

Copyright is owned by the Author of the thesis. Permission is given for a copy to be downloaded by an individual for the purpose of research and private study only. The thesis may not be reproduced elsewhere without the permission of the Author.

Ecology of Native Bees in North Taranaki, New Zealand

A thesis presented in partial fulfilment of the requirements for the degree of

Master of Science

in

Zoology

at Massey University, Manawatū, New Zealand.



Nikki Maria Hartley

2018

Abstract

Studies are increasingly finding that native bees are important pollinators in many systems, in both natural and agricultural settings. With the possible loss of honey bees due to various reasons, it has become clear that relying on major pollinator for the world's pollination needs is problematic. Instead, we must look to native, wild pollinators, such as solitary bees, to avoid declines in pollination rates. However, these native bees are at risk from a number of different factors worldwide including habitat destruction and degradation for agriculture, climate change, and pesticide use. It is therefore important to have a clear idea of the state of native pollinators, to assess how they are affected by these risks.

This thesis gives a novel insight into the abundance and diversity of native bee species in the northern Taranaki area, New Zealand. I examined three main research questions concerning potential threats to native bees: how native bees are affected by varying land uses; how the abundances of native bees respond to different weather variables; and what the floral preferences of native bees in this region are.

572 bees from seven species were caught during the study. Overall, perhaps surprisingly, the abundance of native bees was positively associated with an increase in agricultural intensity and exotic vegetation. However, the results of this study show that species of native bees may respond differently to land use changes -the abundance of the three species of native bees that were collected frequently enough to measure preferences (*L. paahaumaa*, *L. sordidum*, and *L. cognatum*) all showed neutral to positive responses to an increase in agricultural intensity. Whereas, other species were caught much less frequently and may require more native habitat for persistence. This study also showed that weather has a significant impact on the likelihood of encountering native bees, specifically temperature, wind speed, and cloud cover.

This study indicated that these native bees have varying levels of generalisation, and differing preferences for native or introduced plants, when it comes to their floral preferences. The results indicated that the three common species (*L. paahaumaa*, *L. sordidum*, and *L. cognatum*) all forage on many different plant species, including both introduced and native species. This ability to forage on both native and introduced flora may explain the ability of these bees to inhabit areas of high agricultural intensity, while others cannot.

This thesis identified some of the potential threats to native bees in New Zealand and how they may impact native bee populations in North Taranaki. An understanding of these impacts is vital for future conservation management of native bees in New Zealand.

Acknowledgements

I would like to dedicate this thesis to the 572 bees that gave their lives (unwillingly I admit) to make this study possible. Although your lives were cut short, I hope you were able to have a joyous time eating pollen and nectar and industriously building nests before I came along with my net. I hope that your sacrifice will help to lead on to the preservation of your species in the long run.

A huge thank you to my supervisors, Alastair Robertson and David Pattemore. Thank you for your guidance and wisdom on all things bee related. Thank you also for your encouraging words when I was struggling to motivate myself. I am very grateful to Barry Donovan for his expertise on all of New Zealand's bees. Thank you for taking the time to help me identify my bees. You have given me some specialised knowledge that I may be able to help pass on to others, to give our little bees some more recognition in a world ruled by their celebrity cousins the honey bees and bumble bees! Finally thank you to Katherine Holt for her extremely helpful knowledge of identifying pollen grains.

I would like to acknowledge my parents, without whom this thesis would have never been completed. Thank you to my Dad, Stephen Hartley, for encouraging me to pursue my passions with the natural world at university. Thank you to my Mum, Anna Hartley, for being my biggest supporter and a dedicated research assistant.

I am very grateful for the people who took the time out of their day to help me catch bees: Tama Porter, Jamie Darbyshire, and Alarna Stratton - your help was much appreciated!

Thank you to Shelley Ogle and Jo Taylor for all your advice and support, it was so helpful to be following our university paths together!

I hugely appreciated the financial support given to me in the form of two scholarships: the Julie Alley Bursary, and the J P Skipworth Scholarship. These scholarships helped me immensely when working two jobs and studying at the same time became impossible.

Table of Contents

Abstract.....	ii
Acknowledgements	iii
Table of Contents	iv
List of Tables and Figures	vi
1. 1 Ecosystem Services.....	8
1.2 Pollination.....	9
1.2.1 Economic Value of Pollination	9
1.2.2 Insect Pollination.....	10
1.2.3 ‘Global Pollinator Crisis’	11
1.3 Overview of Hymenoptera.....	13
1.4 Bees of New Zealand	13
1.4.1 <i>Leioproctus</i> genus	13
1.4.2 <i>Hylaeus</i> genus	14
1.4.3 <i>Lasioglossum</i> genus	15
1.5 Life Cycle of New Zealand Native Bees	16
1.6 Threats to New Zealand Native Bees.....	17
1.7 Thesis Objectives	18
1.8 Conclusion	19
1.9 Outline of Thesis.....	19
2. Results	20
2.1 Introduction.....	20
2.1.1 Impacts of Agriculture on New Zealand Native bees	20
2.1.2 Effects of Weather on Native Bees	21
2.1.3 Floral Preferences of New Zealand Native Bees	22
2.2 Methods.....	23
2.2.1 Study Period.....	23
2.2.2 Study Site	23
2.2.3 Study Organisms	27
2.2.4 Sampling Method.....	29
2.2.5 Data Analysis	32
2.3 Results.....	35
2.3.1 Overall Abundance and Species Diversity.....	35
2.3.2 Distribution Data.....	36
2.3.3 Diversity of Native Bees in Varying Land uses.....	39
2.3.4 Weather Data	48

2.2.5 Pollen Data.....	52
3. Discussion.....	55
3.1 Introduction.....	55
3.2 Response Diversity of Native Bees to Land Use	55
3.2.1 Response of Native Bees to Agriculture Intensity	55
3.2.3 Conclusion	56
3.3 Species Abundances.....	57
3.3.1 Most Common Species	57
3.3.2 Least Common Species.....	58
3.3.3 Conclusion	59
3.5 Response of Native Bees to Weather.....	59
3.5.1 Conclusion	60
3.6 Interactions of native bees and flowering plants.....	61
3.6.1 Conclusion	62
3.7 Other Results.....	62
3.8 Overall Conclusions.....	63
3.9 Limitations	63
3.10 Study Implications	63
3.11 Future Work.....	64
References.....	67
Appendices.....	71

List of Tables and Figures

Chapter 1	8
Figure 1.1 Honey Bee on an Asteraceae	8
Figure 1.2 Bumble Bee on an Asteraceae	10
Figure 1.3 <i>Leioproctus</i> species on an Asteraceae	13
Figure 1.4 <i>Hylaeus</i> species on a <i>Phormium</i> species	14
Figure 1.5 <i>Lasioglossum</i> species on coriander flowers	15
Figure 1.6 <i>Leioproctus</i> species entering nest	16
Figure 1.7 <i>Hylaeus</i> species before mating	16
Chapter 2	20
Figure 2.1 Map of NZ showing study area.....	25
Figure 2.2 Map of study area showing sites and transects	26
Figure 2.3 Example of study site	26
Figure 2.4 Examples of native bee genera	27
Figure 2.5 <i>Hylaeus relegatus</i> blowing a bubble	28
Figure 2.6 Pollen sampling a <i>Leioproctus</i> species	31
Figure 2.7 Maps showing different farming intensities.....	34
Figure 2.8 <i>Hylaeus relegatus</i> foraging on <i>Phormium</i> species	35
Figure 2.9 Total bee captures and species richness per transect	35
Figure 2.10 Proportions of bee species caught	36
Figure 2.11 Abundances of most common species per transect	37
Figure 2.12 Distribution maps of each species	38
Figure 2.13 Bee captures vs. agricultural land	39
Figure 2.14 Bee captures vs. exotic vegetation	40
Figure 2.15 Species Richness across all sites	41
Figure 2.16 <i>L. paahaumaa</i> captures vs. agricultural land	42
Figure 2.17 <i>L. paahaumaa</i> captures vs. exotic vegetation	43
Figure 2.18 <i>L. cognatum</i> captures vs. agricultural land	44
Figure 2.19 <i>L. cognatum</i> captures vs. exotic land	45
Figure 2.20 <i>L. sordidum</i> captures vs. agricultural land	46
Figure 2.21 <i>L. sordidum</i> captures vs. exotic land	47
Figure 2.22 Bee captures vs. temperature	48

Figure 2.23 Bee captures vs. wind speed	49
Figure 2.24 Bee captures vs. humidity	50
Figure 2.25 Bee captures vs. cloud cover	51
Figure 2.26 Number of plant species bee species foraged on	53
Figure 2.27 Bipartite network of bee plant interactions	54
Table 2.1 Transect and site descriptions.....	24
Table 2.2 ANOVA of bee captures vs. agricultural land	39
Table 2.3 ANOVA of bee captures vs. exotic vegetation	40
Table 2.4 ANOVA of species richness vs. land use intensity	41
Table 2.5 ANOVA of <i>L. paahaumaa</i> vs. agricultural land	42
Table 2.6 ANOVA of <i>L. paahaumaa</i> vs. exotic vegetation	43
Table 2.7 ANOVA of <i>L. cognatum</i> vs. agricultural land	44
Table 2.8 ANOVA of <i>L. cognatum</i> vs. exotic vegetation	45
Table 2.9 ANOVA of <i>L. sordidum</i> vs. agricultural land	46
Table 2.10 ANOVA of <i>L. sordidum</i> vs. exotic vegetation	47
Table 2.11 ANOVA of bee captures vs. temperature	48
Table 2.12 ANOVA of bee captures vs. wind speed	49
Table 2.13 ANOVA of bee captures vs. humidity	50
Table 2.14 ANOVA of bee captures vs. cloud cover	51
Table 2.15 Interaction of bees and floral resources	52

1. General Introduction

1. 1 Ecosystem Services

The fossil record tells us that angiosperms, or flowering plants, first emerged around 125 million years ago, during the Lower Cretaceous. By the Middle Cretaceous, about 100 million years ago, this group experienced a rapid and huge diversification (Hickey & Doyle, 1977). This rapid speciation has been thought to be facilitated by plant-animal mutualisms, specifically the relationship between insects and plants (Kevan, 1990).

Ecosystems are extremely complex, made up of a diverse set of interacting organisms and the physical environment in which they inhabit (Elmqvist et al., 2003). Ecosystems are altered in many ways by humans, the pressures we put on the ecosystems impact on their ability to cope with disturbance (Peterson, Allen, & Holling, 1998). These processes are thought of in terms of ecosystem resilience, defined as “the amount of disturbance a system can absorb and still remain within the same state or domain of attraction” (Elmqvist et al., 2003).



Figure 1.1 Honey bee (*Apis mellifera*) on an Asteraceae species; photo taken by author.

To survive on this planet, humans rely on the ecosystem services provided naturally by organisms on earth. Ecosystem services have been defined as “aspects of ecosystems utilised (actively or passively) to produce human well-being” (Fisher, Turner, & Morling, 2009). Services including: the regulation of gases in the atmosphere, nutrient cycling processes, the production of food, and pollination (Braat & de Groot, 2012; Costanza et al., 1997; Kearns, Inouye, & Waser, 1998).

It has been suggested that the resilience of ecosystems relies, in part, on having a diversity of organisms present in that system (Elmqvist et al., 2003; Peterson et al., 1998). The functioning of ecosystem services relies heavily on biodiversity, as the supply of these services is limited by the diversity of species and populations that are involved in their production (Luck, Daily, & Ehrlich, 2003).

Due to the necessity of all the parts of the ecosystem to be ‘healthy’ and work in concert, any changes to any part of system may dramatically influence the whole ecosystem. Therefore, changes to species populations and diversity through environmental changes influence ecosystem resilience (Elmqvist et al., 2003). This process is described as “response diversity”, where species that carry out the same ecosystem service vary in their responses to environmental changes (Elmqvist et al., 2003; Stavert, Pattermore, Gaskett, Beggs, & Bartomeus, 2017). Although most ecosystems usually undergo disturbance regimes, in most cases these changes have been exacerbated by anthropogenic activities (Elmqvist et al., 2003). Clearing habitat for agriculture is one such activity. Although there would have been disturbances like habitat loss in the past (for example in the form of fire or flood), the ecosystem would have been given a chance to recover after the initial brief event. Now, however, these disturbances are ongoing, as with agriculture, and therefore the biodiversity of the affected area may not get a chance to bounce back (Peterson et al., 1998). One such ecosystem service influenced by the response diversity of organisms is pollination.

1.2 Pollination

Pollination, the process by which pollen is transferred from the male anthers to female stigmas of angiosperms, played a crucial role in the diversification of flowering plants (Kevan, 1990). Insect pollination, or entomophily, facilitated the explosion of angiosperm species (Kevan, 1990; Michener, 2000). The evolution of bees would have been predominately responsible for this, due to their long history of co-evolution with flowering plants (Kevan, 1990; O'Toole, 2013). The diversity of floral structures that we see today is a direct result of the evolutionary arms-race between the flowering plants and their pollinators, where each is trying to exploit the other (Kearns et al., 1998).

1.2.1 Economic Value of Pollination

Plants are the backbone of ecological health on the planet, not only for their role as food for countless species but also as regulators of the atmospheric conditions that allow for survival of life on earth (Sekercioglu, 2010). Pollination, therefore, is a major ecological function as it

allows for the propagation of a vast number of plant species. However, as in most cases, society requires things to have a monetary value to be considered important. Various studies, therefore, have tried to estimate the value of pollination services to humans (Allsopp, de Lange, & Veldteman, 2008; Costanza et al., 1997). Most estimations of the value of insect pollination focus on the honey bee alone; for example, the economic value of honey bees in the United States was estimated to be between \$1.6 and \$5.7 billion (Southwick & Southwick, 1992). In Europe, the value of honey bee pollination was estimated at around €4.25 billion and pollination by non-*Apis* pollinators at around €0.75 billion (S G Potts et al., 2006).

1.2.2 Insect Pollination

There are estimated to be upwards of 250,000 species of modern angiosperms, the majority (~90%) of these are pollinated by animals, mostly insects (Kearns et al., 1998). In almost all floral environments there is a large proportion of the species that are insect pollinated, and thus mostly bee pollinated. The trees of tropical forests, for example, are largely entomophilous species (Michener, 2000). Although most forest trees of temperate forests are wind pollinated, a high number of other flora such as small trees and bushes, are pollinated by bees. Deserts and xeric shrub lands cover about 19% of Earth's land surface area; these areas also play host to an abundance of bee-pollinated plants (Michener, 2000). We rely on insects and their pollination abilities for the huge variety of food we consume today, with over 400 crops pollinated by bees worldwide (O'Toole, 2013). It is estimated that around one-third of global food production depends on insect pollination (Allsopp et al., 2008). These

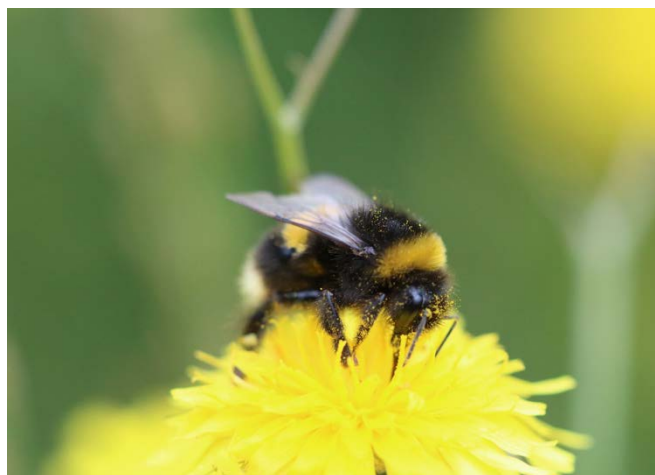


Figure 1.2 Bumble bee (*Bombus* spp.) foraging on a species of Asteraceae; photo taken by author.

figures show the clear importance of pollination by bee species.

