive assemblage of pollinating fauna that differs from the other islands in Oceania because of its different geological origin and temperate climate (Lloyd 1985). However, like other islands, it has a high degree of endemism in the fauna and flora plus an extremely high proportion of introduced naturalised plants (52%) – the highest in the world next to Hawaiʻi (Wilton and Breitwieser 2000). Like other small remote islands, repopulation of locally extinct species from surrounding areas is unlikely because of New Zealand's isolation, high levels of endemism, and vulnerability to invasive species. The low diversity of native pollinators, particularly of bees, characterises New Zealand's vulnerability to a pollinator crisis in the future.

The taxonomic composition of the native pollinator fauna of New Zealand represents an extremely small subset of the diversity of the main pollinator groups found on continents. Some major groups are poorly represented or entirely missing (Lloyd 1985); for example, New Zealand has no native counterpart to the large social bees that are so abundant and diverse elsewhere (Donovan 2007). Its native bees are primarily solitary, low in diversity, and tend to be small (Donovan 2007); and it has few native butterflies and no native hawkmoths (Lloyd 1985). The lack of large, hairy social bees meant managed social bees had to be imported, and this proved essential for agriculture to flourish in New Zealand.Without these imported bees, particularly the honey bee and bumble bee, New Zealand agriculture could not have developed to its present level of productivity.

The subsequent escape and naturalisation of these imported large social bees introduced an entirely new element to the pollinator fauna in natural ecosystems (Lloyd 1985). The total pollinator fauna of New Zealand, including native and non-native species across agricultural and natural ecosystems, can be categorised into five major groups (Newstrom and Robertson 2005): bees (Hymenoptera); flies (Diptera); moths and butterflies (Lepidoptera); beetles (Coleoptera); and vertebrates, including birds (Aves), bats (Mystacinidae), and lizards (Squamata). Recently, Pattemore and Wilcove (2011) documented the role of invasive rats in the pollination of several native plants in New Zealand, thereby adding another sub-group to the vertebrate list. Each of these pollinator groups plays a different role in natural and agricultural ecosystems, and each can sometimes compensate for or even replace each other's services (e.g. Pattemore and Wilcove 2011). However, in certain ecological contexts they can also competitively displace each other (Goulson 2003).

Excluded from the list are wasps, both social and solitary, that visit flowers infrequently for nectar but usually to predate insects (NRC 2007). They are not known to be major pollinators in New Zealand (Barry Donovan, pers. comm.) and have not been seen to carry much pollen (pers. obs.) so are excluded from this functional inventory. However, wasps frequently attack honey bee colonies to rob honey, and in the process will kill so many bees that a bee colony may be destroyed (Matheson 1984; Matheson and Reid 2011). Notwithstanding the New Zealand situation, some wasp species are important pollinators in other countries in other contexts (Proctor et al. 1996; NRC 2007).

We also do not consider other groups of flower visitors such as wētā (Orthoptera), grasshoppers (Orthoptera), or spiders because their role in New Zealand's pollination systems is undocumented and likely to be very minor. Although they have been frequently observed on flowers carrying pollen at night (pers. obs.), their relative importance as pollinators in the worldwide literature is almost nil compared with the five major groups listed above (Proctor et al. 1996). Nevertheless, since their efficacy as pollinators has not been investigated, no conclusion can be reached, but they would not be more important than the currently listed five major groups.

Bees (Hymenoptera)

Worldwide, bees in general are by far the most important pollinators in both agricultural and natural ecosystems because of their diversity, abundance, and precision in transferring pollen efficiently (McGregor 1976; Delaplane and Mayer 2000; NRC 2007). Although most bee species are solitary, the large social bees (e.g. honey bees and bumble bees) are significant in agriculture because of the size of their complex colonies, which are based on a division of labour with cooperative care of the young (Delaplane and Mayer 2000; Donovan 2007).

Honey bees — The honey bee, *Apis mellifera* (Apoidea, Hymenoptera) (Figure 1A), is the premier large-scale managed pollinator for almost all insect-pollinated crops in temperate regions of the world, including New Zealand (Berenbaum 2007; Donovan 2007; NRC 2007). The honey bee is one of the hardest workers in horticulture and agriculture; about NZ$5 billion of the New Zealand GDP is directly attributable to the intensive pollination of horticultural and specialty agricultural crops (John Hartnell, Chair Federated Farmers Bee Industry Group, pers. comm.). Honey bees further contribute indirectly through the pollination of clover, which is sown as a nitrogen regeneration source for pastoral farms, thus benefiting the meat and dairy export industries through the production and sale of livestock and dairy products. Honey bees are the primary source of pollination for horticultural and pastoral land in New Zealand.

Honey bees are unrivalled as pollinators of large-scale monoculture crops and are unlikely to be replaced by any other species in this role because they can: (1) rapidly regenerate from a small colony size of fewer than 10 000 bees per hive to a peak population of up to about 80 000; (2) effectively pollinate a broad range of flowers including small and less favoured flowers; and (3) thrive in managed hives, so colonies can be transported over large distances to crop pollination sites (vanEngelsdorp and Meixner 2010). No other temperate pollinator can be so readily managed and transported in such large colonies. Therefore, the seemingly small beekeeping industry in New Zealand carries out a disproportionate and pivotal role in the agricultural economy because it is the backbone of yields in the agricultural and horticultural sectors for domestic and export products.

Managed honey bees have been kept in New Zealand for over 174 years, beginning as a home craft for honey production in 1839 (Hopkins 1906) and evolving into a progressive professional industry for pollination and honey export today (Donovan 2007). In addition to the original stocks of bees brought to New Zealand, several new races were imported from European countries. Hybridisation among these races resulted in four predominant varieties of bees: *A. mellifera mellifera*, the brown bee or European or English bee; *A. mellifera ligustica*, the three-banded yellow bee or Italian bee; *A. mellifera caucasica*, the 'Caucasian' bee or Near-Eastern bee; and *A. mellifera carnica*, the Carniolan bee (NBA 2009). Live honey bees have not been imported since the late 1950s, in an attempt to keep bee diseases out of New Zealand (NBA 2009).

When honey bees were first introduced they naturalised rapidly and spread as feral colonies throughout New Zealand (NBA 2009). Feral honey bees have been a large component of background pollination in many cultivated crops that never previously required rental of managed hives (NRC 2007), and were once abundant almost everywhere in New Zealand, foraging as 'super-generalists' on an extremely wide range of introduced and native plants (Walsh 1967; Butz Huryn 1995; Donovan 2007).

The reason pollination services could be taken so much for granted in the past is that sufficient pollinators, primarily managed and feral honey bees, have generally been available for crops and pastures. Today, however, feral honey bee populations in New Zealand have been almost entirely eliminated by varroa infestations, which began in 2000 on the North Island and spread in 2006 to the South Island. The few feral colonies still occasionally found are almost always ephemeral. Although feral colonies can and do re-establish each spring as swarms from managed colonies, they will not survive more than a year unless treated to control varroa mites. This means one of the most significant components of 'background pollination' in crops and in natural ecosystems has been permanently lost unless the honey bee can develop defences against varroa mites. Growers and gardeners who previously relied on free pollination services from feral honey bees must now either rent managed colonies or utilise alternative non-*Apis* pollinators.

Honey bees are readily managed in large colonies because they are highly social (eusocial), meaning they live in perennial cooperative colonies in which usually one female, the queen, and several males are reproductively active while most others are non-breeding females called workers (Donovan 2007). Workers feed and monitor the larvae and the queen, protect the hive, and forage for pollen, nectar, water and propolis (resinous substance for hive repair) (Matheson and Reid 2011). Although colonies in New Zealand are perennial because worker bees can forage all year round whenever the air temperature is above 10°C and the weather is clear, honey bees are normally much less active in winter, from late May to August (Barry Foster, President of National Beekeepers' Association, pers. comm.). In spring from August to October, overwintered colonies become active again and begin multiplying, achieving peak populations in time for summer crop pollination services and the honey flow (Winston 1987; Donovan 2007; NBA 2009). During colony build-up, protein-rich pollen is critical for feeding larvae and developing healthy adult bees (Somerville 2005); in particular, it is important for producing substances such as vitellogenin, which is known to influence hormone signalling, food-related behaviour, immunity, stress resistance, and longevity in worker honey bees (Havukainen et al. 2011).

If pollen is scarce, supplemental artificial feed can be purchased by beekeepers. However, this is not the best nutrition because fresh pollen, particularly polyfloral pollen rather than monofloral pollen, affects baseline immunocompetence scores (haemocyte concentration, fat body content and phenoloxidase activity) in individual bees, and at the colony level it affects glucose oxidase activity that enables bees to sterilise food for the colony and brood (Alaux et al. 2010). Furthermore, a major component of pollen grains, p-coumaric acid, is ubiquitous in the natural diet of honey bees and may function as a nutraceutical, regulating immune and detoxification processes in honey bees (Mao et al. 2013). Ideally, sufficient high-protein pollen from natural sources is available in the habitat without the cost of artificial feed but this is becoming harder for bees to find as floral resources disappear.

For many crops, honey bees are in fact not the most effective pollinators on a per bee basis but they have an overwhelming advantage because they produce by far the largest colony populations of any bee species (Delaplane and Mayer 2000). Honey bee colonies can recruit fresh worker bees to a new productive forage source because 'scout' bees communicate their discoveries back at the hive with their dance 'language' (Corbet 1996). Therefore, honey bees can often gain a large share of nectar from a patch before other bees even begin to forage in the patch. Finally, honey bee hives can be easily transported at short notice, so they can be moved in and out of crops quickly. This is useful whenever scout bees draw honey bees away from a target crop (such as non-preferred onion or carrot seed crops) to a more preferred crop nearby (such as clover or brassica), because the beekeeper can move these hives out and bring in fresh, 'naïve' colonies that will then take a another few days to find the competing flowers; meanwhile, the non-preferred crop would be visited and pollinated. Honey bees are super-generalists and will forage on any flower with an accessible reward (Donovan 2007). Their flower preference hierarchy is primarily based on the amount of sugar that can be gained per flower relative to the time and effort of working the flower (Nicolson 2010). The primary advantage of honey bees is that they store surplus honey and generate other marketable products (beeswax, pollen, propolis, royal jelly); these subsidise pollination services to agriculture (Delaplane and Mayer 2000).

Managed honey bee populations are influenced by many factors including pests, diseases, significant stressors such as accidental pesticide exposure, and socio-economic factors driving the price of honey (NRC 2007; vanEnglesdorp and Meixner 2010). Protecting honey bee pollinators is now more critical than ever because varroa mite facilitates other pathogens and in concert they continue to weaken bees (Williams et al. 2010), to the detriment of the beekeeping industry and pollination services in New Zealand. The four main ways to protect honey bees are to prevent and treat diseases and pests, ensure good stewardship in the use of pesticides and agrochemicals, develop good breeding programmes to produce varroa-resistant bees, and provide high-quality bee forage and habitat to improve bee health. The nutritional status of the individual honey bee and the entire colony is fundamental because it influences the ability of bees to withstand and sustain the other multiple stressors listed above.

Bumble bees — Bumble bees, *Bombus* spp. (Apoidea, Hymenoptera) (Figure 1B), are another important managed bee genus for agriculture because they are highly effective on a per bee basis, particularly for complex flowers (Osborne and Williams 1996; Delaplane and Mayer 2000). They are the most significant pollinator for a range of crops because they are large and hairy, so they transfer a great number of pollen grains. For many crops bumble bees are better pollinators than honey bees because they can more efficiently handle deep tubular or complex flowers like red clover and field bean, make better contact with the sexual parts of large flowers like squash and courgettes, and vibrate their wing muscles to 'buzz-pollinate' certain specialised flowers like tomatoes, peppers, and aubergines (Solanaceae) and blueberries (Ericaceae) (Macfarlane and Gurr 1995; Osborne and Williams 1996; Delaplane and Mayer 2000; Donovan 2007). Honey bees cannot buzz-pollinate.

Like honey bees, bumble bees are also super-generalists but they forage differently and do not communicate resource locations to recruit more workers to a new nectar or pollen source (Corbet 1996). They forage as individuals, often in a 'trap-lining' manner, and prefer larger more complex flowers than do honey bees. Because they are heavier than honey bees, they need more nectar sugar per flower to make a visit energetically profitable (Corbet 1996), so they seldom visit the small flowers frequented by honey bees. Unlike honey bees and native bees, bumble bees will fly in cold weather, including wind and rain, and they start earlier in the day and finish later (Delaplane and Mayer 2000; Donovan 2007). This makes them important at high altitudes and latitudes (Corbet 1996).

In the 19th to early 20th century, four bumble bee species were imported to New Zealand to improve pollination rates and seed yields in red clover (*Trifolium pretense*) (Hopkins 1914; Macfarlane and Gurr 1995; Donovan 2007). All four species have naturalised to various degrees (Macfarlane and Gurr 1995; Donovan (2007). The two-banded bumble bee, *Bombus terrestris*, has spread throughout New Zealand and is the most common bumble bee due to the breadth of its flower preferences. It has a relatively short tongue (8.2 mm) – similar in length to that of the honey bee. It is more generalist than the other bumble bee species, with recorded visits to 47 native and over 500 introduced plant species (Donovan 2007). The garden bumble bee, *B. hortorum*, is common in suburban gardens and has spread through the southern North Island and much of the South Island. It has a much longer tongue (13.5 mm) and prefers deep tubular flowers, particularly red clover and a few native and introduced plants (Donovan 2007). The remaining two bumble bees, *B. ruderatus* and *B. subterraneus*, also have long tongues, making both species suitable for pollinating red clover and other complex flowers such as pasture legumes. *Bombus ruderatus* is the second most abundant bumble bee throughout New Zealand, but *B. subterraneus* is restricted to the South Island and is the least known of the four species (Donovan 2007). The narrow diet breadth of long-tongued bumble bees appears to be a worldwide phenomenon; for example, the loss of deep tubular flowers may have contributed to the decline and rarity of long-tongued bumble bees in the United Kingdom (Goulson and Darville 2004).

Bumble bees are primitively social insects with annual nests (Delaplane and Mayer 2000; Donovan 2007). The mated queen overwinters alone underground; in spring she must find and establish a nest to rear the first batch of workers and then forage for them until they are adults (Corbet 1996; Delaplane and Mayer 2000). When the adult workers take over foraging duties, the queen specialises on egg-laying; however, a bumble bee colony reaches only around 300–400 bees. Since no surplus honey is produced or stored, a dearth of nectar puts the colony at risk (Delaplane and Mayer 2000), and the slow start from one queen each spring means populations reach peak levels much later in the season than for honey bees.

Bumble bee colonies were previously considered too small, variable, and expensive to be relied on for field crops (Osborne and Williams 1996) but further research shows bumble bee populations can be increased to make important contributions to many fruit, vegetable and pasture crops (Lye et al. 2010). Partial management by providing custom-built domiciles and a season-long succession of forage can increase the number of colonies of bumble bees in the field (Williams and Osborne 2009); for example, in the United Kingdom, when experiments using agri-environment schemes (AES) were designed to provide more forage for bumble bees by planting targeted mixtures of flowering species, they proved effective (Carvell et al. 2011).

Bumble bees are adaptable to glasshouse pollination. Commercially managed bumble bee colonies in glasshouse crops are now a popular choice for buzz-pollinated tomatoes, peppers, and aubergines, and for other specialty crops such as strawberries. The technique to break the winter diapause of bumble bee queens was developed in 1989 and allowed greater control of the timing of the colony life cycle (Griffiths and Robberts 1996). Commercial colonies for glasshouses quickly spread worldwide. In New Zealand *B. terrestri*s is used in glasshouses (e.g. http://www.biobees.co.nz/Pollination; and http://www.zonda.net.nz/); a cardboard hive contains a colony with 30–100 worker bees and is supplied with sugar syrup if the target crop does not produce nectar. The colony lasts 4–6 weeks in the glasshouse.

Bumble bees are not vulnerable to varroa mite, giving them a potential advantage over honey bees, so further development of management techniques to increase bumble bee pollinators for field and glasshouse pollination is important. However, their small colony populations and lack of surplus honey and other products to subsidise the cost of colony management mean they are not likely to replace honey bees in large-scale operations, but they are ideal in specialty crops.

Solitary bees — New Zealand has only 32 native bee species (26 endemic, 1 indigenous, 5 adventive) (Donovan 2007). All are solitary, as are most of the world's bee species (Delaplane and Mayer 2000; Donovan 2007). The female constructs her nest in a blind tunnel in the ground or in wood, provisions each cell with an egg and with the pollen and nectar the larva will need to develop, then seals the cell and has no further contact (Donovan 2007). The larva overwinters in the tunnel and emerges as an adult bee in the late spring or early summer. Solitary bees do not form colonies, so they do not have queens, workers and drones, although one species (*Lasioglossum sordidum*) is considered to be partially, primitively social because several females share the same tunnel to make their nests (Donovan 2007). Distributions of native bees and records of the flowers they visit are described in the taxonomic treatment of New Zealand bees by Donovan (2007).

The largest group of native bees is *Leioproctus* (Figure 1C–D), with 17 endemic species in one of the most primitive bee families, Colletidae (Donovan 2007). The larger species of *Leioproctus* are good candidates for crop pollination because they are almost as big and hairy as a worker honey bee (Donovan 2007). They have been observed in onion seed and brassica crops (Howlett et al. 2005, 2009), and for crops such as brassica they can transfer large pollen loads comparable with those of honey bees (Rader et al. 2009). They carry pollen packed dry (without mixing with nectar) on their hind legs. In kiwifruit, *Leioproctus* species were ranked as third most effective at transferring pollen (after bumble bees and honey bees) and were found in populations large enough to make a significant contribution to fruit set (Donovan 2007). Their short flight season from November to January coincides with most crop flowering times. In natural ecosystems, they forage on native plants in Asteraceae, Myrtaceae and Fabaceae. Some

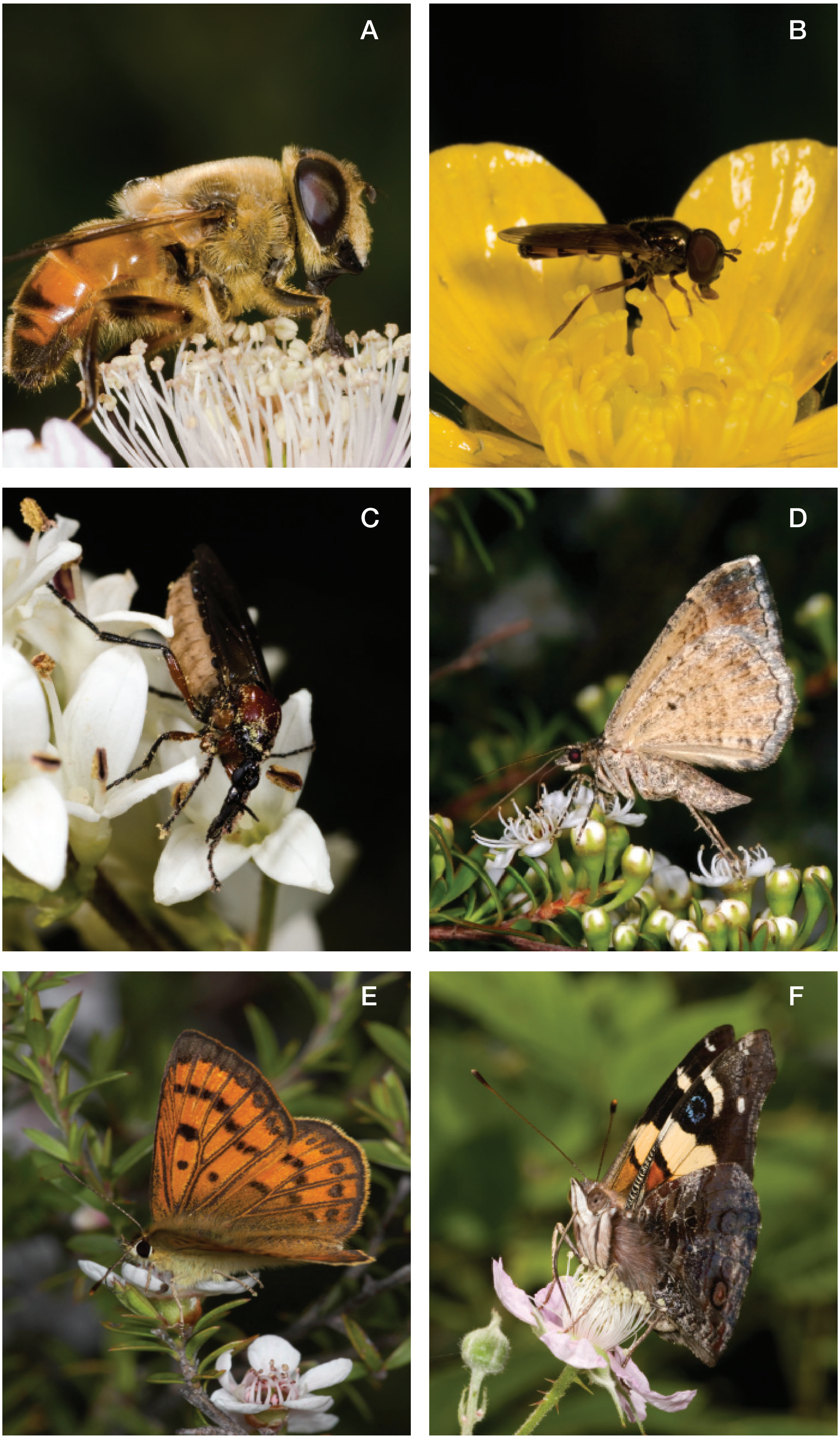

FIGURE 2 Non-bee pollinators in New Zealand: **A**) Introduced drone fly (*Eristalis tenax*) on blackberry (*Rubus fruticosa*); **B**) Hover fly (*Melanostoma fasciatum*) on Buttercup (*Ranunculus*); **C**) Bibionid or St Mark's fly *(Dilophus nigrostigmus)* on Chinese privet (*Ligustrum sinense*); **D**) Geometrid Moth (*Hydriomena deltoidata*) on kanuka (*Kunzea ericoides* **E**) Copper butterfly (*Lycaena salustius*) on manuka *(Leptospermum scoparium*); **F**) Yellow Admiral butterfly (*Vanessa itea*) on blackberry *(Rubus fruticosa*). Photos A, B, C, F by Neil Fitzgerald, D, E by Richard Toft. Copyright Landcare Research.