1.2.3 'Global Pollinator Crisis'

Studies have pointed to a possible 'global pollinator crisis' due to the recorded declines of many pollinator species around the world (Ghazoul, 2005; Holden, 2006; Schmidt-Adam, Murray, & Young, 2009; Westerkamp & Gottsberger, 2002). It has been suggested that wild populations of pollinators are deteriorating, and the managed honeybee populations are not able to compensate for this decline (Burkle, Marlin, & Knight, 2013; Garibaldi et al., 2013; Tylianakis, 2013). Burkle et al. (2013) surmised from historical data of around 120 years, that there had been local extinctions of 50% of bee species in their area of study in Illinois, USA. However, there is debate in the literature that the pollinator crisis is only a honeybee-related problem (Ghazoul, 2005; Simon G Potts et al., 2010; Steffan-Dewenter, Potts, & Packer, 2005). Regardless whether there currently is a pollination crisis or not, the issues identified need to be addressed in order to conserve the diversity of pollinators, and to prevent any such crisis in the future. The issues attributed to the decline of pollinator species have been identified as: habitat loss and fragmentation; pesticide use; climate change; diseases and parasites; and the introduction of non-native plants and competing species (Simon G Potts et al., 2010; S G Potts et al., 2006).

Loss of pollinator species would have dire consequences globally. Pollination is such a keystone process that loss of pollinating species would cause widespread collapses in ecosystems and economies (S G Potts et al., 2006). Due to the high reliance of the food industry on pollination, human food sources, while they may not be completely wiped out, would be heavily disrupted. An example of the loss of pollinators causing major issues can be seen in Sichuan Province, China. Extensive use of insecticides in orchards caused the elimination of bees. Now 40,000 people are employed to carry out the pollination work by hand pollinating all the fruit trees (O'Toole, 2013).

It is thought that honey bees (*Apis mellifera*) are the major insect pollinator in commercial systems (Allsopp et al., 2008). This may be because honey bees are excellent generalists, they can forage on a wide range of flowers. However, reliance on a single pollinator is an inherently risky business due to potential declines of that pollinator (S G Potts et al., 2006). In the case of the honey bee, there have been huge declines in colonies in Europe and America since 2006 (Le Conte, Ellis, & Ritter, 2010; Winfree, Williams, Dushoff, &

Kremen, 2007). These losses have been thought to be caused by a variety of factors, including the parasitic mite *Varroa destructor*, or Colony Collapse Disorder (Le Conte et al., 2010). Not only are honey bees in danger of decline in many areas, but they are also not always the most efficient pollinators. The honey bee has been described as an “eager flower visitor, but an often poor pollinator” (Westerkamp & Gottsberger, 2002). For example, when foraging on some plant species, the honey bee will bite into the side of the flower and rob its nectar. By doing this, the bee does not encounter the anthers or stigma, and therefore does not contribute to the plant’s pollination (O’Toole, 2013).

It is necessary that agriculture increases its range of pollinators to avoid declines in pollination rates (O’Toole, 2013). Relying on only a small number of pollinators is risky, as any losses in their populations could cause major issues. Having a diversity of species would safeguard the systems from collapse if one species were to disappear. Solitary bees and other non-*Apis* bees can be a viable alternative for commercial pollination systems. Some wild bees already implemented in commercial systems include: *Osmia cornifrons*, *Megachile rotundata*, and *Bombus terrestris* (Michener, 2000). A study conducted in the United States questioned whether wild bees would be sufficient for pollinating agricultural crops if honey bees were removed. Using watermelon crops as their model they concluded that native, wild bees were able to provide sufficient pollination services at >90% of their sites (Winfree et al., 2007).

Simply allowing for the protection of wild bee species will be beneficial to both commercial and wild pollination systems. For example, studies have found that having honey bees and other wild bees together in an pollination environment makes for more efficient pollination by honey bees (Artz & Nault, 2011; Greenleaf & Kremen, 2006b). Some studies have even found that wild bees were more effective at pollinating certain crops than honey bees (Garibaldi et al., 2013). O’Toole (2013) suggests that some solitary bees may be more effective at pollinating flowering species than honey bees because their pollen collection behaviours are different. The honey bee packs pollen into its pollen baskets with the help of some nectar to make the pollen stick. This causes the pollen to become unavailable for pollination services. Solitary bees, however, pack pollen densely into their scopae (leg hairs) without the use of nectar, therefore they have more pollen available for pollinating the plant. The common theme emerging from these studies suggests that pollination systems would be improved if wild bee populations were protected; in conjunction with managed honey bee populations.

1.3 Overview of Hymenoptera

Within the Hymenoptera (the insect group comprised of wasps, bees, sawflies, and ants) bees (Apiformes), together with sphecoid wasps (Spheciformes) form the super family Apoidea. Bees have been described as hunting wasps that have abandoned the carnivorous lifestyle of their ancestors, and adopted a vegetarian existence (Michener, 2000; O'Toole, 2002). The oldest fossil bee (*Trigona prisca*) was found in Cretaceous New Jersey amber, dated to be around 74-96 million years old (Michener & Grimaldi, 1988; O'Toole, 2002). The total number of bee species is estimated to be around 17,000, but could be around 30,000 (Donovan, 2007; Michener, 2000). Michener (2000) ranked the seven families of bees into order of most primitive to most advanced: Stenotritidae, Colletidae, Andrenidae, Halictidae, Melittidae, Megachilidae, and Apidae.

Morphologically, some bees can look much like sphecoid wasps, however there are some distinguishing features. Bees possess branched hairs, whereas sphecoid wasps only have simple hairs; the hind basitarsi is usually broader than the succeeding tarsal segments in bees; generally bees have a longer proboscis than sphecoids; and lastly, sphecoid wasps all have silver or golden hairs on the lower part of their face, whereas bees generally do not (Michener, 2000).

1.4 Bees of New Zealand

New Zealand has a relatively small pollinator assemblage, with only a total of 41 species of bees (Donovan, 1980, 2007; Newstrom-Lloyd, 2013). 28 species of these bees are native to New Zealand (27 of these are endemic), the other species were introduced either purposefully or inadvertently by humans (Donovan, 2007). New Zealand's native bees belong to only two families – Colletidae and Halictidae. The three genera of native bees present in New Zealand are *Leioproctus*, *Hylaeus*, and *Lasioglossum*; these bees are generally solitary, small, black, and wasp-like (Donovan, 2007; Newstrom-Lloyd, 2013).

1.4.1 *Leioproctus* genus

The *Leioproctus* genus is very large with 33 subgenera, a high proportion of *Leioproctus* species are found in Australia. This suggests that the 18 species of *Leioproctus* present in New Zealand may have originated in Australia (Donovan, 2007). However, one of the subgenera, *Nesocolletes*, is found only in New Zealand (Donovan, 2007). *Leioproctus* species are the largest of the New Zealand native bees (5-12mm), they are generally black, very

hairy, and mostly carry pollen externally in their scopae. Females are normally larger and stouter than males. They construct their nests, which can occur in aggregations, in bare or mostly bare ground in a variety of different substrates (Donovan, 1980, 2007; Donovan, Howlett, & Walker, 2010). *Leioproctus* species are known to forage both on native flowering species and on many introduced species including kiwifruit (Actinidiaceae), onions (Alliaceae), and some Asteraceae (Donovan, 2007).



Figure 1.3 *Leioproctus* spp. foraging on a species of Asteraceae, photo taken by author.

1.4.2 *Hylaeus* genus

The genus *Hylaeus* occurs almost everywhere, and again is an enormous genus globally with 46 subgenera (Donovan, 2007). New Zealand has eight species of native *Hylaeus* all from the subgenus *Prosopisteron*, these bees are smaller and slimmer than *Leioproctus*, at around 7-9 millimetres long. They are often referred to as ‘masked bees’ due to the white or yellow markings on their faces. Unlike *Leioproctus* and *Lasioglossum*, *Hylaeus* bees collect, and store, pollen and nectar in their crop. As a result, they lack dense vestiture and a scopa, that is typical among other bees (Donovan, 2007). The absence of these features increases their resemblance to sphecoid wasps. It has been suggested that the lack of dense vestiture may cause low effectiveness as pollinators, though this was not the case for the alpine *Hylaeus matamoko* (Bischoff, Campbell, Lord, & Robertson, 2013). The diversity of *Hylaeus* is vast in Australia, which again suggests that New Zealand’s *Hylaeus* species derived from there (Kayaalp, Schwarz, & Stevens, 2013). These bees construct their nests in hollow plant material, for example inside of stems or pre-existing cavities in wood (O’Toole, 2013).

Hylaeus species are also known to forage both on native and introduced flowering plant species including kiwifruit and Rosaceae (Donovan, 2007).



Figure 1.4 *Hylaeus relegatus* on a flax flower (*Phormium* spp.), photo taken by author

1.4.3 *Lasioglossum* genus

Lasioglossum is another large genus that has a cosmopolitan distribution (Danforth, 1999). There are four species of native *Lasioglossum* present in New Zealand (Donovan, 2007).

These bees are predominately black, and are smaller than *Leioproctus*, at around half the size of worker honey bees. They, like *Leioproctus*, carry pollen externally in their scopae on their hind legs (Donovan, 2007). Their nesting behaviour is also like that of *Leioproctus* species, as they too nest in the ground and nests can be aggregated. It is suggested that females may re-nest in the same tunnel that they overwintered in (Donovan, 2007). *Lasioglossum* species have a wide foraging range with both native and introduced flowering species (Donovan, 2007).



1.5 Life Cycle of New Zealand Native Bees

As far as we know, the lifecycle of the 28 species of native bees in New Zealand are essentially the same. As solitary species, females work alone to construct a nest; there is no caste system; and no overlap of generations, so the female usually dies before her offspring emerge from the nest (O'Toole, 2013). The nest generally consists of a blind tunnel that is either pre-existing, such as inside branches or stems (*Hylaeus*), or the female excavates in soil (*Leioproctus* and *Lasioglossum*) (Donovan, 2007). These nests contain cells that are individual chambers excavated at the end of the tunnels or branching off from them. Or in the case of *Hylaeus*, the cells are lying end to end in the tunnel inside the plant material (O'Toole, 2013).



Figure 1.6 *Leioproctus* spp. entering its nest in a dirt bank; photos taken by author.

These females collect pollen and nectar which is deposited in the cells, in a process called mass-provisioning. An egg is then laid on the food and the female seals the cell, the growing bee has no contact with the rest of the nest until it has emerged (Donovan, 2007; O'Toole, 2013). The female continues to forage for food and construct more brood cells until she dies. On the other hand, the life of a male solitary bee is simpler, they are mostly concerned with foraging on flowers for their own energy source, and finding females to mate with (Michener, 2000).



Figure 1.7 Male *Lasioglossum* spp. approaching female *Lasioglossum* spp. to mate; photo taken by author.

New Zealand's native bees are generally on the wing from the beginning of spring (August/September) to the end of summer (February/March) (Donovan, 1980). At the end of the warm months the adult bees die, and the offspring spend the winter in their brood cells growing into adult bees, ready to emerge the next spring (Donovan, 2007). Some species of New Zealand native bees nest in what is termed aggregations; when ground nesting species excavate many nests in a small area, which results in small areas of earth covered in nest holes (Michener, 2000).

1.6 Threats to New Zealand Native Bees

There is a risk of native pollinator decline in New Zealand. Some studies worldwide have suggested a possibility of negative effects on native bee populations due to the introduction of competing pollinator species, such as honey bees and bumble bees (Goulson, 2003; Roubik, Moreno, Vergara, & Wittmann, 1986). However, other studies show that there is no quantitative evidence to suggest that honey bees are impacting negatively on native fauna (Butz Huryn, 1997; Paini, 2004).

It has also been suggested that the honey bee may have a negative competitive effect on native bees in New Zealand (Donovan, 1980). However, it is thought that although they may overlap in their floral preferences, native bees and introduced bees have such wide differences in their requirements for nesting sites that competition is reduced (Donovan, 1980). Furthermore, Donovan (2007) states that native bees have been successfully competing with introduced bees for over a century now, therefore it is likely they will continue to do so. Another study has found that native bees are more likely to compete with each other rather than with honey bees, as they share different floral resources. Only when the densities of honey bees and native bees are very high in one area there may be competition for resources (Iwasaki, 2017). However, the data concerning possible native bee declines is not yet available, and there continues to be an increase in commercial bee hives, this therefore may cause issues in the future (Newstrom-Lloyd, 2013).

The main risks to populations of New Zealand native bees have been identified as anthropogenic causes such as: deforestation and agricultural intensification causing habitat loss and fragmentation; the use of chemicals in agriculture; and climatic changes due to human activity (Donovan, 2007).

The loss of native bees in New Zealand would cause detrimental effects in the environment, with the potential decline of plants that may be reproductively tied to these species. For example, some studies have found a link between declines of pollinators and declines of plants that depend on those species for pollination (Biesmeijer et al., 2006). The New Zealand economy would also be impacted as some species of native bees are known to be important in pollinating a number of commercial crops, including: carrots, kiwifruit, and onion seed crops (Donovan, 2007; Howlett, Lankin-Vega, & Pattemore, 2015). Rader et al. (2012) found that wild pollinators were able to provide consistent pollination services to mass-flowering fields of pak choi (*Brassica rapa* spp. *chinensis*) comparable to the services provided by honey bees.

1.7 Thesis Objectives

This thesis examined the potential impacts of the above threats to native bees in New Zealand. This study aims to answer three main questions: firstly, how is native bee abundance and diversity impacted by agriculture and other land uses; secondly, how weather variables influence the foraging activity of native bees; and lastly, what are the floral preferences of native bees. Along with these main questions, the general distribution and diversity of native

bees in the study area will be examined. This study also aims to shed light on the need to protect native pollinator diversity, instead of relying on the few introduced pollinators. The results will have implications for the conservation of these native bees, ecosystem health, and the agricultural industry.

1.8 Conclusion

This Literature review covered the current scientific knowledge around insect pollination, specifically bee pollination. An overview of New Zealand's native bees was included, threats to native bees were also identified. This review shows that there are gaps in the current knowledge surrounding native bees in New Zealand, particularly the impacts of threats to native bees. This thesis attempts to address some of these knowledge gaps by examining the effects of agriculture, weather, and the floral preferences of native bees.

1.9 Outline of Thesis

The following chapter investigates questions about the abundance and diversity of native bees in the Taranaki region of New Zealand. This study gives an insight into the distribution of native bee species in North Taranaki, how native bees in this region are affected by different land uses and different weather variables, and investigates the floral preferences of these bee species. The final chapter discusses the results of this study along with implications of these results including conservation options. Lastly, potential avenues for future research are discussed.

2. Results

2.1 Introduction

2.1.1 Impacts of Agriculture on New Zealand Native bees

As New Zealand is an agriculturally driven economy, it is essential to understand the effects this intensive land use has on the native bees. Donovan et al, (2010) states that the environmental modifications, mainly due to agriculture, over the past 200 years have had a profound impact on the native bee species; nearly wiping them out from parts of their historic ranges. The effects farming has on the bees can be positive or negative, and range from loss of native plants, pesticide use, and even the unintentional creation of new habitats (Donovan, 2007). The abundance and species richness of bees is positively correlated with floral abundance and richness (Kremen et al., 2007). Thus, it follows that destruction of floral resources due to agriculture may cause a reduction in bee abundance and species richness. The degradation and fragmentation of native bee habitats may result in reduced gene flow between populations and lowered persistence rates (Kremen et al., 2007).

This theme of agricultural intensification causing declines in pollinator species is widespread. A study in California concluded that the intensification of agricultural practices had a negative impact on native bee abundances (Klein et al., 2007). A review by Kremen et al, (2002) looked at 16 studies that were conducted over four continents, the main trend identified from all the studies was that there was a decline in pollination by wild pollinators due to increasing agricultural intensity.

However, some studies have found that there are differences between the responses of solitary bees and social bees due to increasing agricultural intensities. One study, carried out in Indonesia, found that increasing agricultural intensities increased the abundance of solitary bees whilst decreasing the abundance of social bees (Klein, Steffan-Dewenter, Buchori, & Tscharntke, 2002).

One of the aims of this study is to monitor the response diversity of native bee species in areas of high agricultural intensity and other land uses. This will allow us to estimate the impact that the agricultural industry is having on native bees in New Zealand. There are several ways that the agricultural industry can affect native bees. The destruction, degradation, or fragmentation of habitat to create more agricultural land is a huge issue, as it causes the elimination of potential food sources for the bees (Davis, Reid, & Paxton, 2012). Agrochemicals such as pesticides and herbicides have been known to cause negative effects

on the health of honey bees (Pettis, Lichtenberg, Andree, Stitzinger, & Rose, 2013; Thompson, 2010), the same may be true for New Zealand's native bees (Donovan, 2007). Although, studies have suggested a wide range of sensitivity of bees to pesticides (Arena & Sgolastra, 2014), and without any specific data for New Zealand's native bees it is difficult to make assumptions. Conversely, agricultural intensification may also have positive impacts of the native bees. For example, farming practices can unintentionally open up new areas for nest sites, such as dirt banks or clay tracks (Donovan, 2007; Hart, 2007). I predict that the native bees species may show varying tolerance to intensified agriculture but overall there will be fewer bees in areas of very high intensity agriculture. I also predict that areas with high proportions of exotic vegetation will have fewer native bees than areas of low exotic vegetation.