Leioproctus species specialise on a few plant species in just one of these plant families (Donovan 2007). Because they nest in the ground, often in large, aggregated groups, they are challenging to manage for agriculture but successful trials of nest removal and re-establishment have been conducted (Donovan et al. 2010).

The second important group of native bees, *Lasioglossum* (Figure 1E), has three endemic and one indigenous species, and belongs to a less primitive bee family, Halictidae (Donovan 2007). They also carry pollen packed dry on their hind legs and are ground nesters (Donovan 2007). The most common species, *Lasioglossum sordidum*, forages in many crop plants (e.g. onion, brassicas) (Howlett et al. 2005, 2009), but because they are small and less hairy they transfer much less pollen than *Leioproctus* (Rader et al. 2009). The long flight season of this species means it forages on a very wide range of plant species and is regarded as a generalist. The small body size and ground-nesting trait make this species less valuable for management, but unmanaged populations in crops can be very high (Howlett et al. 2009).

The third group of native bees are the masked bees, *Hylaeus* (Figure 1F) and *Hyleoides* with six endemic and three adventive species; they too are Colletidae (Donovan 2007). These species nest in wood, which makes them promising candidates for management in agriculture because wood bee nests can be transported. However, they do not transfer much pollen because they carry it internally instead of on their hind legs and regurgitate it for their brood (Donovan 2007). They also lack hairs for picking up pollen on their bodies (Donovan 2007). For these reasons, species in this group are not considered good candidates for developing managed populations in agriculture.

Three managed, non-native solitary bee species were deliberately imported to New Zealand for agriculture (Donovan 1980, 2007). Two are promising wood-nesting bees in Megachilidae: the red clover mason bee (*Osmia coerulescens*) and the lucerne leafcutting bee (*Megachile rotundata*), which were both imported as specialist bees to pollinate lucerne seed crops (Donovan 2007). The third imported solitary bee, the ground nesting alkali bee (*Nomia melanderi*, Halictidae), was also imported to pollinate lucerne. The successful work from the 1970s to 1990s to develop these bees for agriculture in New Zealand has not been continued so most of the managed non-native solitary bee populations remain small, with some feral populations still existing (Donovan 1980, 2007). Their full potential to assist crop pollination has not yet been realised, so they remain an untapped resource in New Zealand's agricultural pollination systems. Management of these bee species in North America is well advanced (Delaplane and Mayer 2000) and this could also be achieved in New Zealand.

An unmanaged, non-native solitary bee that recently arrived accidentally is the adventive wool carder bee, *Anthidium manicatum* (Megachilidae). This bee, originally from Europe, was discovered in Napier and Nelson in 2006 (Donovan 2007) and has since spread. It is not used for crop pollination and is potentially a damaging invasive species that harms other pollinating insects because it is the only insect in New Zealand that aggressively defends patches of flowers against other flower-visiting insects (Donovan 2007). The wool carder bee attacks honey bees and bumble bees by ripping their wings with its spiny abdomen, leaving its victim unable to fly (Donovan 2007). There are anecdotal reports of expanding populations visiting an increasing diversity of plant species in gardens in Nelson (Donovan 2007) and the bee has spread to Hamilton (Gary Harrison, Landcare Research, pers. comm.). Donovan (2007) suggests this bee has the potential to colonise most of New Zealand. Because of its aggression towards other pollinators it is not a desirable species to develop for pollination in agricultural or natural ecosystems.

Flies (Diptera)

While the abundance and diversity of Diptera is high in New Zealand, no comprehensive treatment is available. Important families are bristle flies (Tachinidae) and hoverflies (Syrphidae). One of the most common large syrphid flies, the drone fly, *Eristalis tenax*, (Figure 2A) resembles a honey bee. Most syrphid flies are smaller, for example *Melanostoma fasciatum* (Figure 2B) and many feed on pollen (Holloway 1976; Hickman et al. 1995). In the *Bibionidae* an important pollinator is the March or St. Mark's fly, *Dilophus nigrostigmus* commonly seen in spring with abundant pollen on the dorsal surface (Figure 2C). The effectiveness of flies as pollinators is thought to be generally low due to small pollen loads and inconstancy to flowers (Proctor et al. 1996, Kearns 2001). However, both of the most common flower visitors, the drone fly and the March fly carry significant pollen loads that are comparable to those found on honey bees (Rader et al. 2009). Flies are important pollinators for many plants worldwide and have been implicated in the pollination of more than 100 different cultivated pant species (Ssymank et al. 2008). Flies are common flower visitors of a range of crops in New Zealand including onion, brassicas, radish, carrots, and white clover (Howlett et al 2005; Howlett et al 2009, Rader et al 2009).

Moths and butterflies (Lepidoptera)

Lepidoptera are represented in New Zealand by an extremely low diversity of butterfly species (11 endemic, 2 native, and 17 introduced or transient species) (Gibbs 1980; Parkinson and Patrick 2000) but a high diversity of moths (over 1800 species) (Dugdale 1988; Parkinson and Patrick 2000). In New Zealand, one of the important moths found visiting flowers is the geometrid *Hydriomena deltoidata* (Figure 2D), but little is known about moth pollinator effectiveness or abundance. However, lepidopteran larvae depend on specific host plants, and because many of these relationships are obligate, conservation efforts are necessary. Without the host plants, larvae will not develop; for example, New Zealand's copper butterfly, *Lycaena salustius* (Figure 2E), feeds only on pōhuehue (*Muehlenbeckia* spp.) and the yellow admiral butterfly (*Vanessa itea*) (Figure 2F) feeds only on stinging nettles (*Urtica* spp.) (Monarch Butterfly New Zealand Trust 2010). The status of butterflies in New Zealand is monitored by the Monarch Butterfly New Zealand Trust (2010) but, like moths, the importance of butterfly pollinators in New Zealand is not well understood (Newstrom and Robertson 2005). However, they are considered insignificant for crop pollination because they do not deposit much pollen, tend to travel large distances between flowers, and require host plants for reproduction (Proctor et al. 1996). Moreover, their population sizes are small and they do not make nests.

Beetles (Coleoptera)

Although beetle pollination is important for primitive flowering plant species, especially in the tropics (Proctor et al. 1996), very little is known about population trends in beetles or their role in pollinating flowers in New Zealand (Newstrom and Robertson 2005). Similarly, beetle pollination in North America has received little attention (NRC 2007). Few crops are pollinated by beetles except in the tropics (NRC 2007). In New Zealand,

FIGURE 3 Bird pollination and compensation in New Zealand: **A**) Tui (*Prosthermadera novaeseelandiae*) on Puriri (*Vitex lucens*); **B**) Bellbird (*Anthornis melanura*) on Kohekohe (*Dysoxylum spectabile*); **C**) Bellbird on five finger (*Pseudopanax arboreus*) **D**) Honey bee (*Apis mellifera*) on five finger; **E**) Stitchbird (*Notiomystis cincta)* on Kohekohe; **F**) Silvereye (*Zosterops lateralis*) on Wattle (*Acacia* sp.). Photos A,B,C,D,E by Abe Borker; D by Richard Toft. Copyright Landcare Research.

beetles do not play a significant role in pollinating crops because they are less effective than bees and flies in carrying pollen to a neighbouring plant for outcrossing and they tend not to carry large amounts of pollen. However, beetle pollination has not been well investigated in New Zealand.

Vertebrates

Birds (Aves) — For some New Zealand native plant species, the most effective vertebrate pollinators are nectar-feeding birds. These are perching bird pollinators, in contrast to the hovering humming birds that feed on nectar in North America and the Neotropics (Proctor et al. 1996). Of the eight species of indigenous perching bird pollinators in New Zealand (Godley 1979), three make the majority of flower visits: the tūī (*Prosthemadera novaezelandiae*; Figure 3A), the bellbird (*Anthornis melanura*; Figure 3B–C), and the self-introduced silver eye (*Zosterops lateralis*; Figure 3F) (Kelly et al. 2006). A fourth nectar-feeding bird, the stitchbird (*Notiomystis cincta*; Figure 3E), was originally distributed throughout the North Island but has been extinct on the mainland since 1883, leaving only one natural population on Little Barrier Island. In addition, populations have been successfully restored and managed on three other offshore islands (e.g. Tiritiri Matangi) and a mainland sanctuary (Castro 2013). Other New Zealand birds, now extinct, may also have been nectar feeders (Tennyson and Martinson 2006). The importance of bird pollinators for some bird-adapted flowers has been demonstrated by Anderson et al. (2011) where absence of birds is not compensated by other pollinators; for example, seed set and plant density are reduced in *Rhabdothamnus solandri* on mainland sites of the North Island.

Nevertheless in many cases, birds and insects, including native and honey bees, commonly share flowers typical of bird pollination (pers. obs.), while birds have also been observed visiting small flowers typical of insect pollination (Castro and Robertson 1997). Of the 28 plant species regularly visited by birds, six are commonly used by honey bees in producing market-quality monofloral honey, including pohutukawa (*Metrosideros* spp.), rewarewa (*Knightia excelsa*), and kāmahi (*Weinmannia racemosa*). Nine other typical bird plant species are called ‘surplus honey producers’ because they provide more honey than needed for honey bee colony maintenance (Butz Huryn 1995; Newstrom and Robertson 2005). In some cases honey bees may partially compensate for the absence of birds; for example, five-finger (*Pseudopanax arboreus*) (Figure 3C–D). However, the level of compensation by honey bees depends on the size and shape of the flower and how well the bee contacts the anthers and the stigma.

In agricultural systems one of the few temperate crops documented as pollinated by birds is *Feijoa sellowiana*, which can also be pollinated by managed honey bees (Stewart 1989; Free 1993). Otherwise, birds are not important in most agricultural or horticultural crops because they are too heavy for most flowers and tend to damage small flowers.

Bats, rats and lizards — Three other groups of vertebrates pollinate plants: native bats, lizards, and introduced rats. These are not important in crop pollination but play important roles in native plant pollination. Pattemore and Wilcove (2011) have shown the great importance of bats in moving pollen in several native plants and discovered the role played by introduced invasive rats in degraded ecosystems.

Of the two ancient and unique nectar-feeding bats in New Zealand, the only one surviving is the lesser short-tailed bat (*Mystacina tuberculata*, Mystacinidae). The greater short-tailed bat (*M. robusta*, Mystacinidae) is presumed extinct because it has not been sighted since ship rats invaded Stewart Island in 1967 (Lloyd 2005). Populations of the lesser short-tailed bat have been so decimated that it is listed as endangered and of ‘highest conservation priority’ by the Department of Conservation (undated). Like birds, bats visit flowers with copious dilute nectar rewards, including plant species used by honey bees for market honey, such as pohutukawa and rewarewa (Butz Huryn 1995; Newstrom and Robertson 2005).

The role of lizards in pollination has largely been ignored except for some investigations on islands (Olesen and Valido 2003; Newstrom and Robertson 2005). Whitaker (1987) has shown that lizards have a role in New Zealand pollination for *Metrosideros excelsa*. Lizard populations have declined on the mainland but larger populations can be found on offshore islands such as Little Barrier Island (Pattermore and Wilcove 2011).

CURRENT CONDITIONS AND TRENDS

The above list of pollinator groups is a preliminary step toward creating a functional inventory of pollinators for New Zealand. Further analysis and more investigation in the field may change the list and will certainly lengthen and refine it. Nevertheless, even at this broad scale, the contrast between natural and agricultural systems is evident. Pollination in agricultural ecosystems is dominated by insect pollinators; in contrast, and in terms of quantity of pollen transferred per visit, natural ecosystems are dominated by vertebrate pollinators. However, natural systems also include large populations of highly diverse insect groups, particularly bees and flies, that are important for both their effectiveness and abundance, and they also include a range of unexplored moth, butterfly and beetle pollinators (Godley 1979; Lloyd 1985; Newstrom and Robertson 2005; McAlpine and Wotton 2009).

Natural ecosystems

Pollinator declines and their consequences differ in each system. In natural systems, the loss of native vertebrate pollinators, especially birds, is one of the most serious pollinator declines in New Zealand – at least for plants tightly adapted to bird pollination (Kelly et al. 2006). Other vertebrates, particularly bats and lizards, have also severely declined. Although they undoubtedly played a large role in natural ecosystems in the past, compensation for these can be derived from introduced birds and invasive rats, so eliminating rats without restoring bats, for example, could be detrimental to some plant species in areas without bird pollinators (Pattemore and Wilcove 2011). This illustrates the complexity of pollination systems in terms of trade-offs in managing pollinators while attempting other conservation goals, particularly the elimination of invasive introduced species. In natural ecosystems, feral honey bees may have compensated for vertebrate declines; if so, their loss (due to varroa infestations) worsens the impact of the vertebrate losses, at least for plant species that honey bees could successfully pollinate.

In terms of numbers of individuals, the most ubiquitous and abundant, and therefore most important, pollinators for both natural and agricultural systems are bees and flies. They service almost all types of medium to small flowers depending on how well they match the flower morphology and therefore how well they can access rewards and contact the anthers and stigma. Declines in hymenopteran or dipteran species have not been reported because only baseline data are available so far (Howlett et al. 2005, 2009). Although Donovan (2007) reported that native bees have successfully coexisted with introduced feral bees since the 1800s, this conclusion was based on natural and feral population levels. Recently, commercially managed honey bee hives have increased greatly, particularly in Northland and the East Coast of the North Island where bees are introduced to remote areas of native bush to extract mānuka honey, and this increase may cause problems in the future if the hives are highly overstocked. Some evidence of negative effects of honey bees in native systems has been found in the Tongariro National Park (Murphy and Robertson 2000). Competition for pollen and nectar resources by an extremely high density of commercially managed honey bees may adversely affect native insects particularly if the same site is overstocked year after year. Concern about how commercially managed honey bees may outcompete native bees has prompted investigations in Australia (Paini and Roberts 2005), and is an important issue in some countries (Gross and Mackay 1998; Goulson 2003). On the other hand, mānuka and other flowers may be abundant enough to sustain high populations of honey bees and all the native insects, particularly in the absence of birds. However, the carrying capacity of these native habitats based on volumes of nectar and pollen, rate of extraction by honey bees versus native insects, and density of flowers has not been determined so the continued co-existence of honey bees and native bees under these new circumstances is unknown.

Agricultural ecosystems

In agricultural systems, the loss of feral honey bees has been a massive loss for those crops and pastures that relied on background pollination. For the time being, commercially managed honey bees can continue to be viable if varroa treatments keep working. However, varroa is developing resistance to current treatments in the North Island (Goodwin and Taylor 2007), so the viability of commercially managed honey bees will depend on the development of new treatments. Beekeepers estimate that the eventual increase and spread of this resistance will be more difficult to manage than the initial arrival of varroa. Resistance is now a problem in North America and Europe, where beekeepers have battled varroa for over 20 years. If trends in New Zealand follow the overseas pattern of increasing varroa resistance accompanied by continual varroa-induced viruses and other pathogens, then sudden large-scale colony loss events could eventuate, to the detriment of New Zealand agricultural production.

Globally there is some concern that as human populations and agriculture continue to increase, the rate of increase in honey bee populations is not keeping pace with the demand for pollination (Aizen and Harder 2009). This may also be true for New Zealand, where future demand for colonies may exceed supply (Goodwin 2007). While the recent increase in hive numbers and new beekeepers in New Zealand over the last five years, as registered by AsureQuality, appears encouraging, this does not necessarily reflect more bees for pollination because much of the new activity is directed to harvesting high-value mānuka honey without using hives for pollination. However, meeting the demand for more honey bee colonies is a matter of building up bee populations and making splits to produce new hives. The rate at which this can be achieved is more important than the total number of hives in management because it is the rate of colony losses that will drive up the cost of supplying bee colonies for pollination. The limiting factor here is the economics of beekeeper livelihoods and their ability to sustain the ever increasing rates of hive losses caused by varroa resistance and other threats (discussed below).

The prospect of large-scale colony loss events in New Zealand comparable with those that have repeatedly taken place overseas raises important questions. What pollinator groups could compensate for the losses to agriculture? Does New Zealand have a diversity and abundance of non-*Apis* alternative pollinators comparable with those found overseas? Can these alternative pollinator populations fill the gap until honey bee populations are restored following a major colony loss event? As discussed above, the only candidates for managed alternative pollinators are bumble bees, one group of native bees (*Leioproctus*), and some flies. Unmanaged diverse insects can contribute but may not be able to be built up to the required population levels or be manipulated to supply large-scale crops at the right time.

Bumble bees would be suitable for many crops but would probably only partially compensate for the scale of honey bee pollination conducted in New Zealand, and New Zealand's native bees do not have the diversity and abundance of the large hairy native bee species in continental regions. Populations of native *Leioproctus* species are promising but their ground-nesting habit means developing management methods for transportation of nests will be difficult. However, permanent sites with populations of these native bee species can be developed, and these could serve as alternatives if nest site areas are not disturbed and are supported with the necessary bee forage plants. The use of native bees in agriculture has not been explored to its full extent and many crops such as kiwifruit could benefit (Donovan 2007).

While flies can be important pollinators, they can also cause harm, so attempting to increase fly populations on farms might be viewed unfavourably. For example, while blowflies (Calliphoridae) pollinate some flowers (Heath 1982), some are agents of flystrike, so promoting flies as pollinators would probably be resisted by sheep farmers.

The fundamental question large-scale crop farmers ask when considering alternative pollinators to replace honey bees is whether or not these can be supplied at short notice in the numbers required to pollinate the entire crop in a few weeks. Building up alternative pollinators around the farm so they will be on site in sufficient numbers when required is an option that has yet to be explored. With honey bees, pollinator populations are already at a peak when they are introduced to the crop for pollination and the bees are moved in and out for just those weeks that they are needed.

Nevertheless, alternative pollinators are important supplemental pollinators with synergistic effects when mixed with honey bees. In some crops they are often more efficient and can be the primary or only pollinator; however, these results are from overseas where different types of native bees are involved. Keeping a high diversity of pollinators available for agriculture will mitigate an over-reliance on honey bees, especially in crops that formerly relied entirely on background pollination. Although non-A*pis* alternative pollinators in New Zealand have some limitations for large-scale crops, it is critically important to protect and restore them by increasing their populations through habitat improvement and by developing management techniques for domestication or at least partial management.

At the same time, the urgency to protect honey bees is due to the magnitude of the combined effects of four major ongoing threats: (1) marked acceleration of new diseases and pests compounded by varroa and the development of resistance to treatments; (2) ongoing misuse of pesticides and issues with new systemic pesticides in pollen fed to larvae; (3) the narrow genetic base for breeding bees with resistance to varroa; and (4) loss of traditional nutritious floral resources.

The likelihood of a major colony loss event in New Zealand can be assessed by examining events overseas in North America and Europe. The four major threats listed above work in concert not just overseas but also in New Zealand and it is the ability of these four threats to create synergistic adverse impacts on honey bees that leads to the high risks of large-scale widespread colony losses (Williams et al. 2010; USDA 2012). Because New Zealand has been coping with varroa for 10–15 years less than overseas countries, the lessons learned there may help prevent large losses here. However, this will depend on two factors: first, how well and how quickly measures are put in place to remove or reduce the multiple threats against bee health, and second, how fast varroa resistance to treatment spreads throughout New Zealand and/or new varroa treatments can be developed.

Overseas research may help identify new treatments for varroa, but working out how to reduce the four threats to bees will be specific to New Zealand. It is beyond the scope of this chapter to discuss each of these threats and their mitigation in New Zealand other than to highlight two issues. For the first threat, strong measures are needed to battle current diseases and prevent the introduction of new diseases. In this respect the New Zealand American Foulbrood programme is world leading (American Foulbrood Pest Management Strategy: http://afb.org.nz/). A helpful measure in this regard would be to review the scientific basis for the risk analyses originally conducted in 2004 and 2009 for importing honey from Australia, because if honey were to be imported it would open a new risk pathway for the entry of new honey bee diseases to New Zealand. Overseas, the reasons for the syndrome known as colony collapse disorder (CCD) remain unresolved, but it is clear that varroa and the diseases it facilitates play a significant role (Williams et al. 2010). Contributing factors are numerous and the focus has now turned to all types of large-scale colony collapses/losses in general rather than just the syndrome originally defined as CCD (Williams et al. 2010; USDA 2012). Overseas, the increasingly high level of bee colony losses has become a major concern for pollination of crops in the last few years. In light of this and the reality of these same four threats in New Zealand, the scientific evidence supporting the idea that New Zealand could manage the risks of new diseases from honey imports is increasingly called into question.