2.1.2 Effects of Weather on Native Bees

The weather can have a considerable effect on pollinators. Weather variables such as temperature, light intensity, solar radiation, wind speed, humidity, and cloud cover can influence the flight period of bee species (Heard & Hendrikz, 1993; Papanikolaou, Kühn, Frenzel, & Schweiger, 2017).

Bees vary in their ability to fly at different temperatures from species to species. The period in which a bee is able to forage is termed its "microclimatic window" (Corbet et al., 1993). Studies have shown that honey bees do not fly in temperatures below 9°C (Burrill & Dietz, 1981), whereas some species of bumble bees start foraging at lower temperatures than honey bees and many other bee species (Corbet et al., 1993; Donovan, 2007). A study has shown that the stingless bee *Tetragonula carbonaria* only initiates flight when the temperature is over 18°C (Heard & Hendrikz, 1993).

The extent to which the other weather variables affect the foraging of bees may vary. Heard and Hendrikz (1993) found that temperature and solar radiation were the most important factors affecting the foraging of *T. carbonaria*, whereas vapour pressure, humidity, cloud cover, and wind speed did not cause significant effects.

However, another study found that although temperature had the greatest effect on the flight activity of the stingless bee (*Melipona asilvai*) but there was also a positive correlation between flight activity and a humidity increase (Souza, Carvalho, & Alves, 2006).

There is little quantitative data on the microclimatic range of New Zealand native bees. This study, therefore, aims to provide information as to how these weather variables may affect the native bees. These data may be important in light of the changing climate, as the foraging activity of the native bees may be altered due to these changes. Any shifts in the bee's foraging activity may result in an ecological mismatch between the foraging period of the bees, and the flowering period of their host plants (Polgar, Primack, Williams, Stichter, & Hitchcock, 2013; Rader, Reilly, Bartomeus, & Winfree, 2013). This could result in changes in the pollination services provided by bees. For example, Rader et al. (2013) predicted that under the most extreme IPCC scenario, pollination services provided by honey bees may decrease. However, they also predicted that the pollination services provided by wild, native pollinators would increase to buffer the impacts caused by climate change.

The impact of weather conditions on the activity patterns of native bees is important for taking advantage of the conditions for peak sampling. Researchers in the future will be able to use this information to design efficient sampling techniques.

We predict that the native bees will be greatly affected by weather conditions, specifically temperature and wind speed.

2.1.3 Floral Preferences of New Zealand Native Bees

The relationship between flowering plants and pollinating species can be complex. Very few plant species rely on only one pollinator for reproduction and vice versa (Memmott, Waser, & Price, 2004). Rather, there is a degree to how specialised or generalised both the plant and the animal can be (Kearns et al., 1998). For example, some species of bees, i.e. honey bees, are very broad generalists; they are happy to visit many different flowering species. On the other hand, bees like squash bees (*Peponapis* and *Xenoglossa*), only forage on species from the squash and pumpkin genus (*Curcubita*) (O'Toole, 2013). The width of a pollinator's foraging niche, or how specialised for certain flora a pollinator is, has been identified as a potential cause for declines in populations (Davis et al., 2012). Specialised or oligolectic bees (i.e. species that forage on only a few plant species) may be more susceptible to extinction if their few host plants are in danger of becoming extinct (O'Toole, 2013). Polylectic bees, i.e. those that are more generalised and forage on a wide variety of plants may, however, be buffered from extinction as it will be less likely that all their food sources will disappear (Davis et al., 2012; Michener, 2000).

New Zealand has a naturalised flora assemblage. Ever since European settlement, the number of plants introduced to New Zealand has been about eight species per year (Atkinson & Cameron, 1993). The total number of naturalised plants in New Zealand is 2436, which can be compared with the native total of about 2414 species (de Lange & Rolfe, 2010; Howell & Sawyer, 2006). A large number of New Zealand's native bees are known to forage on introduced plant species (Donovan, 2007).

The final aim of this research is to study the floral preferences of the native bees, including looking at the ratio of introduced and native plants that the native bee species are foraging on, and how generalised or specialised these bees are in their foraging habits. This information may be important in terms of the bees' survival. For example, if the bees are foraging on high numbers of introduced plant species, then the destruction of native flora may not have such a large effect on the bee species, compared with if they were only foraging on native flora. Also, if they are more specialised then they may be more at risk of population decline. These results may also tell us whether the bees can exploit areas of development, such as farmland, where there are higher levels of introduced plant species. I predict that the native bees will vary in their floral foraging preferences from species to species.

2.2 Methods

2.2.1 Study Period

This study was conducted from mid-August 2016 to mid-March 2017 in North Taranaki, New Zealand. This study was carried out over the summer months as the bees are most abundant during the warmer months (Donovan, 1980). Sampling was conducted in all weather conditions apart from heavy rain, as the bees were most likely not flying in this weather.

2.2.2 Study Site

Eight transects were chosen throughout the North Taranaki area. These were roads that passed through areas with varying levels of farming intensity, including: dairy, dry-stock, croplands, and some native remnant vegetation. 8 – 10 sites were located along each of the roads where sampling was carried out.

These sites were spaced at a general distance of 3km apart. However, some sites were spaced closer, or further than 3km depending on the availability of safe areas to park the vehicle and safely carry out the sampling. At each of these sites the GPS coordinates were recorded.

Table 2.1 Transect and site descriptions, including the farming intensities of each transect.

Transect	Number of Sites	Transect Location	Transect Land Use Description	Coordinates of First Site in Transect
Pukearuhe (P)	10	Sites follow Pukearuhe Road, beginning further inland at the Mimi river bridge and ending at White Cliff Bay next to the coast	This site transects through farmland and areas of native bush.	-38.96525, 174.45006
Farm (F)	10	Sites are spread over a farm at 1140 Pukearuhe Road.	This area is heavily populated with native bush and most of the farmland is dry-stock land.	-38.89437, 174.52658
Uruti (U)	9	Sites follow Uruti Road from its beginning until the intersection of Uruti and Kaka Roads just after a tunnel.	This area is mostly dry-stock farms with patches of native bush.	-38.94854, 174.5326
Kaipikari Upper (KU)	10	Sites follow Kaipikari Road, from its intersection with State Highway 3 to further inland.	This transect goes through both dairy and dry-stock land with small patches of native bush.	-39.05041, 174.3978
Mimi (M)	8	Sites follow Mimi Road from its intersection with Pukearuhe Road to its end at the intersection with State Highway 3. The sites continue down the opposite side of the road, following Mangamaio Road further inland.	Most of this site is situated alongside a river/stream that is running through mostly dry-stock land with patches of bush. The Mangamaio part of the site runs through a valley with native bush on either side.	-38.9714, 174.45102
Lepperton (L)	9	Sites begin following Richmond Road, they then are situated in a loop with sites throughout the Lepperton area and ending on Waitara Road.	These sites are mostly situated in dairy farm land with small patches of native bush.	-39.02446, 174.21492

Otaraoa (O)	10	Sites begins near Tikorangi, where they then follow Otaraoa Road and end in Tarata.	This site has a mixture of dairy and dry-stock land with patches of bush.	-39.03111, 174.27341
Kaimata (K)	10	Sites begin at the Tarata saddle rest area on Tarata Road where they continue through the Kaimata, Everett Park, and Hurangi areas.	This site passes through large areas of bush with a mixture of dairy and dry-stock land.	-39.16818, 174.3562
Total	Total			
Transects:8	Sites:76			

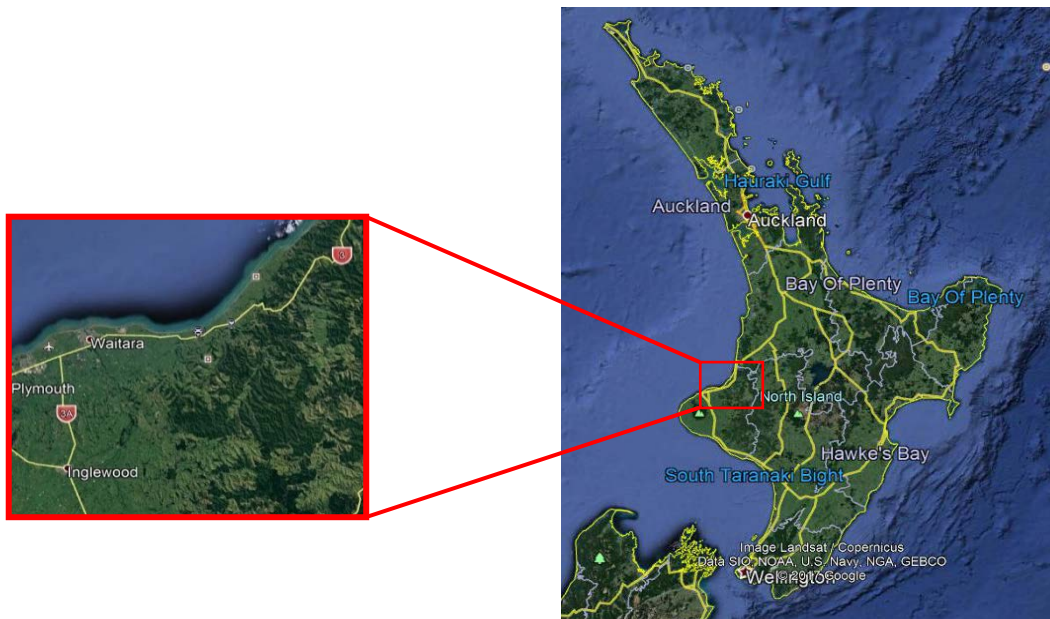


Figure 2.1 Map of New Zealand highlighting the study area of North Taranaki (Google Inc., 2018)

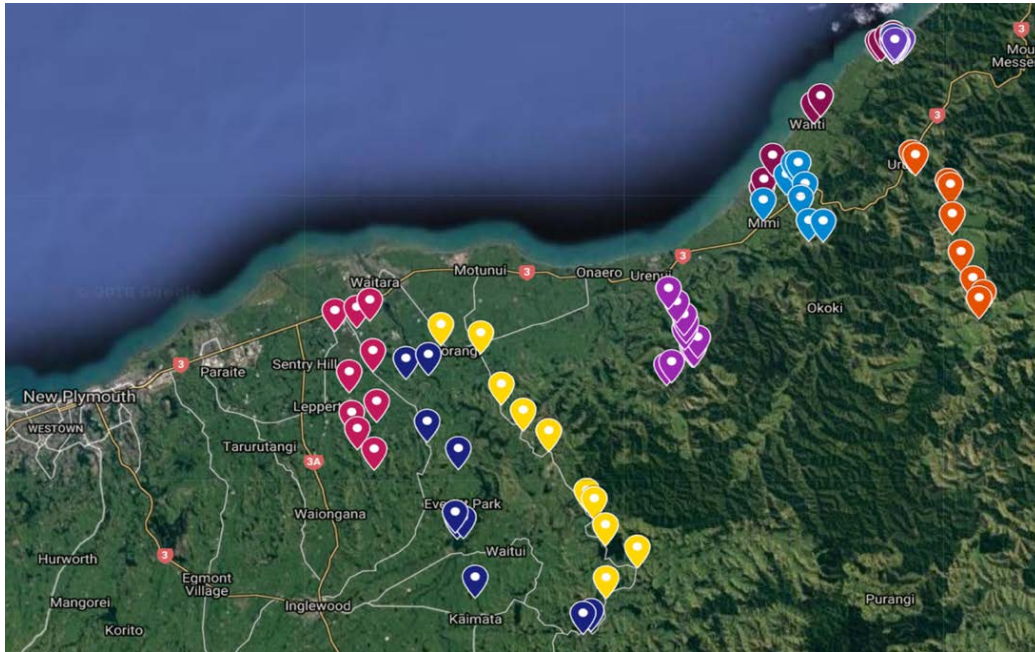


Figure 2.2 Transects and sites in the North Taranaki region (Google Inc., 2018).



Figure 2.3 Example of one site (KU10) used in this study; photo by author.

2.2.3 Study Organisms

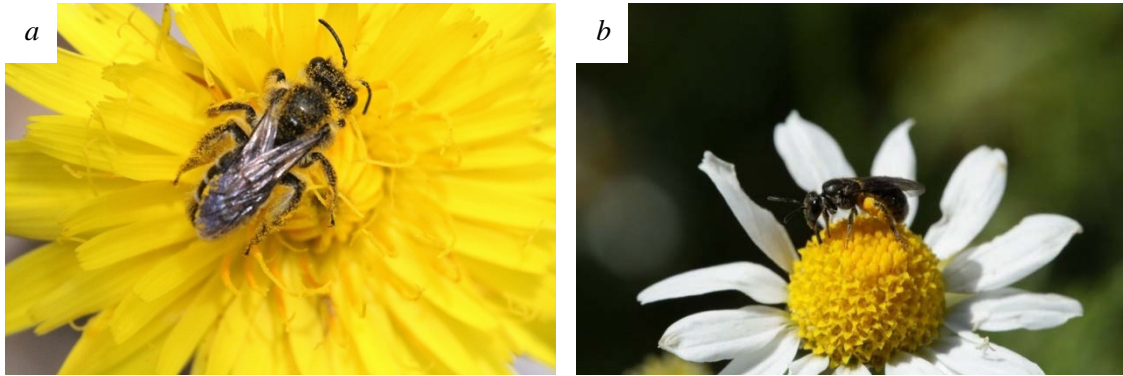


Figure 2.4 *a*- *Leioproctus* spp. foraging on an Asteraceae spp.; *b*- *Lasioglossum* spp. foraging on an Asteraceae flower. Photos taken by author.

The organisms focused on in this study were the native bees of New Zealand, of which there are three different genera: *Leioproctus*, *Hylaeus*, and *Lasioglossum*.

Leioproctus paahaumaa: This species was recently described by Barry Donovan (2007). The name *paahaumaa* means white beard for the dense long white vestiture on the clypeus of the males. This species has a cosmopolitan distribution across the North Island, as well as several islands around the North Island. Donovan (2007) suggests that *L. paahaumaa* prefers to forage on Asteraceae species rather than other native sources. These bees nest in the ground in different substrate, including: bare clay, dirt banks, domestic lawns, and sandy soil.

Leioproctus huakiwi: This species is another one that was recently described by Barry Donovan (2007). This species has a wide distribution over New Zealand and can be found in most vegetated areas. The known flight period for *L. huakiwi* is from October through to April. This species does not seem very specialised in its foraging, it can utilise a number of different floral sources, including many introduced species – in particular kiwifruit (*Actinidia deliciosa*) (Donovan, 2007). The name *huakiwi* is the Maori name for kiwifruit, this species is named for their high abundances found on kiwifruit.

Leioproctus pango: Another recently described species by Barry Donovan (2007). This species can be throughout most of New Zealand and is relatively common. The flight period for this species is from September to March. *L. pango* has a strong preference for Fabaceae but also collects pollen from a wide range of plant families. *L. pango* has a variety of nesting preferences, including: sandstone and mudstone cliffs, fine sand, bare soil, riverbeds, and clay/silt roadsides (Donovan, 2007). The etymology of the name *pango* is the Maori word for



Figure 2.5 *Hylaeus relegatus* blowing a bubble, which is thought to be a method of concentrating the pollen, on a *Phormium* spp. Photo taken by author.

black, since most of the specimens have completely black vestiture, or nearly so.

Leioproctus monticola: Described during the 1920s by Theodore Cockerell, this species is widely distributed throughout mountainous regions in New Zealand. This species can be found on the wing from November to May. *L. monticola* seems to be rather specialised in their floral habits, with most of the records being found collecting pollen on *Hebe* species, this may limit their distribution. The nesting habits of this species are not well known, there is on record of an adult male being found in a burrow in a clay bank (Donovan, 2007).