The second issue to highlight in the suite of threats to honey bees in New Zealand is the problem of malnutrition and starvation in bees due to continuing loss and removal of traditional honey bee floral resources. Bee health in general is inextricably linked to the other threats since weakened bees are less able to withstand long-term varroa, new diseases, and pesticide exposures. One of the most straightforward methods to rapidly improve bee health is to increase the supply of high-quality food, particularly where bee forage has been lost.

RESTORING FLORAL RESOURCES

The dearth of floral resources for bees on farms is not unique to New Zealand; it is a worldwide result of biodiversity losses in both natural and agricultural ecosystems (NRC 2007). Lack of floral resources for all types of bee pollinators is a major issue in Europe and North America, where programmes have been established to promote planting of bee forage on farms and roadsides. Many of these programmes are subsidised by government funding (NRC 2007). In general, interest in planting for bees is increasing in many countries, such as Australia (Leech 2012) and the United Kingdom (Kirk and Howes 2012). In New Zealand the lack of bee forage is partly caused by land-use changes and partly by the failure of programmes designed to modernise and intensify agriculture to consider replacement bee forage when noxious weeds are controlled. The latter failure has arisen because in the past it was always possible to take pollination for granted.

Decline of floral resources

As biodiversity has declined due to extensive land-use changes and continuing intensification of agriculture, flower diversity and abundance have also declined, thereby contributing to worldwide pollinator declines (NRC 2007). New Zealand has an additional problem: many key traditional flowers on which beekeepers have relied are now recognised as invasive weedy plants that threaten native plant diversity and are subject to mass removal. This ongoing elimination of weeds due to farming practices, legislative controls, and biocontrol programmes is reducing traditional floral resources on farms as well as on public and private land.

Programmes to replace the removed plant species by planting alternative native or non-invasive introduced plants will help restore previous levels of bee forage resources. For this to succeed, key forage plants in the bee colony life cycle will have to be replaced by plant species offering good nutrition at the same time of year. This may not be possible for all the key forage plants being eliminated, because it will depend on many factors including timing, nutrition levels, and regional conditions. Consequently, a list of all available bee plants and their seasonal contributions to the bee colony life cycle can help suitable replacement plants to be selected.

Constructing a basic list of bee plants

Common widespread bee forage plants — Beekeepers are not usually large landowners, so they traditionally rely on placing apiaries on farms and public or private land with sufficient bee forage plants. The most common traditional bee forage plants are listed in *Practical Beekeeping in New Zealand* (Matheson and Reid 2011). However, this is not a list of plants recommended for planting for bees – for example, it includes some species now classed as noxious weeds – but instead comprises a list of common and widespread plants bees use for pollen and nectar. It is arranged according to the different beekeeping 'seasons' that correspond to stages in the honey bee colony life cycle.

Beekeepers in New Zealand divide the year into four major seasons based on colony stages (Matheson and Reid 2011). The first season, *Winter – Early Spring*, lasts 4 months (June to September); during this, a nucleus of overwintering bees (<10 000 bees per hive) survives cold weather until the advent of warm weather, which is accompanied by the first early-spring flowering when bee populations start to build up. The second season, *Spring – Early Summer*, lasts 2 months (October to November); during this, the colony rapidly builds to peak population levels in preparation for pollination services and honey harvesting. The third season, *Summer*, lasts 4 months (December to March); the colonies must now be at their full strength and size (about 60 000–80 000 bees per hive) to perform pollination services and harvest honey. Finally, the fourth season, *Autumn – Early Winter*, lasts 2 months (April to May); colony size starts to reduce, brood numbers decrease, and individual bees fatten for surviving the

TABLE 1 List of Native Bee Plants from the Federated Farmers Bee Industry Group Bee Plant Guides of November 2009 shows all species that were selected by beekeepers as good bee forage and by farmers and nurseries as suitable for planting on farms. These plants are listed according to their regions in the 10 regional Bee Plant Guides on www.treesforbeesnz.org or http://www.fedfarm.org.nz/membership/Industry-Groups/Trees-for-Bees

Bee Plant Guide region number	Botanical name	Common name	Flowering time	Life form	Height (m)
2	*Aciphylla colensoi*	Giant speargrass		Tufted	1
3	*Alectryon excelsus*	Tītoki	Oct–Dec	Tree	10
2	*Alseuosmia macrophylla*	Karapapa	Aug–Dec	Shrub	2
3	*Aristotelia fruticosa*	Mountain wineberry	Oct–Dec	Tree	2.5
4	*Aristotelia serrata*	Wineberry	Sep–Dec	Tree	10
7 & 10	*Astelia nervosa*	Kakaha	Oct–Dec	Tufted	1.5
2	*Brachyglottis repanda*	Rangiora	Aug–Oct	Tree/Shrub	6
7,8,9	*Carmichaelia arborea*	South Island broom		Tree/Shrub	3
1,2,3,4,8,9	*Carmichaelia australis*	North Island broom	Oct–Feb	Shrub	2
8	*Carmichaelia glabrescens*	Pink tree broom	Dec	Shrub	3
4,5,6,7,8,9	*Carmichaelia odorata*	Scented broom		Shrub	3
8	*Coprosma lucida*	Karangū		Tree/Shrub	4
4	*Coprosma robusta*	Karamū		Tree/Shrub	6
1,2,3,4,5,6,7,8,9,10	*Cordyline australis*	Cabbage tree	Oct–Dec	Tree	15
7	*Cordyline banksii*	Bank's cabbage tree	Nov–Jan	Tree	6
7	*Cordyline indivisa*	Mountain cabbage tree	Dec–Jan	Tree	8
6,7,8,9,10	*Discaria toumatou*	Matagouri	Oct–Jan	Tree/Shrub	5
1,2,3,4,7.9	*Elaeocarpus dentatus*	Hīnau	Oct–Feb	Tree	15
2,10	*Elaeocarpus hookerianus*	Pōkākā	Oct–Jan	Tree	8
2,3,7,8,9,10	*Fuchsia excorticata*	Tree fuchsia	Jun–Jan	Tree/Shrub	12
1,2,4	*Geniostoma rupestre* var. *ligustrifolium*	Hangehange	Sep–Nov	Shrub	3
5,6,7,8,9	*Hebe salicifolia*	Koromiko	Jan–Feb–(Apr)	Shrub	3
1,4,5	*Hebe speciosa*	Napaka		Shrub	2
8	*Hebe spp.* e.g. *gracillima*	Hebe		Shrubs	
2,3,5	*Hebe stricta*	Koromiko		Shrub	4
3,4,5,6,7,8,9,10	*Hoheria angustifolia*	Narrow-lv. lacebark	Dec–Mar	Tree	10
1,2,3	*Hoheria populnea*	Lacebark	Mar–Apr–(Jun)	Tree	5
10	*Hoheria salicifolia*	Koromiko	Jan–Feb–(Apr)	Shrub	3
1	*Iscaria toumatou*	Matagouri	Oct–Jan	Tree/Shrub	5
1,3	*Ixerba brexioides*	Tāwari	Nov–Jan	Tree	10
1,2,3,4,5	*Knightia excelsa*	Rewarewa	Oct–Dec	Tree	30
1,2,3,4,5,6,7,8,9,10	*Kunzea ericoides*	Kānuka	Sep–Feb	Tree/Shrub	15
1,3,7,9,10	*Leptecophylla juniperina*	Prickly mingimingi		Shrub	2
1,2,3,4,5,6,7,8,9,10	*Leptospermum scoparium*	Mānuka	Sep–Mar	Tree/Shrub	5
1,2,3,4,7	*Leucopogon fasciculatus*	Mingimingi	Sep–Nov	Shrub	5
10	*Leucopogon fraseri*	Mingimingi	Sep–Nov	Shrub	0.2
2,5,6	*Lophomyrtus bullata*	Ramarama	Nov–Feb	Tree/Shrub	6
10	*Melicope simplex*	Poataniwha	Sep–Nov	Shrub	4
5,6	*Melicope ternata*	Whārangi	Sep–Oct	Shrub	8
4,5,6,10	*Melicytus ramiflorus*	Whiteywood	Nov–Feb	Tree	10
1,2,3,4,	*Metrosideros excelsa*	Pohutukawa	Dec–Jan	Tree	20
1,2,3,4,5,6,7	*Metrosideros robusta*	Rātā	Nov–Jan	Tree	25
1,3,4,5,6,7,8,9	*Metrosideros umbellata*	Sth. rātā	Nov–Jan–(Mar)	Tree/Shrub	15
2,3,5,6,7,8,9	*Myoporum laetum*	Ngaio	Jul–Apr	Tree/Shrub	10
2,5,6,9,10	*Myrsine divaricata*	Weeping matipou	Jun–Nov	Shrub	3
2	*Nestegis cunninghamii*	Black maire	Oct–Nov	Tree	20
10	*Olearia arborescens*	Tree daisy	Oct–Jan	Tree/Shrub	4
2	*Olearia furfuracea*	Akepiro	Oct–Jan	Tree/Shrub	5
5	*Olearia paniculata*	Akiraho	Mar–May	Tree/Shrub	6

1,2,7	*Olearia rani*	Heketara	Aug–Nov	Tree/Shrub	7
1,2,3,4,5,6,7,8,9,10	*Phormium tenax*	NZ flax	Nov–Dec	Tufted	5 flw stalk
3	*Pittosporum crassifolium*	Karo	Sep–Dec	Tree/Shrub	9
1,2,3,4,5,6,7,8,9,10	*Pittosporum eugenioides*	Lemonwood	Oct-Dec	Tree	10m
3,4	*Pittosporum ralphii*	Karo	Sep-Dec-(Jun)	Shrub	4m
1,2,3,4,5,6,8,9,10	*Pittosporum tenuifolium*	Kohuhu	Oct-Nov	Tree	6m
2	*Pittosporum umbellatum*	Haekaro	Sep-Jan	Tree	7m
5,6	*Plagianthus regius*	Ribbonwood	Sep-Nov	Tree	6m
2	*Pomaderris kumeraho*	Kumarahou	Sep-Oct	Shrub	3m
1,2,3,4,5,6,7,8,9	*Pseudopanax arboreus*	Five-finger	Jun-Aug	Tree	8m
1,3,4,7,9,10	*Pseudopanax colensoi*	Three-finger	Oct-Mar	Tree/Shrub	5m
2,4,5,6,8,9,10	*Pseudopanax crassifolius*	Horoeka	Jan-Apr	Tree	15m
1,4,6,7	*Quintinia acutifolia*	Westland quintinia	Oct-Nov	Tree	12m
1	*Quintinia serrata*	Quintinia	Oct-Nov	Tree	9m
2,10	*Raukaua edgerleyi*	Raukawa	Sep-Dec	Tree	10 m
1,3,4,7	*Rhopalostylis sapida*	Nikau palm	Nov-Apr	Tree	15m
2,10	*Schefflera digitata*	Seven-finger	Feb-Mar	Tree	8m
1,3,4,5,6,8,9,10	*Sophora microphylla*	Weeping kowhai	Aug-Nov	Tree	10m
5,6	*Sophora prostrata*	South Island kowhai	Sep-Nov	Shrub	2m
3,4	*Sophora tetraptera*	North Island kowhai	Sept-Nov	Tree	10m
1,2,3,4,5,6,7,8,9,10	*Weinmannia racemosa*	Kamahi	Dec-Jan	Tree	20m
2	*Weinmannia silvicola*	Tawhero	Sep-Dec	Tree	15m

TABLE 2 List of Introduced Bee Plants from the Federated Farmers Bee Industry Group Bee Plant Guides of November 2009 shows all species that were selected by beekeepers as good bee forage and by farmers and nurseries as suitable for planting on farms. These plants are listed according to their regions in the 10 regional Bee Plant Guides on www.treesforbeesnz.org or http://www.fedfarm.org.nz/membership/Industry-Groups/Trees-for-Bees

Bee Plant Guide Region Number	Botanical Name	Common Name	Flowering Time	Life Form	Height
1	*Callistemon salignus*	Bottlebrush	Sep – Feb	Tree/Shrub	7 - 8m
8	*Callistemon splendens*	Bottlebrush	Oct	Shrub	2m
5 & 6	*Callistemon* spp.	Bottlebrush	Oct – Dec	Shrub	2m
1,2,3,4,5,6,7,8,9	*Chamaecytisus palmensis*	Tree Lucerne	May-Oct	Tree	5m
1	*Citrus sinensis*	Orange	Jan – Dec	Tree	10m
9,10	*Corylus avellana*	Hazelnut	Sept – Nov	Shrub	4.5m
1,2,3,4,5,6	*Corymbia ficifolia*	Red flowering gum	Dec – Feb	Tree	10m
1,2,3,4,7,8,9,10	*Eucalyptus cinerea*	Silver dollar gum	Dec – Feb	Tree	15m
10	*Eucalyptus crenulata*	Silver gum		Tree	8m
1,2,3,4,7,8,9	*Eucalyptus globulus*	Blue gum	Aug – Nov	Tree	40m
10	*Eucalyptus gunnii*	Cider gum		Tree	37m
1,2,3,4,5,6,7,8,9	*Eucalyptus leucoxylon*	White ironbark	Mar – Nov	Tree	30 m
7,8,9,10	*Eucalyptus melliodora*	Yellow box	Dec – Feb	Tree	30m
7,8,9,10	*Eucalyptus pauciflora* subsp. *niphophila*	Snow gum	Sep – Nov	Tree	18m
8	*Eucalyptus rodway*	Swamp peppermint	Mar – Jun	Tree	15m
8,10	*Eucalyptus viminalis*	Ribbon gum	Jul – Apr	Tree	40m
4,5,6	*Grevillea* spp.	Grevillea	Sep – Nov	Tree/Shrub	9m
8	"*Grevillea* spp. e.g., *'Clearview David'*, or *Victoria'*"	Grevillea		Tree/Shrub	2.5m
5,6	*Lavandula* spp.	Lavender	Sep – Dec	Shrub	1m
8	*Lavandula stoechas*	Lavender	Sept – Dec	Shrub	1m
7	*Malus sylvestris*	Crabapple		Tree	6 - 10m
1,3,4,5,6,7,8,9,10	*Malus xdomestica*	Apple	Sep – Nov	Tree	6 - 10m
1,3,7,9,10	*Prunus persica*	Peach	Aug – Oct	Tree	6 - 10m
1,2,3,4,5,6,7,8,9,10	*Pyrus communis*	Pear	Sep – Oct	Tree	6 - 10m
1,2,3,4,5,6,7,8,9,10	*Rosmarinus officinalis*	Rosemary	Sep – Nov	Shrub	1.5m
1,2,3,4,5,6,7,8,9,10	*Salix babylonica*	Weeping willow	Aug – Sep	Tree	25m

winter. Individual bees live as few as about 9 weeks in summer but up to several months during winter; however, lifespan can vary depending on the climate and level of nutrition (Winston 1987).

In this cycle, bees have critical requirements for high-level nutrition during two seasons (Winter – Early Spring and Autumn – Early Winter) when fewest species of plant flower in New Zealand (cf. figure 8 in Newstrom and Robertson 2005, p. 37). At these times, bees are at risk from 'pollen dearth' (lack of sufficient pollen). During spring build-up, if the colony does not have a consistent supply of high-protein pollen, then the multiplying population will start to crash or fail to thrive because the nurse bees will sacrifice the youngest brood to feed them as protein to the older brood, thus creating gaps in the cohorts (Winston 1987). During autumn as the colony prepares for winter, a lack of pollen and nectar sources means adult bees cannot store plentiful fat (Somerville 2005); the weakest, most malnourished bees will not survive the winter and if conditions are severe, malnutrition or low pollen and honey stores will cause the colony to dwindle or collapse (Williams et al. 2010).

The Matheson and Reid (2011) list parallels the flowering peaks in the New Zealand flora, with the highest number of common bee forage species flowering from early through late summer. Removing the 10 major weeds and one toxic plant (karaka, *Corynocarpus laevigatus*) leaves the list with 78 tree, shrub, vine, herb, and crop species. Fourteen species flower in Winter – Early Spring (5 native and 9 introduced); 25 flower in Spring – Early Summer (13 native and 12 introduced); 24 flower in Summer (8 native and 16 introduced) and only 4 flower in Autumn – Early Winter (2 native and 2 introduced). The list includes 14 herbaceous introduced weeds (particularly in summer and autumn) and only one native herbaceous species, reflecting the lack of herbs in the native New Zealand flora (Wilton and Breitwieser 2000).

Of the 10 major weeds on the list, two species are on the National Plant Pest Accord weed list: one tree, *Salix fragilis* (crack willow), flowering in Winter – Early Spring, and one herb, *Calluna vulgaris* (Ling heather), flowering in Summer (Ministry for Primary Industries 2012). Eight weed species are on various Regional Plant Pest Management Strategies (RPPMS) (www.biosecurityperformance.maf.govt.nz). Two are trees: sycamore (*Acer pseudoplatanus*) flowers in Spring – Early Summer, and Chinese privet (*Ligustrum sinense*) flowers in Summer. Four are shrubs: gorse (*Ulex europaeus*) flowers in Winter – Early Spring, and barberry (*Berberis* sp.), buddleia (*Buddleia salvifolia*), and broom (*Cytisus scoparius*) flower in Spring – Early Summer. Finally, two are herbs: Spanish heath (*Erica lusitanicus*) flowers in Winter – Early Spring, and thyme (*Thymus vulgaris*) flowers in Spring – Early Summer.

The most important floral resources to restore are the Winter – Early Spring species *Salix fragilis*, *Ulex europaeus*, and *Erica lusitanica* when little else is available to replace the losses. For beekeepers in many regions, the single most significant pollen dearth problem is the loss of gorse because it is one of the few plants that flower from autumn through winter and into early spring and it also provides good levels of crude protein (16-25%) in the pollen (Somerville 2005). In many regions, it is the most beneficial plant that reliably produces good winter survival and spring build-up for bees. A second problem in some regions is the loss of crack willow, but other willow species could be explored to take its place. In many regions, October is a critical period for pollen dearth because most of the common willows finish flowering but clover flowering has not yet started. Because of these regional variations, the first step in restoring lost floral resources was to conduct a regional analysis of bee forage for the entire flowering calendar.

The 2009 Federated Farmers Bee Plant Guides — In August 2009, the question of how to restore lost floral resources for honey bees was taken up by the Federated Farmers Bee Industry Group (FF-BIG), with John Hartnell as chair and Shona Sluys as policy advisor. They initiated a project in collaboration with Landcare Research and the Oceania Pollinator Initiative to search for solutions to the increasing problem of pollen dearth caused by the removal of traditional bee forage. The project, Trees for Bees NZ, aimed to create a bee plant list for the full flowering calendar so farmers could plant these to help restore lost floral resources. Although many bee plant lists already exist for New Zealand and other countries, the species they contain need to be examined carefully before promoting them for planting on farms. The species must be verified to have good nutrition, must not be weeds, and should not be impractical, unavailable, or otherwise useless. Multi-use plants that fit into the farm operations are more likely to be adopted by farmers, particularly if they offer some economic gain.

For this project, information on bee forage plants was obtained from two sources: a search of the New Zealand literature and a beekeeper survey to evaluate plants as pollen and nectar sources. The resulting 10 regional Bee Plant Guides are available online (Federated Farmers of New Zealand 2013; Landcare Research 2013a). Tables 1 and 2 provide the combined list of all species published in the 10 regional guides for native and introduced plants respectively. This list is neither comprehensive nor exhaustive but does provide accurate recommendations for good bee forage species to plant on farms in each of the 10 regions.

The regions were arbitrarily designated based on floristic changes and the quality of information available. From North to South, they comprise: (1) Northland and Auckland; (2) Bay of Plenty and Waikato; (3) Gisborne and Hawke's Bay; (4) Taranaki, Manawatu, Wanganui, and Wellington; (5) Nelson and Tasman; (6) Marlborough; (7) West Coast; (8) Canterbury; (9) Otago; (10) Southland. Plant species for each regional list were selected from the Landcare Research Trees for Bees NZ database using a sequence of steps to rank and eliminate plant species.

Step 1. Expand the diversity of the bee forage list: The first step used a search of the New Zealand literature to construct a full list of plants bees are known to visit. Four major sources were available to build a basic list: (1) Nectar and Pollen Sources of New Zealand (Walsh 1967), which included an annotated list of 240 native and introduced bee forage plants based on beekeeper information; (2) Butz Huryn (1995), which used an extensive literature search to identify 140 native plant species visited by honey bees; (3) Jeffs (1983), which listed 46 bee forage plant species selected for a tree-planting programme to provide shelter, bee forage and employment; and (4) Matheson (1984), which listed 89 plants based on beekeeper information. The combined list from these four sources resulted in 345 bee forage plants known to be used by bees in New Zealand. Sixty-five species in Butz Huryn were also in Walsh, while 15 species in Jeffs were in Walsh and 14 in Butz Huryn. The plant list in Matheson (1984), the first edition of *Practical Beekeeping in New Zealand,* is identical to the list in the fourth edition by Matheson and Reid (2011), which has been discussed above. All plant names were updated and checked for synonymy using the Landcare Research Plant Names database (Landcare Research 2013b).

Step 2. Determine rankings of each plant species: The second step determined which species have the highest rankings as pollen and nectar sources for bees on the basis of current experience of expert beekeepers. We asked 18 beekeepers from different regions to evaluate all 345 plant species for pollen and nectar value to bees. They scored the plants using qualitative categories: 'none' = 0, 'poor' = 1, 'average' = 3, 'good' = 5, and 'excellent' = 10 or, if necessary, 'unknown' = na. The beekeepers included comments about the usefulness or harmfulness to bees, and about the abundance of the plant. All weedy species were included to track the role of weed species for beekeepers in each region.