Lasioglossum sordidum: This species is abundantly found throughout most of the North and South Island. *L. sordidum* is a very common species and can be expected to be present wherever there are suitable floral resources and nest sites. This species can be seen on the wing from August to June. *L. sordidum* has a very wide foraging niche and will forage on almost any flowering plant that it can access the floral resources of. This is another species with a wide range of nesting substrates, including: beaches, riverbeds, gravel, clay, soil, and

cliffs. This species is so abundant due to its ability to forage on a wide variety of flowering plants and nest in a wide range of substrates (Donovan, 2007).

Lasioglossum cognatum: this species is native to New Zealand but are also found in Australia. It is suggested that the species arrived in New Zealand in the ballast of sailing ships from Australia (Donovan, 2007). *L. cognatum* seems to be distributed mainly across the middle and upper North Island, though it has been found in a few locations in the South Island. Its flight period is from July to April and it exhibits a wide range of floral hosts, mostly of introduced flowering plants. There is not much information for their nest preferences in New Zealand, but there is a record of a *L. cognatum* nest in a sandstone bank (Donovan, 2007).

Hylaeus relegatus: this species has a very wide distribution over New Zealand, which suggests that this bee can exist in a wide range of conditions. This bee exploits a wide variety of introduced and native flowers. The flight period for this species is from October to April. *H. relegatus* nests in branches, flax, stems, and wood. This species has also been found to nest in man-made wooden blocks with holes drilled in them (Donovan, 2007). Of the species of *Hylaeus* present in New Zealand, *H. relegatus* is the most common and largest, it has been suggested that the main variable limiting its distribution is a lack of nest sites (Donovan, 2007).

2.2.4 Sampling Method

Bee Sampling

Multiple invertebrate sampling techniques were used to catch bees at each site, including: sticky traps, pan traps, plant traps and net sampling.

The sticky traps consisted of a wooden stake that had two pieces of A4 sized corflute stapled on either side, one side yellow, the other white. Two pieces of A4 sized transparency film were covered in a thin film of an adhesive for insect traps. These sheets were held in place on the corflute using bull clips. The stakes were then driven into the ground until they were around 70cm above the ground. After around a week in the field the film sheets were collected by covering them with plastic wrap.

The pan traps consisted of 2L ice cream containers (17 x 17 x 9cm) painted with Dulux Weather Shield Bold Yellow paint, filled with approximately 400ml of a preservative solution. This preservative consisted of 10gms of sodium benzoate in 1 litre of water with

5ml of apple scented dishwashing liquid. This trap design was derived from Larsen, et al, (2014). Sodium benzoate was used as a preservative rather than propylene glycol as Larsen et al (2014) showed that sodium benzoate traps caught more Hymenoptera than propylene glycol traps. A wire netting with 13mm x 13mm gaps was taped over the top of the containers to prevent animals/children from consuming the contents. These pan traps were then placed out at site for a minimum of three days before being collected. The contents of the pan traps were drained through CHUX® Superwipes® dish cloths, the holes in the dishcloth being 1.6 × 0.9mm. The insects left on the cloths were wrapped up and placed into small plastic ziplock bags, with 21ml of 99% ethanol and 9ml of water. These bags were kept in a sealed container until their contents were transferred into small glass screwtop vials.

The plant traps consisted of pak choi (*Brassica rapa* subsp. *chinensis*) plants that had been propagated from seed and transferred into 3L plant bags with fertilised soil. When they started flowering, 3-4 pak choi plants were placed at each replicate prior to net sampling. These plants were used to attract the bees to the flowers for catching via net sampling.

Net sampling was carried out, at first, for 5 minutes at each site, and involved searching in an approximately 20m radius around the sample site for any native bees. Once caught, the bees were stored in small screw top containers and the details pertaining to that bee's capture were recorded on a recording sheet. The details recorded were: the number of the bee, date caught, site caught at, temperature, humidity, estimated cloud cover, wind speed, wind direction, where the bee was found/which plant it was found on, a weather description, and the time of capture. It was later surmised that a 5 minute sampling period was not long enough to sufficiently sample the area so the time was increased to 10 minutes of sampling. This time was a compromise between sampling the site sufficiently and efficiency.

The captured bees were then stored in a chilly bin with ice packs until they could be moved into a freezer after sampling was completed. After freezing overnight at 18°C, the bees were pollen sampled and then transferred into small zip lock plastic bags and back into the freezer for storage.

Identification of the bees was carried out using a dissecting microscope and a dichotomous key written by Donovan (2007), also by consulting Barry Donovan for help identifying the more difficult specimens (Personal Communication, 2017).

Weather Sampling

Weather sampling included measuring the temperature, wind speed, humidity, and a weather description (overcast, cloudy, or sunny) for the period in which a particular bee was caught. The temperature, wind speed, and humidity was recorded from the MetService website (Meteorological Service of New Zealand, 2018). The weather description was recorded by observation.



Figure 2.6 Pollen sampling a *Leioproctus* spp. with gelatin-fuchsin; photo taken by author.

Pollen Sampling

Pollen sampling of the bees was carried out by pollen staining and fixation with gelatin-fuchsin, a method adapted from Beattie (1971a). To make the gelatin mixture, 50grams of gelatin was heated in distilled water, then 150ml of glycerine was mixed in. A few crystals of basic fuchsin was then added until the mixture turned pink; the solution was then filtered through glass wool and stored in small plastic containers. The gelatin-fuchsin was then kept in the refrigerator at 4°C until used. To use in pollen sampling, a small cube (2 x 2 x 2 mm) was cut, this was then dabbed all over the bee to pick up any pollen. The pollen-filled gelatin-fuchsin was then melted on to a slide, using a portable battery powered element, and covered with a slide cover.

After pollen sampling the bees were pinned with labels affixed to the pin denoting: name of collector, date of collection, location, and what the bee was caught on.

Identification of pollen from the plant and bee samples was carried out using a compound microscope and the help of Katherine Holt (personal communication, 2017). Note that the

classification of the plant species was usually not to species due to the difficult nature of identifying fresh pollen to fine taxonomic scale. Within the Apiaceae and Asteraceae several distinct types were identified, however, they could not be identified to species; therefore there may be one or more species.

Pollen sampling was not carried out for *Hylaeus relegatus* as it was assumed that the pollen would be too difficult to sample in high enough numbers due to their ingestion of the pollen. Male bees of all species were likewise not sampled as they lack the dense vestiture of the female bees.

2.2.5 Data Analysis

Three main research questions were investigated during this study: the response diversity of native bees to land-use changes; the response of native bees to weather variables; and the interaction of native bees and floral resources. The distributions of each species were also recorded.

Species Distribution Maps and Land-Use Descriptions

Species distribution maps and land-use descriptions were developed using Google Earth Pro (Google Inc., 2018) and the New Zealand Land Cover Database (Landcare Research, 2015).

At each replicate, using the measuring tool on Google Earth, a 500m radius was measured out, with the site located at the centre. The land uses were distinguished using the Land Cover Data Base (LCDB) as a layer of the base Google Earth map. This allowed for the estimation of the proportion of each land use category within the 500m radius area.

The land use categories were derived from the LCDB, these categories were: high producing exotic grassland, short rotation crop, indigenous forest, exotic forest, mānuka/kānuka, waterbody, settlement, gorse/broom, herbaceous freshwater vegetation, and low producing exotic grassland.

Response Diversity Analysis

For analysing response diversity of bees to varying land uses, the above categories were combined to create four land-use variables: ‘Agricultural Land’, ‘Woody Vegetation’, ‘Exotic Vegetation’, and ‘Native Vegetation’. Agricultural land consisted of the categories: high intensity exotic grassland, short rotation crop, and low producing exotic grassland. Woody vegetation consisted of: indigenous forest, mānuka/kānuka, gorse/broom, and exotic forest.

Exotic vegetation included: high producing exotic grassland, short rotation crop, gorse/broom, exotic forest, and low producing exotic grassland. Native vegetation included: indigenous forest, and mānuka/kānuka. The other vegetation types were not deemed to be present at high enough percentages to be included in the analysis.

The categories of land-use intensity (high, medium, and low) were calculated using the percentage of agricultural land/exotic vegetation. High Intensity = 80 % < agricultural land; medium intensity farming = 50 % < agricultural land; and low intensity farming = 50% > agricultural land. Using this system there was calculated to be a total of 25 high intensity farming replicates, 29 medium intensity, and 22 low intensity replicates.

The analysis of these data was carried out using R (R Core Team, 2018). Multiple univariate analyses were used on this data. For each of the land use variables (agricultural land, woody vegetation, exotic vegetation, and native vegetation), a generalised linear model (glm) on the number of bees caught per site, with a Poisson dispersion was evaluated using chi-squared on the test statistic. This analysis was carried out to examine the response diversity of native bees to different land-use variables.

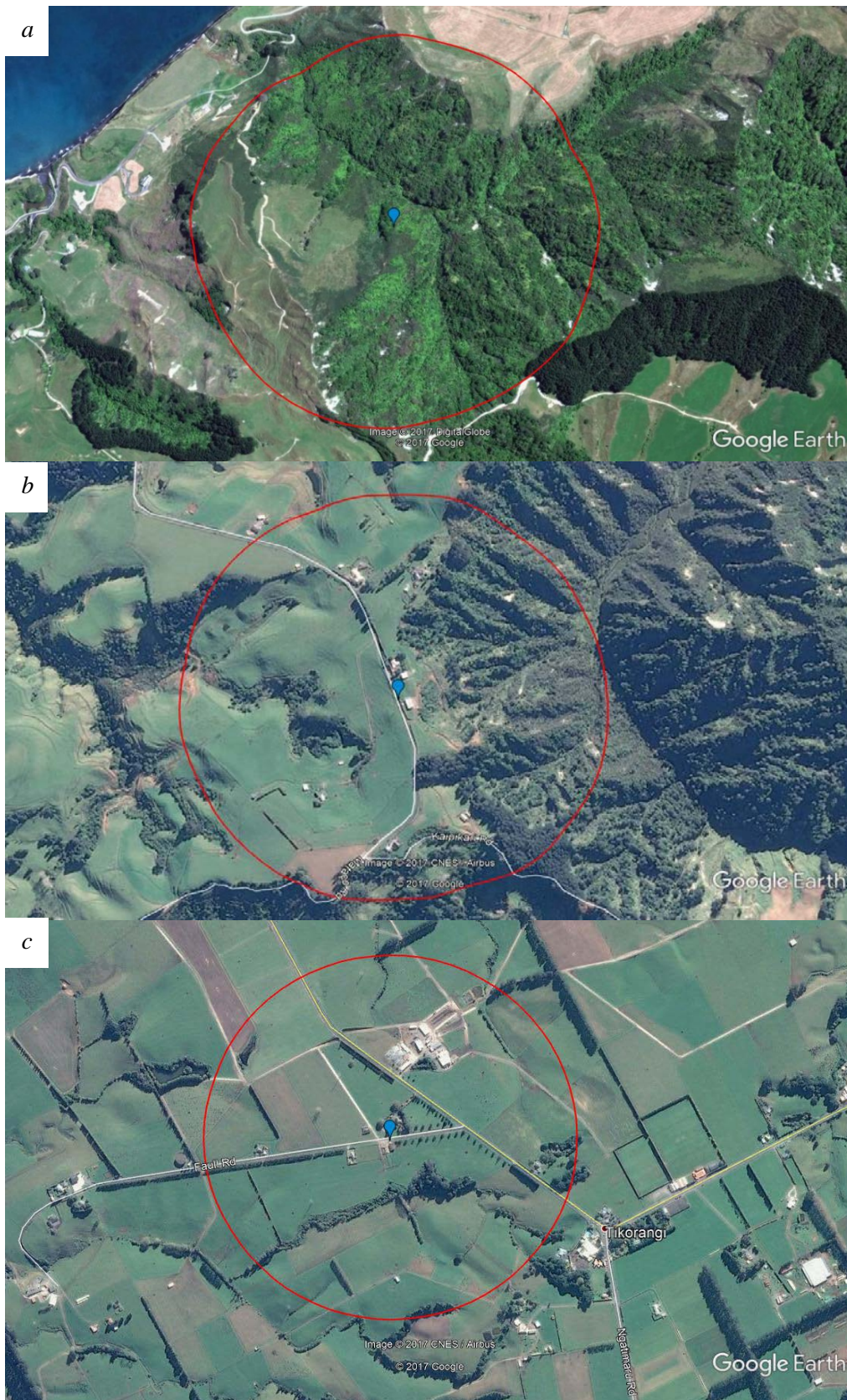


Figure 2.7 Maps showing the different farming intensities within the 500m² (red circle). *a*- low intensity (F2); *b*- medium intensity (KU5); *c*- high intensity (O1). Maps derived from Google Earth Pro (Google Inc., 2018).

Weather Data Analysis

The response of bees to weather variables (temperature, wind speed, humidity, and weather type) was analysed using R (R Core Team, 2018). A glm with Poisson dispersion was generated for each weather variable, and tested with a chi-squared statistic.



Figure 2.8 *Hylaeus relegatus* foraging on a *Phormium* spp; photo taken by author.

Pollen Data Analysis

The pollen samples were analysed by generating graphs and a bipartite network to describe the interaction between the bees caught and their floral preferences

2.3 Results

2.3.1 Overall Abundance and Species Diversity

A total of 572 specimens were handled during this study, seven species from the family Colletidae. These bees were all caught via the net sampling method. The sticky trap method did not generate good results, only one bee was caught using this method. The pan trap method did generate some results, however, time restrictions meant that the samples were unable to be processed for this study.

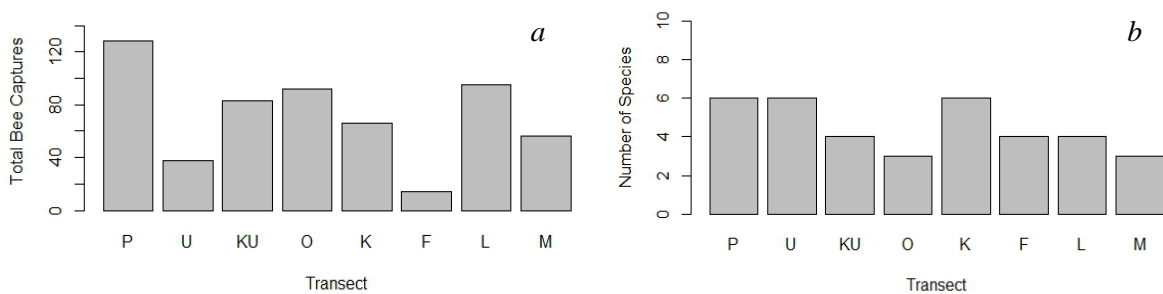


Figure 2.9 *a*- Total bee captures per transect. *b*- Total number of species found at each transect.

Seven species of native bees were caught in this study: *Lasioglossum sordidum*, *Lasioglossum cognatum*, *Hylaeus relegatus*, *Leioproctus paahaumaa*, *Leioproctus huakiwi*, *Leioproctus pango*, and *Leioproctus monticola* (Fig. 2.10). A total of 307 of the bees were female, with 265 males. Bees were caught at every transect sampled (Fig. 2.9), although a few sites within the transects did not generate any bees.

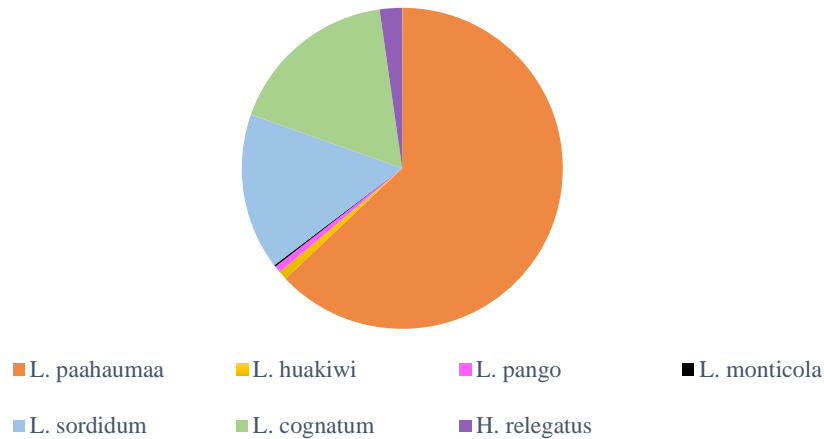


Figure 2.10 Proportion of each species of native bees caught during this study: *L. paahaumaa* (62.9%), *L. huakiwi* (0.9%), *L. pango* (0.7%), *L. monticola* (0.2%), *L. sordidum* (15.7%), *L. cognatum* (17.3%), *H. relegatus* (2.3%).

Refer to Table 1 in the appendix to see the complete bee captures. The three species, *L. paahaumaa* (63%), *L. cognatum* (17%), and *L. sordidum* (16%) were the most prevalent species of native bees caught during this study, with *L. paahaumaa* being the most common of the three.

2.3.2 Distribution Data

The distribution of all seven species of bees differed. *L. sordidum* and *L. cognatum* had a cosmopolitan distribution across all sites, as did *L. paahaumaa*, as you can see from the Figure 2.11. These three species were caught at nearly every transect.

L. huakiwi, *L. pango*, *L. monticola*, and *H. relegatus* were the least common species found during this study. As seen in Table 1 in the appendix, only very few numbers of each of these species were found.

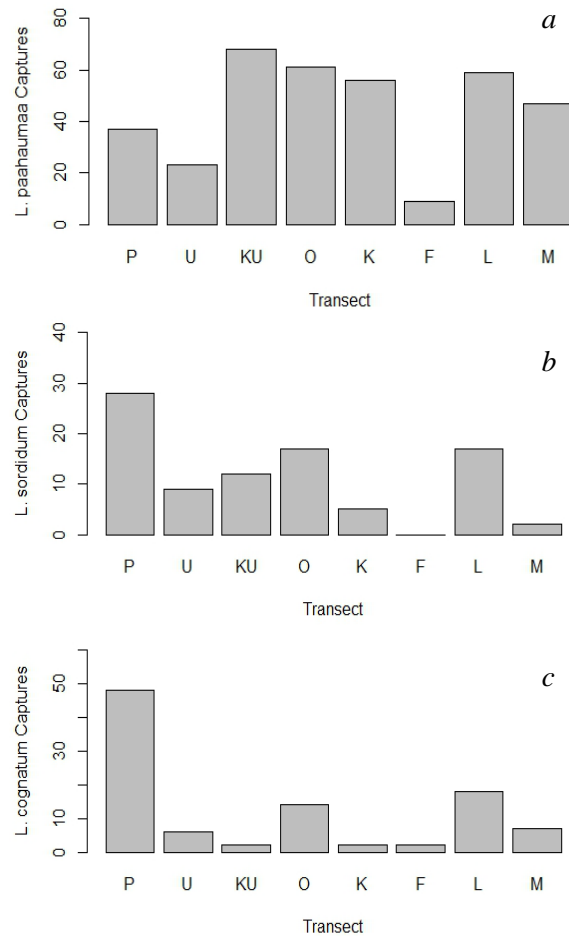


Figure 2.11 Abundances of the three most common species at each transect (a- *L. paahaumaa*, b- *L. sordidum*, and c- *L. cognatum*).

Interestingly, only one specimen of *L. monticola* was found at site K2. *L. pango* was only found at a couple of sites near the coast. *H. relegatus* was similarly only found at a few more coastal sites. *L. huakiwi*, on the other hand, although only found in low numbers, seemed to be present at more inland sites (Figure 2.12).

Although there were not enough specimens of the less common species to analyse their abundances with varying agricultural intensity, we are able to see the level of farming intensity of each of the sites where they were captured.

L. monticola: was only found at K2, this site has a farming intensity of medium. *L. pango*: was only found at sites with a low or medium agricultural intensities. *L. huakiwi*: was found at mostly medium intensity sites and one high agricultural intensity site. *H. relegatus*: was found at mostly low intensity sites and one high intensity site.

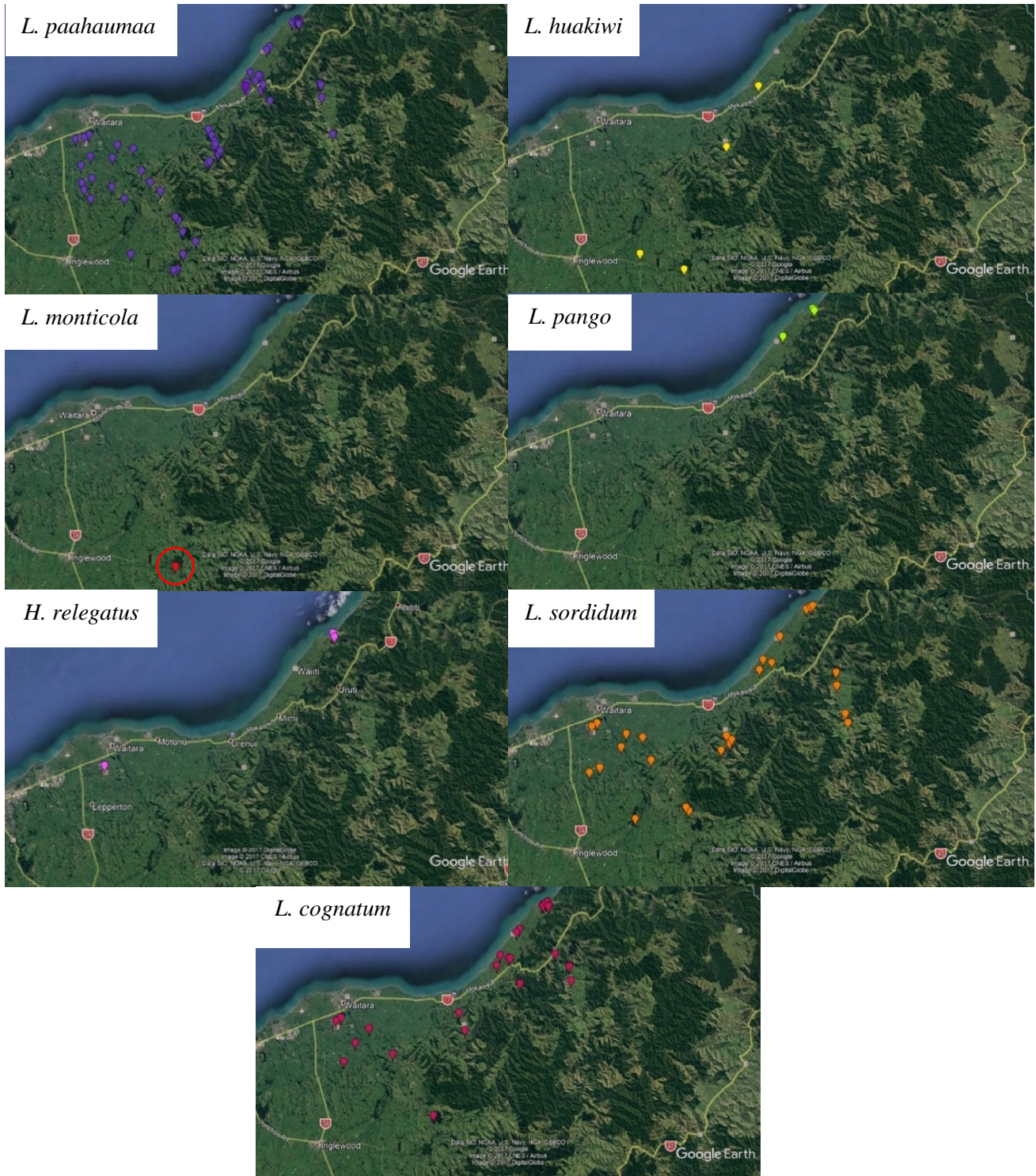


Figure 2.12 Distribution maps of each species at the sites they were found (Google Inc., 2018).

Overall, these four species of less common native bee species were mostly found at sites with low to medium agricultural intensity.

2.3.3 Diversity of Native Bees in Varying Land uses

Total Species Response to Varying Land Uses

These results show the response diversity of native bees to the land use variables agricultural land and exotic vegetation. The categories woody vegetation and native vegetation were analysed separately as the impacts of these categories on native bees were more or less the inverse of the relationships shown below. For example, the response of native bees to woody vegetation was the inverse of the response to agricultural land, likewise for native and exotic vegetation (refer to the appendix for these results).

One of the research aims of this study was to examine the response diversity of native bees in the North Taranaki area to increasing agricultural intensity. Overall the native bees showed a positive (Figure 2.13) and significant (Table 2.2) response to increasing agriculture intensification.

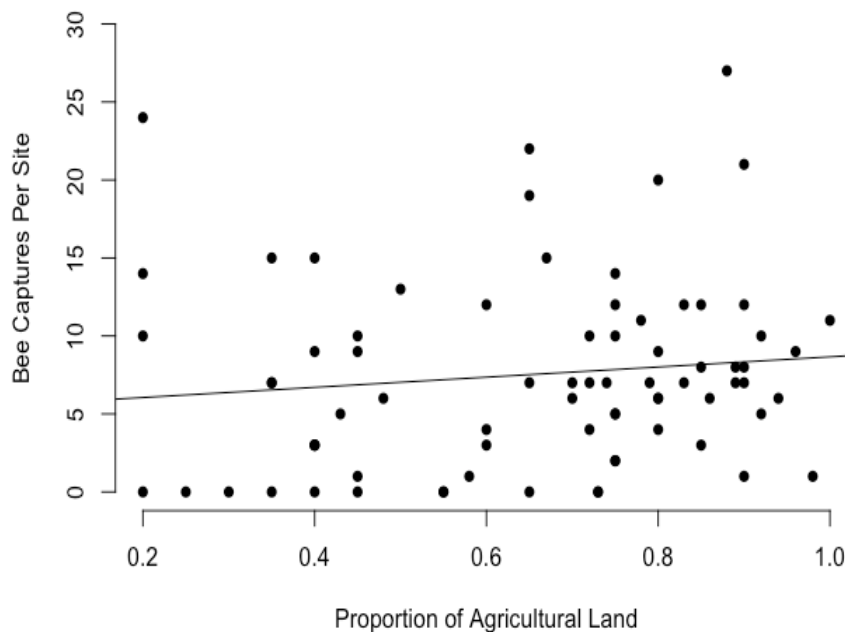


Figure 2.13 Bee captures per site vs. the proportion of agricultural land.

Table 2.2 Results of an ANOVA of bee captures per site vs the proportion of agricultural land.

	DF	Deviance Resid.	DF Resid.	Dev	Pr(>Chi)
Null			75	404.81	
Agricultural	1	5.2157	74	399.60	0.02238

Similar trends are found when comparing the numbers of bees with increasing levels of exotic vegetation. There is a significant increase in the number of bees in sites with higher proportions of exotic vegetation (Figure 2.14, Table 2.3).

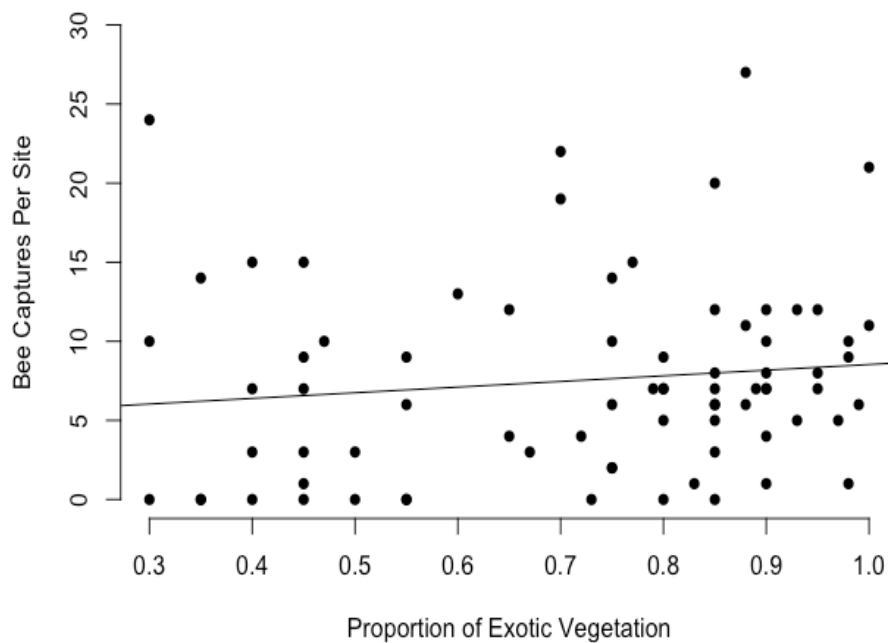


Figure 2.14 Bee captures per site vs. the proportion of exotic vegetation.

Table 2.3 Results of an ANOVA of bee captures per site vs. the proportion of exotic vegetation

	DF	Deviance Resid.	DF Resid.	Dev	Pr(>Chi)
Null			75	404.81	
Exotic Veg	1	5.8268	74	398.99	0.01578

Land use intensity did not have a significant effect on the species richness of native bees, as you can see in Figure 2.15 and Table 2.4. The results show that all three land use categories had similar mean species richness. The maximum number of species caught at a site was four, out of a potential seven.

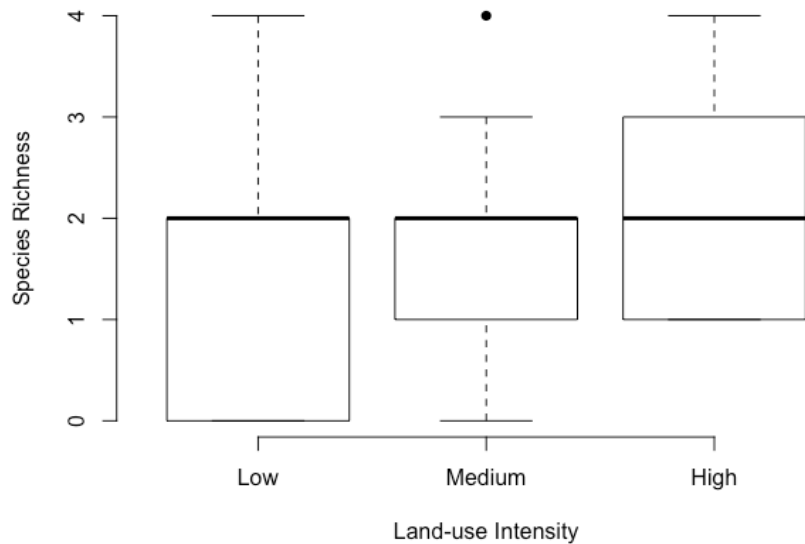


Figure 2.15 Species richness across all sites of low, medium, and high land use intensity.

	DF	Deviance Resid.	DF Resid.	Dev	Pr(>Chi)
Null			75	65.916	
Land-use	1	1.6531	74s	64.263	0.1985

Table 2.4 Results of an ANOVA of species richness vs. land use intensity.

Response of the Common Species to Varying Land Uses

The three most common species found during this study (*L. paahaumaa*, *L. cognatum*, and *L. sordidum*) were analysed separately to give greater insight into how each species responds to changes in land use.

Response of L. paahaumaa to Varying Land Uses

The results of this study show that the numbers of *L. paahaumaa* caught did not increase significantly with an increase in the proportion of agricultural land (Figure 2.16, Table 2.5).

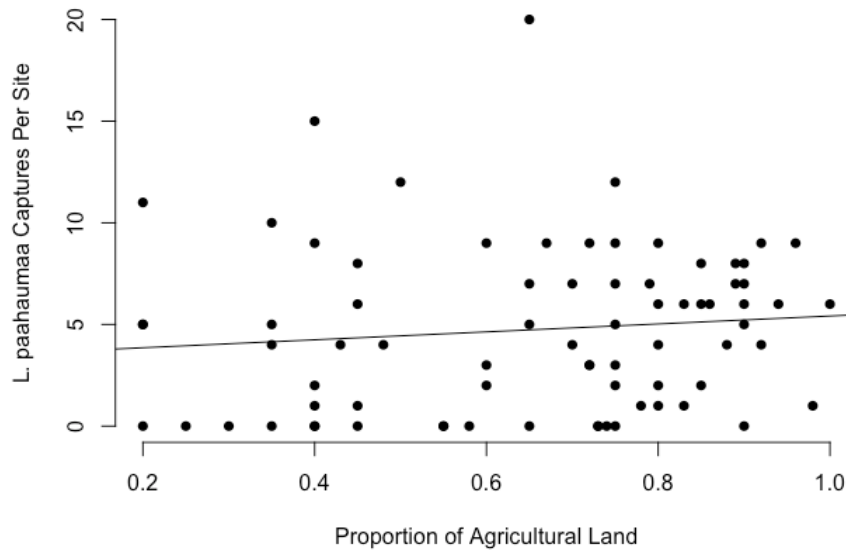


Figure 2.16 *L. paahaumaa* captures per site vs. the proportion of agricultural land.