Step 3. Eliminate weeds from the list: In the third step, all weeds were flagged by filtering out plant species listed in the National Plant Pest Accord (NPPA) and Regional Pest Plant Management Strategies (RPPMS). Plants listed on the NPPA are unwanted organisms under the Biosecurity Act 1993 and must not be sold, propagated or distributed even though some are high-value bee plants. Four species with high pollen or nectar scores were on the NPPA list (Table 3). Plants on RPPMS lists should not be planted for various reasons and are subject to certain rules in each region. Thirteen species with high pollen or nectar scores were on various RPPMS lists (Table 4). Two of the most important bee forage plants, gorse and broom, are under an RPPMS for all 10 regions. Some high-value bee plants are under an RPPMS only for the North Island or the South Island and a few are managed in only one or two regions (Table 4). In the published Federated Farmers regional Bee Plant Guides, plant species scoring high for nectar or pollen but also on the NPPA and relevant RPPMS lists were specifically named to alert people not to plant them, since some of these proscribed weeds are well-known high-value bee forage. In addition, the Department of Conservation (DOC) national weed list contained about 20 high-value bee forage plants that are aggressive weeds in certain locations but these were not specified on the published Bee Plant Guides because the DOC weed list, although a national list, targets each weed based on regional concerns. Since these vary from region to region, are sometimes limited to certain areas, and require consultation with DOC in each location, we did not name them in the published Bee Plant Guides.

TABLE 3 List of National Plant Pest Accord Weeds noted on the Federated Farmers Bee Industry Group Bee Plant Guides of November 2009 that must not be planted or propagated even though they are traditionally good bee forage in New Zealand. These noxious weeds are a threat to natural ecosystems in New Zealand and should be replaced by non-weedy bee forage plants

National Plant Pest Accord Weeds	
Common name	**Latin name**
Crack Willow	*Salix fragilis*
Grey Willow	*Salix cinerea*
Lantana	*Lantana camara*
Scottish Heather	*Calluna vulgaris*

TABLE 4 Regional Plant Pest Management Weeds noted on the Federated Farmers Bee Industry Group Bee Plant Guide of November 2009 that are subject to restrictions and should not be planted even though they are traditionally good bee forage in New Zealand. These weeds create problems in the regions indicated in the table and should be replaced by other non-weedy bee forage plants

	Common Name	Latin Name	Number Regions Listed	Auckland & Northland	Waikato & Bay of Plenty	Gisborne & Hawk's Bay	Taranaki, Manawatu, Wanganui & Wellington	Marlborough	Nelson & Tasman	West Coast	Canterbury	Otago	Southland
1	Gorse	*Ulex europaeus*	10	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes
2	Scotch Broom	*Cytisus scoparius*	10	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes
3	Blackberry	*Rubus fruticosa*	7	yes	yes	yes	yes	no	yes	no	yes	no	yes
4	Spanish Heath	*Erica lusitanica*	5	yes	no	no	yes	no	no	yes	yes	no	yes
5	Barberry	*Berberis darwinni & B. glaucocarpa*	4	both	+	++	both	no	no	no	no	no	no
6	Buddleja	*Buddleja davidii & dysophylla*	4	*	*	*	**	no	no	no	no	no	no
7	Hawthorn	*Crataegus monogyna*	4	yes	no	yes	no	no	no	no	yes	no	yes
8	Privet	*Ligustrum sinense*	3	yes	yes	yes	no	no	no	no	no	no	no
9	Himalyan honeysuckle	*Leycesteria formosa*	2	no	yes	no	no	no	no	yes	no	no	no
10	Sycamore	*Acer pseudoplatanus*	2	no	no	no	no	no	no	no	yes	no	yes
11	Cherry Laurel	*Prunus laurocerasus*	1	no	no	no	no	no	no	no	no	no	yes
12	Flowering Currant	*Ribes sanguineum*	1	no	no	no	no	no	no	no	yes	no	no
13	Thyme	*Thymus vulgaris*	1	no	no	no	no	no	no	no	yes	no	no

* *B. davidii* ** *B. dysophylla* + only *B. darwinii* ++ only *B. glaucocarpa* no not listed

Because the goal was to construct a list of plants intended for planting for bees, a conservative approach was taken by also eliminating other known weeds not on the NPPA or RPPMS lists and any potentially weedy species. Decisions about potential weeds were conservative but are temporary, because many good species need closer examination and may not need to be excluded as weedy. For example, all wattles and all willows (except *Salix babylonica*) were left off the list until further investigation. The importance of weed issues for New Zealand cannot be emphasised enough, because bee forage plant lists found in magazines or on websites often include weedy species that should not be planted – as on any island nation, invasive weeds are serious threats to native plants.

Step 4. Organise into regional sub-lists: The fourth step listed the highest ranking bee plant species within each region on the basis of distribution information in the database. If a plant species in a given region had no survey score but the species is known from other sources to be important, it was included on the basis of its national average rank. The plant list changed along the latitudinal gradient with some species added or dropped, but there was also considerable overlap among regions. Plant species were selected first according to their ranking scores for pollen (from excellent to average) then according to their ranking scores for nectar.

Step 5. Filter for farm practicality and conditions: The final filter assessed the practicality of plants for farms and was based on advice from regional nurseries. A plant list that farmers can use with confidence must be based on practical plants: those suitable to the region, easy to establish, effortless to maintain, economical, and preferably with multiple uses such as shelter, fodder, timber, and erosion control. This step eliminated all herbs as impractical, including the four Spring – Early Summer herbs and the 11 Summer herbs listed in Matheson (1984). Crop plants were also eliminated because they are subject to economic decisions by the farmer and are not part of a dedicated permanent bee forage plot. However, crop plants, particularly *Brassica* spp., are extremely important in building up and maintaining bee colonies, especially since they are planted at large scales (James Callaghan, Midlands Apiaries, beekeeper, pers. comm.). Plantations of bee forage crops are desirable but were beyond the scope of the bee plant guides for farmers and are often temporary plantations due to crop rotations.

This step eliminated expensive or high-maintenance plant species, or those unsuited to particular growing conditions (e.g. frost, drought, high winds). For each region, the top ranking 20–24 native plant species and 14–16 introduced plant species were selected. Many native species were candidates because of the Butz Huryn (1995) input. However, introduced species were lacking because all weeds and all herbs were eliminated and input from the original sources was insufficient. A flowering calendar based on national flowering times for most of the species used in the Bee Plant Guides (Table 5), and a frequency chart of the number of species in flower each month (Figure 4), show more research is needed to fill out the list from February to August (Autumn through Winter) when few plant species are flowering in New Zealand (cf. figure 8 in Newstrom and Robertson 2005, p. 37).

Extending and refining the basic list of bee plants

The 10 Federated Farmers regional Bee Plant Guides represent a selection of the best bee plants based on current beekeeper evaluations, elimination of weeds, regional distributions of high-ranking plants, and compatibility with farm situations. However, because insufficient information was gained on plants for pollen-dearth times, a second Tree for Bees NZ project was initiated under the governance of the Bee Friendly Farming Group (BFFG) with Ross Little as chair and collaboration from AsureQuality, Landcare Research, GNS Science, Federated Farmers Bee Industry Group (FF-BIG), National Beekeepers' Association (NBA), Foundation for Arable Research (FAR), and the Oceania Pollinator Initiative (OPI). This new research project was supported by a Ministry for Primary Industries Sustainable Farming Fund grant (MPI-SFF Project 10/009) from November 2010 to 2013 (Ministry for Primary Industries undated) and many industry groups and companies (Landcare Research 2013a). It focuses on finding the most nutritious plants that flower in the two critical pollen-dearth times: autumn, when bees are preparing to overwinter, and late winter to early spring, when bee populations are growing. Losses of traditional forage plants are most critical at these pivotal times. For example, invasive introduced plants like gorse, broom and willow have traditionally been relied on but are now subject to major removal and control programmes.

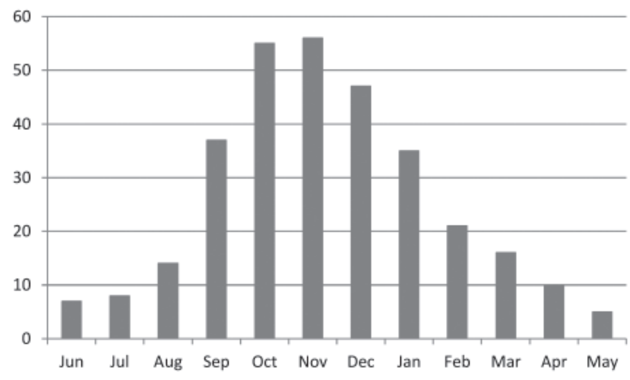

FIGURE 4 Total number of selected Bee Plant species in Figure 4 that are likely to flower in each month of the year based on the species listed in the Federated Farmers Bee Industry Group Bee Plant Guides of November 2009. The season for pollination services and honey flow is from November to February. Pollen Dearth for Spring Build up can occur in August, September and October on farms with low flower diversity especially after willows finish flowering and before clover flowers. Pollen Dearth for Winter Preparation can occur in March, April and May when few species are in flower. Y axis is the number of species, X axis is the month.

The focus of this second project is not only on finding plants that flower in these critical pollen-dearth times but also on finding the best nutrition. For bees this means high-protein pollen, which is much more difficult than nectar to supplement with artificial food. Pollen from flowers is the only natural source of protein for bees to feed their brood. Although they can derive protein from alternative sources including artificial protein supplements, colonies thrive best on a diversity of natural pollen. The diversity and abundance of pollen with high protein is critical for the success of the colony because the larvae need it to grow and develop (Roulston and Cane 2000; Roulston et al. 2000). The total protein intake of the colony will influence the number and strength of bees available for pollination; thus, when colonies collect too little pollen, whatever the protein content, or when the protein content is below 20%, whatever the volume collected, the colony will reduce the area of brood being reared (Somerville 2005). Finding plant species with the highest protein pollen and the largest quantity of pollen per unit of vertical area will help maximise nutrition while taking up least space on the farm. To

TABLE 5 Flowering times for the native and introduced Bee Plant Species listed in Table 1 and 2. Plant species from the Federated Farmers Bee Industry Group Bee Plant Guides of November 2009. Flowering seasons are categorized according to the bee colony life cycle as per Matheson and Reid 2011 (Pages 74 to 82). Flowering times are derived from Webb et al. 1988 Flora of New Zealand Vol. IV and reports by beekeepers. The flowering periods reflect the start and stop times at the national level and will be earlier or later according to latitude or region. Symbols: 1 = full flowering, x = partial or sporadic flowering; E = Introduced plant species; N = Native plant species