Table 2.5 Results of an ANOVA of *L. paahaumaa* captures per site vs. the proportion of agricultural land.

	DF	Deviance Resid.	DF Resid.	Dev	Pr(>Chi)
Null			75	298.66	
Agricultural	1	2.9682	74	295.69	0.08492

There is again similar results for the effects of increasing proportions of exotic vegetation on the numbers of *L. paahaumaa* caught (Figure 2.17, Table 2.6). There is no significant effect of exotic vegetation on captures of *L. paahaumaa*.

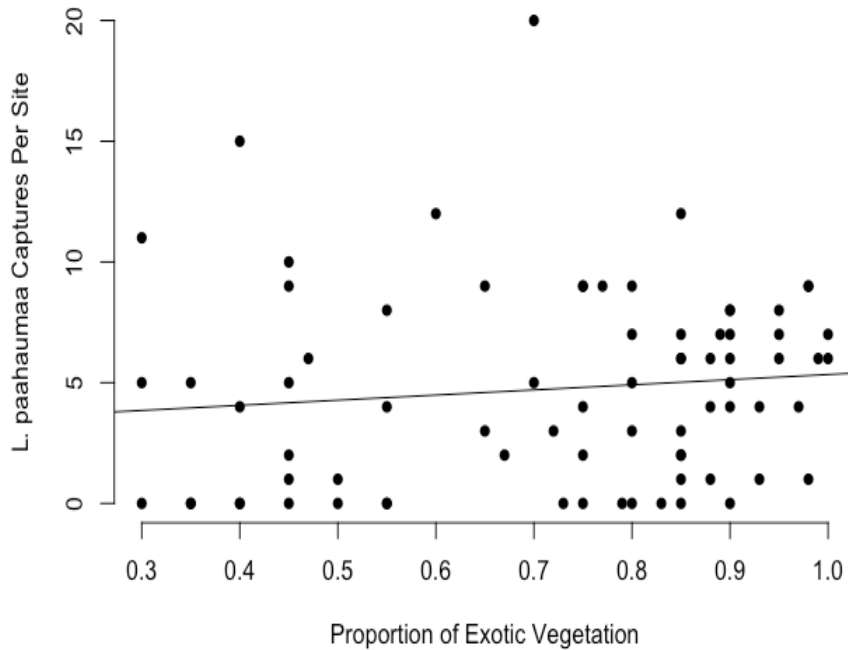


Figure 2.17 *L. paahaumaa* captures per site vs. the proportion of exotic vegetation.

Table 2.6 Results of an ANOVA of *L. paahaumaa* captures per site vs. the proportion of exotic vegetation.

	DF	Deviance Resid.	DF Resid.	Dev	Pr(>Chi)
Null			75	298.66	
Exotic Veg	1	3.2713	74	295.39	0.0705

Response of L. cognatum to Varying Land Uses

L. cognatum shows different trends to that of *L. paahaumaa*. There is a significant increase in the numbers of *L. cognatum* caught with an increase in the proportion of agricultural land (Figure 2.18, Table 2.7).

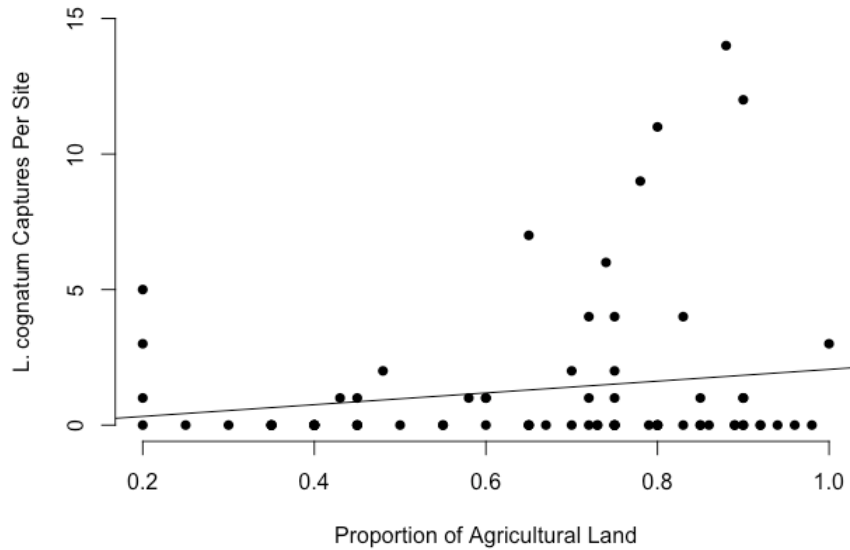


Figure 2.18 *L. cognatum* captures per site vs. the proportion of agricultural land.

Table 2.7 Results of an ANOVA of *L. cognatum* captures per site vs. the proportion of agricultural land.

	<i>DF</i>	<i>Deviance Resid.</i>	<i>DF Resid.</i>	<i>Dev</i>	<i>Pr(>Chi)</i>
Null			75	293.10	
Agricultural	1	14.239	74	278.86	0.000161

The number of *L. cognatum* caught increases with an increase in the proportion of exotic vegetation at each site (Figure 2.19, Table 2.8).

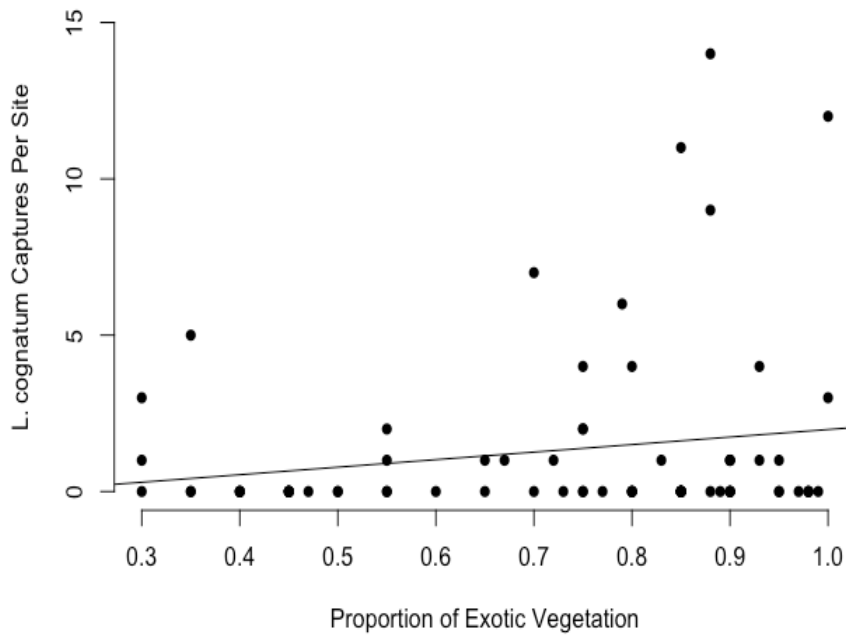


Figure 2.19 *L. cognatum* captures per site vs. the proportion of exotic vegetation.

Table 2.8 Results of an ANOVA of *L. cognatum* captures per site vs. the proportion of exotic

	DF	Deviance Resid.	DF Resid.	Dev	Pr(>Chi)
Null			75	293.10	
Exotic Veg	1	16.547	74	276.55	4.746e-05

vegetation.

Response of L. sordidum to Varying Land Uses

There is no negative effect of the proportion of agricultural land on the numbers of *L. sordidum* caught (Figure 2.20, Table 2.9).

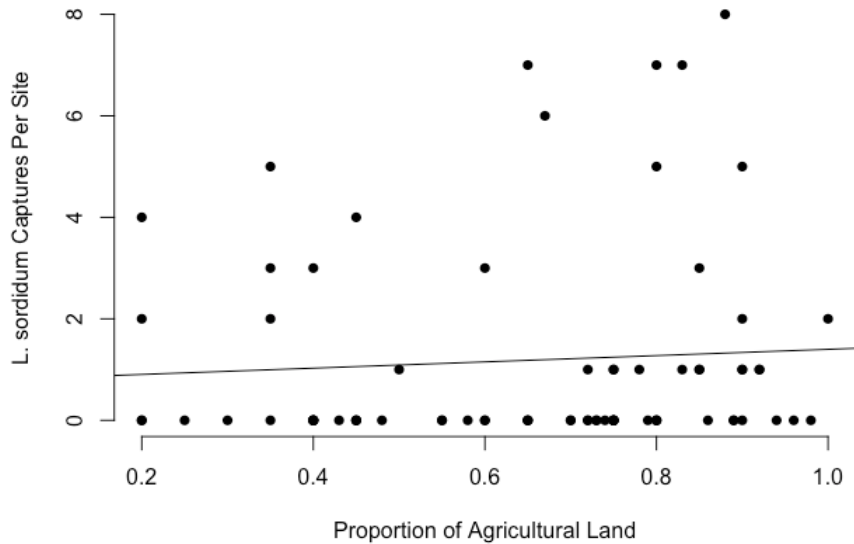


Figure 2.20 *L. sordidum* captures per site vs. the proportion of agricultural land.

Table 2.9 Results of an ANOVA of *L. sordidum* captures per site vs. the proportion of agricultural land.

	DF	Deviance Resid.	DF Resid.	Dev	Pr(>Chi)
Null			75	213.99	
Agricultural	1	1.203	74	212.78	0.2727

These results show that the proportion of exotic vegetation has no negative effect on the numbers of *L. sordidum* caught (Figure 2.21, Table 2.10).

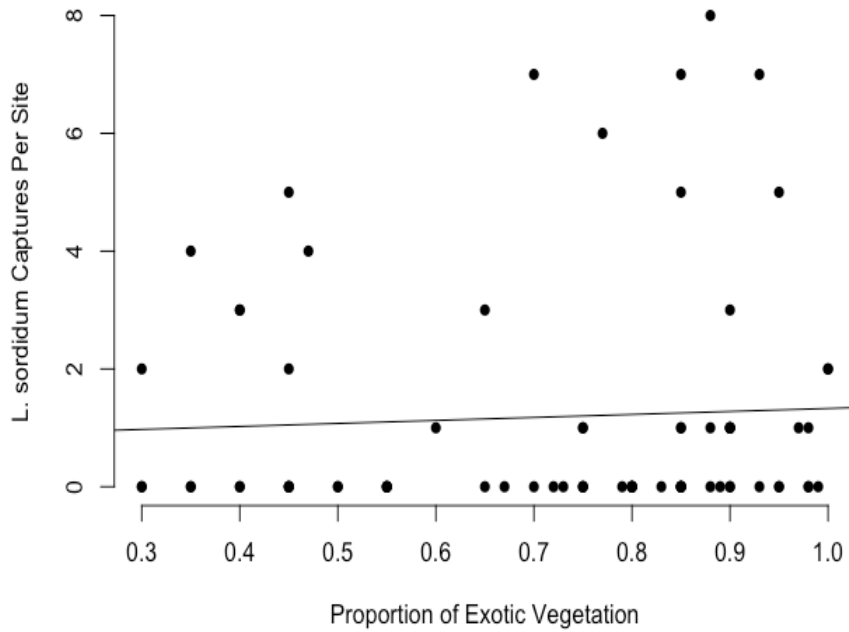


Figure 2.21 *L. sordidum* captures per site vs. the proportion of exotic vegetation.

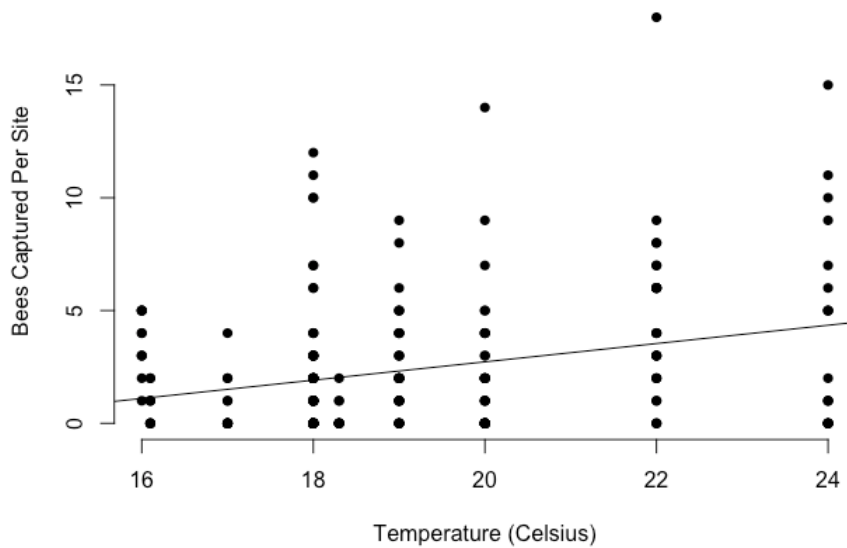
Table 2.10 Results of an ANOVA of *L. sordidum* captures per site vs. the proportion of exotic vegetation.

	DF	Deviance Resid.	DF Resid.	Dev	Pr(>Chi)
Null			75	213.99	
Exotic Veg	1	0.7435	74	213.24	0.3885

2.3.4 Weather Data

The second research question covered in this study was how weather variables might affect the numbers of native bees caught. Four different weather variables were analysed in this study. Overall, weather seemed to play an important part in relation to bee captures.

The temperature had a significantly positive effect on the numbers of native bees caught. There was an increase in bee numbers with higher temperatures (Figure 2.22, Table 2.11).



More native bees were caught during days where the temperature was above 17°C.

Figure 2.22 Bee captures per site vs. temperature (Celsius).

Table 2.11 Results of an ANOVA of bee captures per site vs. temperature (Celsius).

	DF	Deviance Resid.	DF Resid.	Dev	Pr(>Chi)
Null			238	815.67	
Temp	1	67.727	237	747.94	< 2.2e-16

Wind speed also had a significant impact on the numbers of native bees caught during this study. There was a decrease in the number of bees caught with increasing wind speeds (Figure 2.23, Table 2.12).

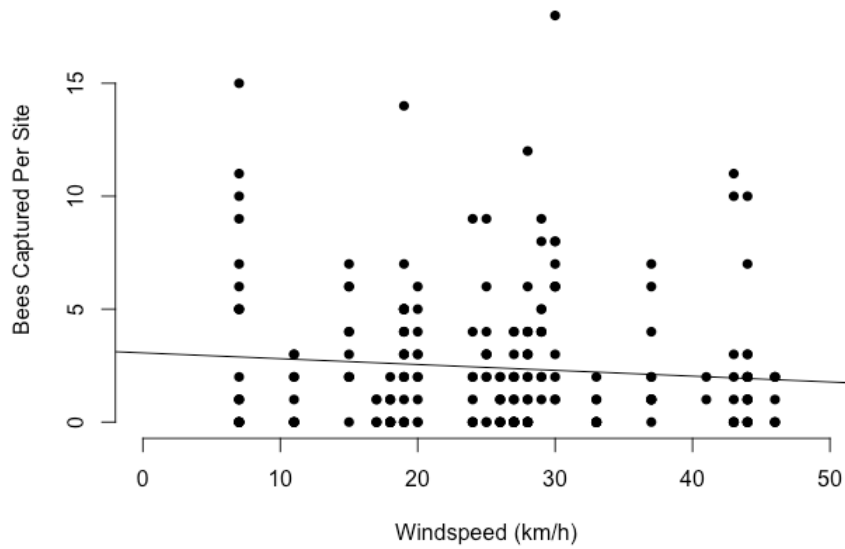


Figure 2.23 Bee captures per site vs. wind speed (km/h).

Table 2.12 results of an ANOVA of bee captures per site vs. wind speed (km/h).

	DF	Deviance Resid.	DF Resid.	Dev	Pr(>Chi)
Null			238	815.67	
Windspeed	1	7.658	237	808.01	0.005652

The humidity did not have an effect on the presence of native bees in the study area. There seemed to be a slight increase in the numbers of native bees caught with higher levels of humidity, although the results of an ANOVA show that this is not statistically significant (Figure 2.24, Table 2.13).