		Flowering Period	Winter/Early Spring				Spring/Early Summer		Summer				Autumn/ Early Winter	
			Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May
N	*Fuchsia excorticata*	Jun-Jan	1	1	1	1	1	1	1	1				
N	*Myrsine divaricata*	Jun-Nov	1	1	1	1	1	1						
N	*Pseudopanax arboreus*	Jun-Aug	1	1	1									
N	*Myoporum laetum*	Jul-Apr		1	1	1	1	1	1	1	1	1	1	
E	*Eucalyptus viminalis*	Jul-Apr		1	1	1	1	1	1	1	1	1	1	
N	*Alseuosmia macrophylla*	Aug-Dec			1	1	1	1	1					
N	*Olearia rani*	Aug-Nov			1	1	1	1						
E	*Eucalyptus globulus*	Aug-Nov			1	1	1	1						
E	*Prunus persica*	Aug-Oct			1	1	1							
N	*Brachyglottis repanda*	Aug-Oct			1	1	1							
E	*Salix babylonica*	Aug-Sep			1	1								
N	*Leptospermum scoparium*	Sep-Mar				1	1	1	1	1	1	1		
N	*Kunzea ericoides*	Sep-Feb				1	1	1	1	1	1			
E	*Callistemon salignus*	Sept to Feb				1	1	1	1	1	1			
N	*Pittosporum umbellatum*	Sep-Jan				1	1	1	1	1				
N	*Pittosporum crassifolium*	Sep-Dec				1	1	1	1					
N	*Pittosporum ralphii*	Sep-Dec-(Jun)	x			1	1	1	1	x	x	x	x	x
N	*Raukaua edgerleyi*	Sep-Dec				1	1	1	1					
N	*Weinmannia silvicola*	Sep-Dec				1	1	1	1					
N	*Aristotelia serrata*	Sep-Dec				1	1	1	1					
E	*Lavandula* spp.	Sep-Dec				1	1	1	1					
E	*Lavandula stoechas*	Sept-Dec				1	1	1	1					
E	*Malus xdomestica*	Sep-Nov				1	1	1						
E	*Corylus avellana*	Sept-Nov				1	1	1						
E	*Eucalyptus pauciflora subsp. niphophila*	Sep-Nov				1	1	1						
E	*Grevillea* ~~spp~~.	Sep-Nov				1	1	1						
N	*Plagianthus regius*	Sep-Nov				1	1	1						
N	*Leucopogon fasciculatus*	Sep-Nov				1	1	1						
N	*Leucopogon fraseri*	Sep-Nov				1	1	1						
N	*Melicope simplex*	Sep-Nov				1	1	1						
N	*Geniostoma rupestre* var. *ligustrifolium*	Sep-Nov				1	1	1						
N	*Melicope ternata*	Sep-Oct				1	1							
N	*Pomaderris kumeraho*	Sep-Oct				1	1							
E	*Pyrus communis*	Sep-Oct				1	1							
E	*Rosmarinus officinalis*	Sep-Nov				1	1	1	1	1	1	1	1	
N	*Pseudopanax colensoi*	Oct-Mar					1	1	1	1	1	1		
N	*Carmichaelia australis*	Oct-Feb					1	1	1	1	1			
N	*Elaeocarpus dentatus*	Oct-Feb					1	1	1	1	1			
N	*Elaeocarpus hookerianus*	Oct-Jan					1	1	1	1				
N	*Iscaria toumatou*	Oct-Jan					1	1	1	1				
N	*Knightia excelsa*	Oct-Dec					1	1	1					
N	*Olearia arborescens*	Oct-Jan					1	1	1	1				
N	*Olearia furfuracea*	Oct-Jan					1	1	1	1				
N	*Pittosporum eugenioides*	Oct-Dec					1	1	1	1				
N	*Discaria toumatou*	Oct-Jan					1	1	1	1				
N	*Alectryon excelsus*	Oct-Dec					1	1	1					

		Flowering Period	Winter/Early Spring				Spring/Early Summer		Summer				Autumn/ Early Winter	
			Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May
N	*Aristotelia fruticosa*	Oct-Dec					1	1	1					
N	*Astelia nervosa*	Oct-Dec					1	1	1					
N	*Cordyline australis*	Oct-Dec					1	1	1					
N	*Quintinia acutifolia*	Oct-Nov					1	1						
N	*Quintinia serrata*	Oct-Nov					1	1						
N	*Pittosporum tenuifolium*	Oct-Nov					1	1						
N	*Nestegis cunninghamii*	Oct-Nov					1	1						
E	*Callistemon splendens*	Oct					1							
N	*Rhopalostylis sapida*	Nov-Apr						1	1	1	1	1	1	
N	*Lophomyrtus bullata*	Nov-Feb						1	1	1	1			
N	*Melicytus ramiflorus*	Nov-Feb						1	1	1	1			
N	*Metrosideros umbellata*	Nov-Jan-(Mar)						1	1	1	x	x		
N	*Cordyline banksii*	Nov-Jan						1	1	1				
N	*Ixerba brexioides*	Nov-Jan						1	1	1				
N	*Metrosideros robusta*	Nov-Jan						1	1	1				
N	*Phormium tenax*	Nov-Dec						1	1					
N	*Hoheria angustifolia*	Dec-Mar							1	1	1	1		
E	*Corymbia ficifolia*	Dec-Feb							1	1	1			
E	*Eucalyptus cinerea*	Dec-Feb							1	1	1			
E	*Eucalyptus melliodora*	Dec-Feb							1	1	1			
N	*Weinmannia racemosa*	Dec-Jan							1	1				
N	*Metrosideros excelsa*	Dec-Jan							1	1				
N	*Cordyline indivisa*	Dec-Jan							1	1				
N	*Carmichaelia glabrescens*	Dec							1					
N	*Pseudopanax crassifolius*	Jan-Apr								1	1	1	1	
N	*Hebe salicifolia*	Jan-Feb-(Apr)								1	1	1	x	
N	*Hoheria salicifolia*	Jan-Feb-(Apr)								1	1	1	x	
N	*Schefflera digitata*	Feb-Mar									1	1		
E	*Eucalyptus leucoxylon*	Mar-Nov	1	1	1	1	1	1				1	1	1
E	*Eucalyptus rodway*	Mar-Jun	1									1	1	1
N	*Hoheria populnea*	Mar-Apr-(Jun)	x									1	1	x
N	*Olearia paniculata*	Mar-May										1	1	1
E	*Chamaecytisus palmensis*	May-Oct	1	1	1	1	1							1

date, protein values for c. 120 species of trees and shrubs have been measured (Trees for Bees NZ, unpubl. data).

Furthermore, information is needed on plants toxic to bees, mammals and other organisms. Literature searches after publication of the Bee Plant Guides showed one species (horse chestnut, *Aesculus hippocastanum*) recommended for Canterbury to be on a list of toxic plants that may harm bees (Skinner 1997). The toxicity of horse chestnut is not well understood but toxicity may be due to saponins and would probably harm bees if they were forced to use only this species during a drought. For this reason it is excluded from Table 2. As mentioned above, karaka is also toxic to bees and should not be planted. Some species listed as toxic to bees are not always harmful, depending on time of year, location, or variations in climate (e.g. kōwhai (*Sophora* sp.), *Tilia*, *Rhododendron*) (Skinner 1997). In addition, any plant contributing to honey toxic to humans should not be planted. For example, when bees collect honeydew from passion vine hoppers (*Scolypopa australis*, Ricaniidae) feeding on tutu (*Coriaria arborea*), the honey can be toxic to humans (NBA undated), but tutu is a popular pioneering species still planted in many revegetation programmes in New Zealand. Further searching for international information on toxicity is an important component of expanding and refining the basic bee plant list.

To test the planting combinations and designs from the data, several experimental demonstration plots of bee forage have been installed: two on arable farms, one on a small sheep and beef farm, and one on a mixed orchard and livestock farm. The flowering calendar in these demonstrations is organised so bees can attain peak populations on spring flowers, prepare for winter on autumn flowers, but will have no or few other plants during the pollination period to prevent competition with the target crop. The home range of a typical bee apiary is 2–5 km so the full calendar needs to be covered within those spatial limits – preferably the least distance.

Finally, expanding the basic bee plant list also increases the diversity of groups that can help restore floral resources for bees. Many already active planting programmes, such as council programmes for erosion control, riparian strips, and shelter, or programmes for farm forestry, are using these opportunities to include bee forage plants, thereby serving a double purpose for each planting programme.

POLLINATOR SECURITY IN NEW ZEALAND

If pollinator services in New Zealand can no longer be taken for granted, what is required to achieve pollinator security? Both natural and agricultural systems have suffered major losses of key pollinators; the most obvious are birds and bats in natural ecosystems and feral honey bees in natural and agricultural ecosystems. These losses can be compensated for in various ways. Restoration programmes are in progress for vertebrates in natural ecosystems on islands, mainland sanctuaries, and other habitats, but the complex networks of native and introduced invasive species are only beginning to be understood. Since invertebrate pollinator populations in natural systems are not being actively monitored to detect declines, it is unknown if there are problems for either pollinator or plant populations. Pollinators from natural ecosystems may be crucial for supplying the diversity and abundance of alternative non-Apis pollinators if these are needed to help compensate for honey bee losses in agriculture. Although not ideal, these alternatives already contribute to crop and pasture pollination; consequently, their protection is important for both natural and agricultural ecosystems because this diversity helps spread the risks caused by over-reliance on the managed honey bee.

The second component of pollinator security in New Zealand – protecting the commercially managed honey bee – is already in jeopardy. The absence of an in-depth economic analysis of the real value of honey bees to the New Zealand economy has contributed to a persistent lack of urgency about the level of threats facing honey bees. Although managed non-*Apis* pollinators now available in New Zealand will not be able to provide the current level of pollination services delivered by honey bees to agriculture, increasing their contribution by developing better management methods will still be important in improving pollinator security. Using managed alternative pollinators to spread the risks would mitigate pollination losses if honey bee populations are slow to recover from major colony loss events.

Nevertheless, the most urgent and significant issue is how to protect the health and survival of commercially managed honey bees and prevent large-scale colony losses. Positive timely action would not only reduce the cost of pollination services in large-scale agriculture, but would also address the four threats to pollinator security in agriculture. Understanding these four threats and how to reduce them is a challenge for New Zealand. Looking overseas may amount to looking into the future for New Zealand pollination services. Focusing on remedies and prevention measures specific to New Zealand can help reduce the currently high risk of large-scale, widespread colony losses. One underpinning threat, the loss of traditional bee forage resources, can be remedied by replacing lost nectar and pollen sources with key nutritious plants during pivotal pollen-dearth times on farms, as well as on public and private land. Proper nutrition is fundamental to all the threats facing honey bees, because healthy bees in strong colonies will better withstand diseases and pests, especially varroa, and exposure to pesticides. Although the beekeeping industry seems to be a small component of agriculture in New Zealand, it underpins all the bee-pollinated crops and pastures that make up a large proportion of New Zealand's economy, and because of this, its importance can hardly be overstated.

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