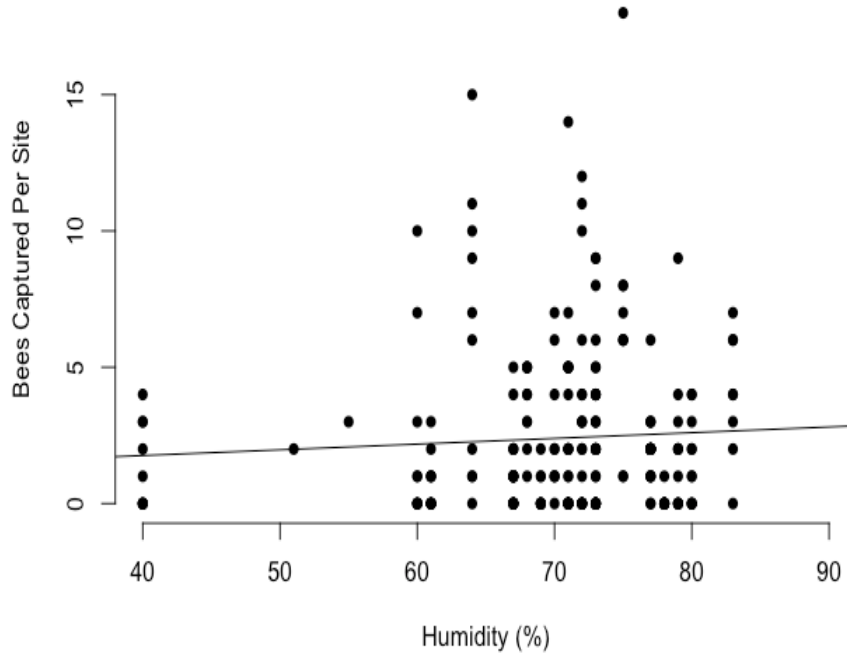


Figure 2.24 Bee captures per site vs. humidity (%).

Table 2.13 Results of an ANOVA of bee captures per site vs. humidity (%).

	DF	Deviance Resid.	DF Resid.	Dev	Pr(>Chi)
Null			238	815.67	
Humidity	1	3.3833	237	812.29	0.06586

Cloud cover also showed a significant effect on the native bees in this study. On sunny days, significantly more bees were caught whereas fewer bees were caught on cloudy or overcast days (Figure 2.25, Table 2.14).

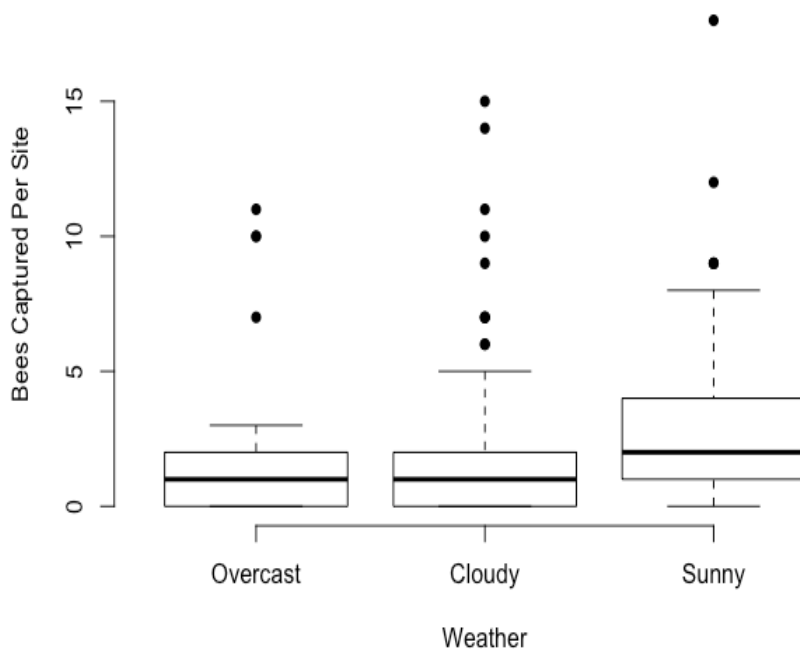


Figure 2.25 Bee captures per site vs. cloud cover.

Table 2.14 Results of an ANOVA of bee captures per site vs. cloud cover.

	DF	Deviance Resid.	DF Resid.	Dev	Pr(>Chi)
Null			238	815.67	
Cloud Cover	1	9.9953	236	805.68	0.006754

2.2.5 Pollen Data

The results from analysing the pollen found on the bees, showed that each species varied in the number of different species of plant they foraged on. As you can see in Table 2.15 and Figure 2.26, *L. paahaumaa* were the most generalised of the bees, visiting 17 different species of flowering plants. *L. cognatum* and *L. sordidum* were the next most generalised species visiting over 10 species of flowering plants each. *L. huakiwi*, *L. monticola*, and *L. pango* were the least generalised species, only visiting under five flowering plant species each. Table 2.15 also shows that all the species, except *L. pango* and *L. monticola*, were found on a mixture of introduced and native plants. *L. pango* was only found to have pollen from native species on its body, whereas *L. monticola* was only found to have pollen from introduced species.

Table 2.15 Interactions of native bees with flowering flora from pollen data. Showing the number of native, introduced, and total plant species that the bees visited during the study. Note that due to the difficulty of identifying pollen grains, it was assumed that all the species of Apiaceae, Asteraceae, and Brassicaceae were introduced species as this was the likely case from observation of bee foraging. Note pollen ingested by *H. relegatus* was not examined for identification.

Species	Native sp.	Introduced sp.	Total sp.
<i>L. paahaumaa</i>	4	13	17
<i>L. sordidum</i>	2	11	13
<i>L. cognatum</i>	2	10	12
<i>L. huakiwi</i>	0	4	4
<i>L. pango</i>	4	0	4
<i>L. monticola</i>	0	3	3

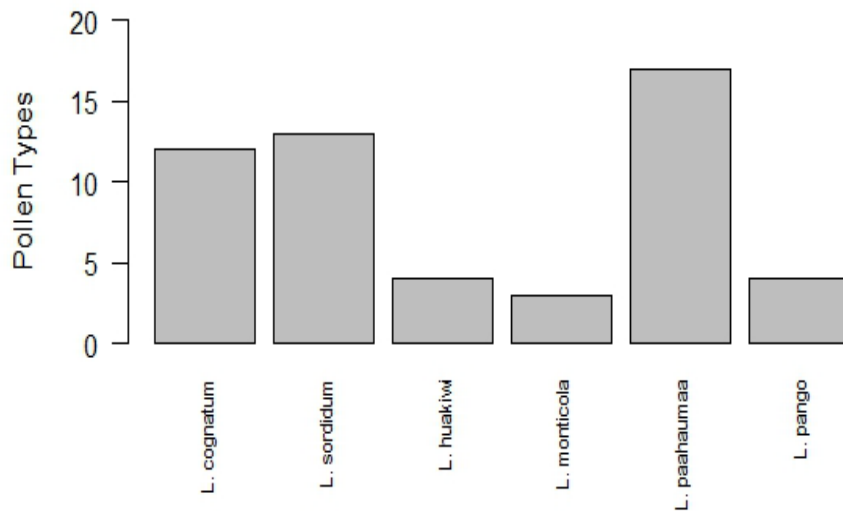


Figure 2.26 Number of flowering plant species that the bees collected pollen from during the study.

The bipartite network in Figure 2.27, depicts the interactions of each native bee species with each species of flowering plant pollen found during this study. There were very strong interactions between *L. paahaumaa*, *L. sordidum*, and *L. cognatum* and three groups of plants, a species of Apiaceae and two Asteraceae species. The network also displays how generalised those species (*L. paahaumaa*, *L. sordidum* and *L. cognatum*) were in comparison to the other three species. As you can see from Figure 2.27, Asteraceae and Apiaceae were popular flowering plant groups for the native bees in this study.

Although *Hylaeus relegatus* was not sampled for pollen, almost all specimens were caught from *Phormium* species or *Cordyline australis*.

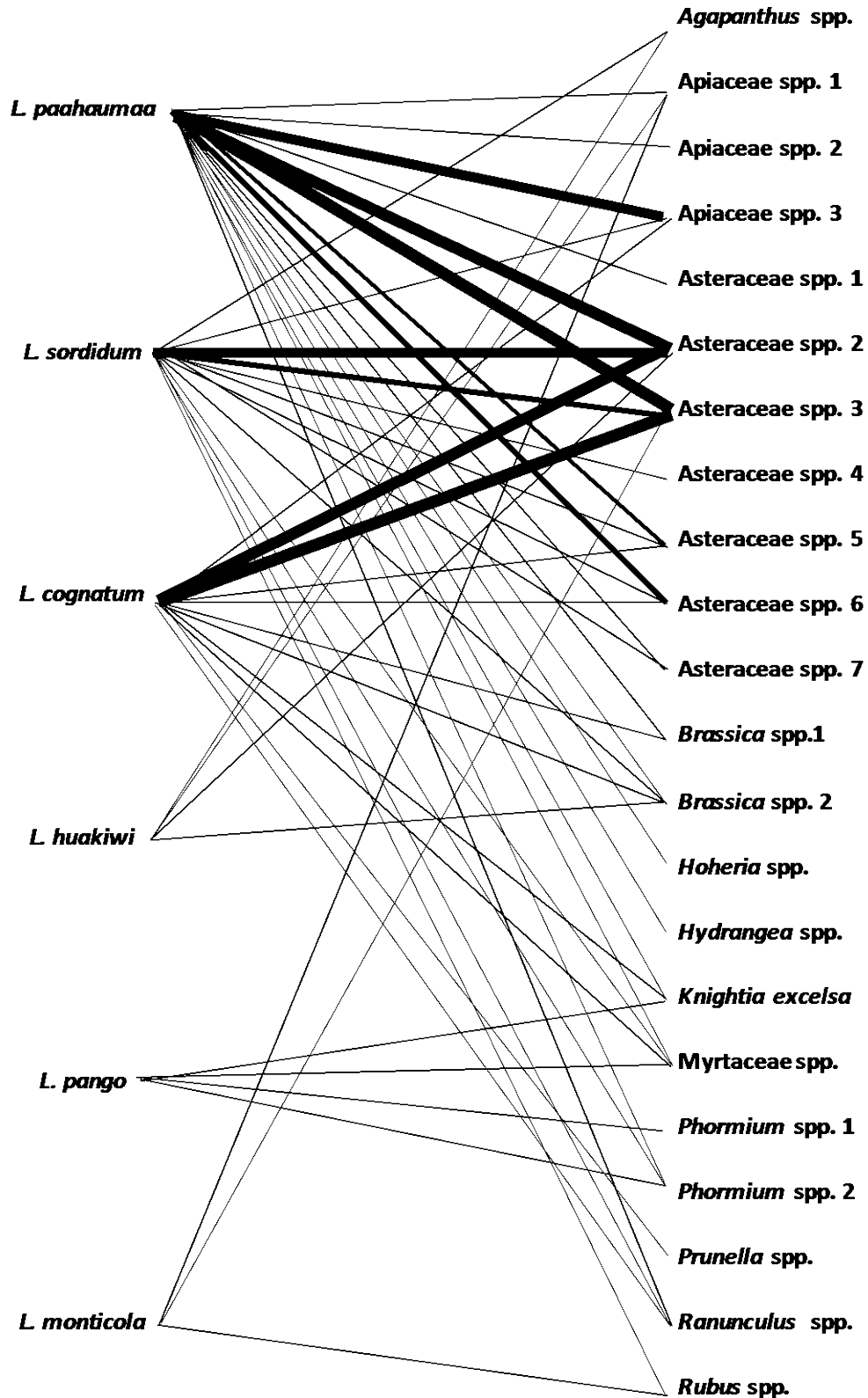


Figure 2.27 Bipartite network showing the interactions of each bee species and the flowering plants they were foraging on during this study. The thicker the line equals a stronger interaction between bee species and that plant species.

3. Discussion

3.1 Introduction

Native, wild pollinators, such as solitary bees, are very important for the health of the ecosystem worldwide (Biesmeijer et al., 2006). They are also important for the pollination of many commercial crop systems. In New Zealand specifically they are significant pollinators of commercial crops including: pak choi, kiwifruit, and carrot (Donovan, 2007; Howlett et al., 2015; Rader et al., 2012). It is vital to know the abundance and diversity of native, solitary bees in order to manage their conservation. Identifying threats to their populations is also paramount for their survival. Potential threats to the health of native bees worldwide, have been identified as: agricultural intensification, pesticide use, and climate change. This thesis aimed to examine the potential impacts of these threats on native solitary bees in New Zealand.

This study examined the abundances and diversity of native bees in the North Taranaki region, New Zealand. Three main research questions were investigated: How native bees respond to different land uses; how native bees are affected by weather conditions; and how the native bees interact with their floral resources. This study was the first of its kind to be carried out in Taranaki, New Zealand, and is the first to systematically sample the bee species found in this area.

3.2 Response Diversity of Native Bees to Land Use

3.2.1 Response of Native Bees to Agriculture Intensity

The results of this study indicate that, overall, the abundances of native bees in the study area are not negatively affected by high levels of farming intensity. This is contradictory to the results of many other studies from other parts of the world, which have found a decrease in the number of native bees in areas of higher farming intensity (Klein et al., 2007; Kremen et al., 2002).

In fact, the results of this study show that the abundance of native bees is positively correlated with increasing agricultural intensities. More native bees were caught in areas with higher levels of agricultural intensity and exotic vegetation. This may be explained by *L. paahaumaa*, *L. cognatum*, and *L. sordidum* being able to exploit introduced vegetation and able to find more nest sites in disturbed areas. These results also differ from a study in New

Zealand that found that native pollinators (including native bees) generally show a negative response diversity to increasing agriculture (Stavert et al., 2017). In this study only two species of native bees (*Lasioglossum cognatum* and *Leioprocutis boltoni*) showed non-negative responses to land use intensification.

Although these results do not follow the trend of some other research, they are similar to a study carried out in an agroforestry area in Indonesia. This study also found that the abundance (but not the number of species) of solitary bees increased with increasing agricultural intensity while the number of social bees declined with increasing agricultural intensity (Klein et al., 2002).

The diversity of native bee species may be affected by increasing farming intensity. The results of this study found that the three most common species of bee present in the study area were *L. paahaumaa*, *L. cognatum*, and *L. sordidum*. The other species (*L. huakiwi*, *L. pango*, *L. monticola*, and *H. relegatus*) were only found in very small numbers and at only a few sites in the study area. The sites where the least common species were found were almost all low and medium farming intensity sites. These results may suggest that the three common species may be able to find habitats in the more disturbed, high farming intensity areas more readily than the other four species. This may be due to being able to exploit the floral resources found in these areas, or being able to find more nest sites. The other species (*L. huakiwi*, *L. pango*, *L. monticola*, and *H. relegatus*) may be more limited in their ability to utilise the floral resources in more disturbed areas, or are unable to find sufficient nest sites. The results, however, show that there is not a significant effect of land use intensity on native bee species richness; perhaps with a more robust data set these results may change.

Although the predictive power of these results is limited due to the sparseness of the data, it may be that these less common species are unable to persist in intensified agricultural environments. The other more common species, however, do have this ability.

3.2.3 Conclusion

The overall the abundances of native bees in the North Taranaki region are not negatively affected by increasing agricultural intensity. Although the data show that there is no significant effect of land use intensity on species richness, this may be due to limited data on

rarer species, as only three species of native bee were commonly found throughout the study area. Therefore, certain species of native bees may be excluded from areas of high agricultural intensity. Overall, these results show that New Zealand native bees species respond differently to land-use changes. This is similar to the results of a study conducted in northern California that found that visitation rates of *Bombus vosnesenskii* on tomato crops are positively correlated with natural habitats, whereas land use does not have a significant effect on the visitation rates of *Anthopora urbana* (Greenleaf & Kremen, 2006a).

3.3 Species Abundances

3.3.1 Most Common Species

L. paahaumaa was the most common species found during this study comprising 62.9% of all the bees caught. As Barry Donovan describes (2007), *L. paahaumaa* seems to be limited by their nest sites – needing bare banks, soil, or cliffs. Donovan suggests that *L. paahaumaa* are well suited to exploit man-made disturbances for nest sites. He also proposes that the species may not have been as common in pre-colonisation New Zealand but spread when there was widespread clearing of forests. Therefore, perhaps *L. paahaumaa* is thriving in the study area of North Taranaki due to the level of disturbance from agricultural practices, which creates nest sites for these bees.

L. cognatum was the second most common species caught during this study (17.3% of all the bees were *L. cognatum*). *L. cognatum* is not endemic to New Zealand as it is also found in Australia. This species has a wide distribution all over Australia (Donovan, 2007). *L. cognatum* has previously been caught in large numbers at New Zealand pasture sites (Malone et al., 2010). This suggests, along with the results of this study, that *L. cognatum* are well adapted at inhabiting agricultural environments. This is even further proved from a study conducted in New Zealand where *L. cognatum* did not show negative responses to increasing land use intensity (Stavert et al., 2017).

L. sordidum was the third most common species caught over the course of this study (15.7% of the bees caught were *L. sordidum*). This species has been recorded to forage on a very large number of both introduced and native flowering plants (Donovan, 2007). It is thought that the introduction of flowering plants from overseas has allowed this species to grow its

population to very high levels (Donovan, 2007). This, along with their ability to nest in a variety of substrates, explains its abundance at high intensity sites during this study.

3.3.2 Least Common Species

As there were only very low numbers of *L. monticola*, *H. relegatus*, *L. huakiwi*, and *L. pango* caught during this study I was not able to carry out separate analyses on these species.

However, these results can still give us an indication about the distribution and abundances of these species in relation to habitat, weather, and floral preferences.

Only one specimen of *L. monticola* was found during this study. The site where it was found had a higher elevation than most of the other sites. This may explain why this species was only found there, as it is known to inhabit areas of high elevation (Donovan, 2007).

Only 13 individual *H. relegatus* specimens were captured during this study. They were almost exclusively captured from *Phormium* or *Cordyline australis*. Although there were not many found, these results seem to suggest that these bees may be limited by floral preferences. However, Donovan (2007) states that this species is also likely to be limited by their nest sites. This may also be true as almost all of the bees were caught at low agricultural intensity sites (with one exception of a bee caught at a high intensity site) which is in accordance with that hypothesis as there are few suitable nest sites in most pasture sites. However, this does not explain why there were not more of these bees caught at the low intensity sites – as they were only found at three out of a possible 22 low agricultural intensity sites.

Five specimens of *L. huakiwi* were caught during this study. The results show that these bees were almost all found at medium intensity sites, with one exception of one individual caught at a high intensity site. Donovan (2007) remarks that this species seems to have the most diverse nest site requirements of all of the *Leioproctus* species. They also seem to be able to forage on a wide variety of both native and introduced plants. Therefore, it is not clear why this species was not present at higher levels during this study.

Four individual *L. pango* were caught over the study period. These bees were all found at sites of either low or medium agricultural intensity. This species is relatively common throughout New Zealand. *L. pango* visits a range of native and introduced plants including

white clover (*Trifolium repens*) (Donovan, 2007). The results of this study suggest that *L. pango* may not be very common in the study area even though it was expected to be present at higher numbers due to its affinity for clover.

3.3.3 Conclusion

The three common species found in this study (*L. paahaumaa*, *L. cognatum*, and *L. sordidum*) all inhabited similar habitats and locations. The less common species found, however, (*L. monticola*, *L. huakiwi*, *L. pango*, and *H. relegatus*) all seemed to be present in relatively different areas around north Taranaki. This could reflect how each species is limited by nest site requirements and floral preferences. However, it is unclear why some of the less common species were not present in as high levels as would be expected.

3.5 Response of Native Bees to Weather

The second aim of this study was to examine how different weather variables affect the likelihood of capturing native bees. The weather variables measured were temperature, wind speed, humidity, and cloud cover. All but humidity had a significant effect on the presence of native bees.

The results of this study show that the native bees were more likely to be present at higher temperatures of 18°C and above. These results are consistent with those of other studies, that found that bees are more likely to be on the wing in higher temperatures (Heard & Hendrikz, 1993; Souza et al., 2006). However, Iwasaki (2017) found that *Lasioglossum* and *Leioproctus* from a study site in The Remarkables had no response to temperature.

Cloud cover had a significant effect on the presence of native bees. Significantly more bees were caught on cloudy and sunny days, as opposed to overcast days. These results are inconsistent with the results of another study, which found that cloud cover does not have a significant effect on bee abundance (Heard & Hendrikz, 1993). However Iwasaki (2017) found that *Lasioglossum* and *Leioproctus* species showed a similar negative correlation with increased cloud cover.

Wind speed has a negative effect on the presence of native bees. Higher numbers of bees were caught when wind speeds were less than 30km/h. These results are unlike those from

other studies which found that wind speed did not have an effect on the presence of bees (Heard & Hendrikz, 1993).

Humidity did not have a large effect on the presence of native bees in this study. There was a slight increase in the number of bees caught at higher levels of humidity. These results are similar to those of other studies that also found that humidity does not correlate with bee presence (Heard & Hendrikz, 1993). However, other studies have found that high humidity does have a negative effect on bee abundance in Brazil (Souza et al., 2006).

3.5.1 Conclusion

Most of the studies agree that of all the weather variables, temperature plays the biggest role in determining bee abundances with the other variables having less of an effect (Heard & Hendrikz, 1993; Souza et al., 2006). The results of this study show that this seems to be the case for New Zealand native bees. This is logical as it is necessary for the bees to be warmed enough to initiate flight for foraging (Burrill & Dietz, 1981).

The effect of these weather variables on native bees are important to study in order to predict the potential effects of climate change. Other studies have shown that there is a potential mismatch in the phenology of the pollinators and their foraging plants due to changing climates (Polgar et al., 2013; Rader et al., 2013). There is a possibility for this mismatch to occur with native bees' emergence times and the flowering period of their host plants. As these results show that there is a significant positive correlation between bee abundance and temperature, temperature changes due to climate change may have a strong effect (positive or negative) on native bee abundances. For example if the temperature over the summer months is predicted to be warmer in New Zealand, this may cause an increase in the abundance of native bees, to a point. If its summers are to be cooler, this may limit the foraging and nesting abilities of the native bees and therefore, limit the number of native bees present.

The effects of weather variables on the presence of native bees is also important for the sampling designs of future studies. This information will be able to be used to determine the most effective sampling times.

3.6 Interactions of native bees and flowering plants

The final research question investigated in this thesis was the floral preferences of the native bees. This is important as the floral preferences of native bees tells us which habitats are suitable. The relative generalisation/specialisation of the native bees indicates how well the bees will be able to exploit environments. For example a generalist bee will more likely do well in a disturbed environment that has more introduced plants present.

The results of this study have found that the native bees vary in their flower-visiting preferences. Out of the native bees species captured during this study, *L. paahaumaa* was the most generalist species, with 17 different species of flowering plant pollen present after sampling. However, this may be a result of *L. paahaumaa* being the most commonly caught bee in this study. *L. paahaumaa* also appeared to show a preference for Asteraceae species. These results agree with Donovan (2007) who states that *L. paahaumaa* do seem to have a preference for Asteraceae pollen. I have assumed here that these are likely to be introduced species but some native species may also be included. Donovan (2007) also suggests that native Asteraceae may have been the original pollen source for this species..

The next most generalised bee species was *L. sordidum*, and the third-most generalised was *L. cognatum*. These results are similar to descriptions of these species by Donovan (2007), who states that these species are quite plastic in their ability to forage on different plant species. *L. sordidum*, specifically, seem to be a strongly generalist species. Donovan (2007) states that these bees are able to forage on almost any flowering plant that its size allows it to access.

Interestingly, Iwasaki (2017) found that *Lasioglossum* was the more generalist species compared to *Leioproctus*, visiting the widest range of both introduced and native flora. He reported *Lasioglossum* to have visited around 30 plant species. The results of this study that suggest *L. paahaumaa* is the more generalist species may be due to this species being caught in the highest number.

These results suggest that *L. paahaumaa*, *L. sordidum*, and *L. cognatum* are able to persist quite well in environments with high levels of introduced flora, such as agricultural areas. The ability of these three species to persist in these environments may prevent them from becoming extinct due to land-use changes (Davis et al., 2012; Michener, 2000).

The other species were less generalised; however, this result may be due to the very limited number of specimens of each species caught, and not truly reflect their floral preferences. For example, the results from the pollen analysis in my study show that *L. pango* foraged solely on native plant species. However, Donovan (2007) states that *L. pango* do forage on a wider variety of both introduced and native plants than what the results of this study may suggest. There were so few specimens of this species captured during this study so we were unable to gain a representative sample of their floral preferences. In order to do this, further research will need to be carried out.

3.6.1 Conclusion

This results of this study show that native bees vary in the level of generalisation/specialisation in their floral preferences. This may reflect their ability to inhabit areas of disturbance, such as farmland. The more generalist bees such as *L. paahaumaa*, *L. cognatum*, and *L. sordidum* may be able to populate areas of high intensity agriculture due to their ability to forage on many different species of flowering plants.

3.7 Other Results

Another notable result of this study is that the sticky traps used in this study were not ideal for catching native bees. Although the results were not quantified, the sticky traps caught a large variety of other insects but only one native bee, after multiple weeks of trials.

The pan trap caught specimens were not sorted or identified due to time constraints. However, it was observed that a large number of native bees were caught using this method. The only issue with this method is the extra effort needed to sort the samples. In order to identify the bees, they would first need to be separated from the other insects, and then thoroughly dried before identification. Also, the pollen load information is lost using this method.

For this study, therefore, sweep-net sampling was the most effective method of sampling since it is a simple, and thorough method that allows for easy sorting, identification, and collection of pollen loads of bees. However, this method only allowed for sampling at one point in time. In contrast, pan traps and sticky traps are able to collect samples over a longer period of time than sweep netting, provided that bees are attracted to these traps. This may

allow for a sample that is a greater representation of the sample sites but may under-sample trap shy species.

3.8 Overall Conclusions

1. The abundance of native bees in northern Taranaki was not negatively affected by increased agricultural intensity. However, some species may be limited to low agricultural intensity areas. Although these results show that there is no difference in species richness with varying land use intensity this may be due to a small sample size. This must be studied further in order to understand this better.
2. Weather variables of temperature, wind speed, and cloud cover all had a significant effect on the presence of native bees in northern Taranaki, whereas humidity did not.
3. *L. paahaumaa* was the most commonly caught species of native bee in this study, followed by *L. cognatum* and *L. sordidum*.
4. *L. paahaumaa* was the most generalist species, in terms of foraging for floral resources, in this study, followed by *L. sordidum* and *L. cognatum*. This ability to forage on many species of plant may be why they are the most common species found in this study.

3.9 Limitations

Sampling on the roadsides for bees was convenient, but this may have added some unforeseen issues for the sampling process. For example, some studies suggest that bees are less likely to forage on the edge of habitats or on roadsides as a way of adapting to anthropogenic disturbance (Kremen et al., 2007; Ricketts, 2001). Sampling on roadsides also limited the available floral resources, as all the plants on roadsides were those that are able to exploit disturbed environments.

3.10 Study Implications

The results of this study provide a novel insight into the abundance and species richness of native bees in the northern Taranaki region, New Zealand. This thesis also identifies the potential threats to native bees in New Zealand, and examines the impacts of some of these threats. It is vital to understand what these impacts are, in order to manage the conservation of native bees in the future. Previous work has shown the importance of native bees in pollination systems, both natural and commercial (Donovan, 2007; Howlett et al., 2015;

Rader et al., 2012). Therefore, it is in the interest of all to protect these species from extinction.

The results of this study indicate that there is a potential for some species of native bees to be unable to persist in areas of high intensity agriculture. This information is very valuable as farmers are able to be encouraged to make an effort to preserve the diversity of native bees by, for example, planting bee-friendly plants or restricting their use of pesticides. Diversity has been identified as vital to ecosystem resilience (Elmqvist et al., 2003; Luck et al., 2003), where a lack of diversity can have negative impacts on ecosystem services. A lack of diversity of native bees may cause a reduction in pollination rates in these systems. Therefore, it is key to have an understanding of the native bee diversity in order to examine pollination levels.

This thesis also shows how weather can have an effect on the presence of native bees in the region. With the predicted climatic changes, the native bees in New Zealand may be facing changes in their behaviours. Therefore, it is important to have an understanding about how the bees may be impacted by these changing conditions. These results also give information to improve and refine future bee sampling techniques.

Lastly, these results provide further detail on the floral preferences of the native bee species present during this study. Knowing the floral preferences of native bees is helpful for planning conservation management and for predicting the presence/absence of native bees.

Overall, these insights allow for better predictions surrounding the presence of native bees in these areas. This information is necessary in order to better conserve and protect New Zealand's native bees in the face of ever-changing environments.

3.11 Future Work

The data from this study are able to be used in the future to create species' distribution models. This would be a very interesting area of research as it would allow us to make predictions about the distributions of native bee species. This information is important for conservation efforts.

An interesting avenue for future research would be to examine the effects of urban environments on the abundance and species richness of native bees as this has not been looked into in New Zealand. The results of this would give an insight as to how people can design urban environments to the advantage of native bees (Bennet, Kelly, & Clemens, 2018).

During this research, an idea of creating nest traps was considered for sampling native bees. These traps were designed in order to specifically lure in *Hylaeus* species. The design consisted of a small, rectangular block of wood, with holes of various different sizes drilled into its front face. The idea was that the cavity nesting *Hylaeus* would attempt to nest in these drilled tunnels. These nest traps could be drilled onto fence posts or trees. These traps would then be left for a couple of summers and then collected again. *Hylaeus* nests are able to be seen in the trap due to the presence of a cellophane-like material, which they use to line their nests, in the holes. These traps were only very briefly trialled during this study. However, there were some *Hylaeus* observed using the nest traps. Therefore, these traps seem promising not only for recording the presence of these bees but also for translocations, or for increasing bee densities in sites where nest sites are limiting – which is likely in pasture areas lacking woody species.

There is also the potential for the design of a nest trap for ground nesting species of *Leioproctus* and *Lasioglossum*. This design may consist of containers with varying substrates placed out in the environment. By utilising nest traps, they would be able to be in the environment for longer, and therefore have the potential to catch a fully representative sample of the community composition of each site, more so than only sweep netting.

This study could lead to future research that focusses on how to increase the abundance and diversity of native bees in agricultural environments. These results suggest that planting patches of native bee-friendly flora on farms may increase the abundance of some species of native bees. Another potential future option may be using the nest trap designs discussed above for conservation efforts. These nest traps may be able to be used as a way for farmers, or other interested parties, to increase the abundance and diversity of native bee species on their properties.

Further work is also needed to research the effects of climate change on the phenology of native bees in New Zealand, as the results of this study shows that there is a potential for an ecological mismatch between the bees and their host plants.

References

- Allsopp, M. H., de Lange, W. J., & Veldtman, R. (2008). Valuing insect pollination services with cost of replacement. *PLoS ONE*, 3(9).
- Arena, M., & Sgolastra, F. (2014). A meta-analysis comparing the sensitivity of bees to pesticides. *Ecotoxicology*, 23(3), 324-334.
- Artz, D. R., & Nault, B. A. (2011). Performance of *Apis mellifera*, *Bombus impatiens*, and *Peponapis pruinosa* (Hymenoptera: Apidae) as pollinators of pumpkin. *Journal of Economic Entomology*, 104(4), 1153-1161.
- Atkinson, I. A., & Cameron, E. K. (1993). Human influence on the terrestrial biota and biotic communities of New Zealand. *Trends in Ecology & Evolution*, 8(12), 447-451.
- Bennet, D. G., Kelly, D., & Clemens, J. (2018). Food plants and foraging distances for the native bee *Lasioglossum sordidum* in Christchurch Botanic Gardens. *New Zealand Journal of Ecology*, 42(1), 1-8.
- Biesmeijer, J. C., Roberts, S. P. M., Reemer, M., Ohlemuller, R., Edwards, M., Peeters, T., . . . Kunin, W. E. (2006). Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. *Science*, 313(5785), 351-354.
- Bischoff, M., Campbell, D. R., Lord, J. M., & Robertson, A. W. (2013). The relative importance of solitary bees and syrphid flies as pollinators of two outcrossing plant species in the New Zealand alpine. *Austral Ecology*, 38(2), 169-176.
- Braat, L. C., & de Groot, R. (2012). The ecosystem services agenda: bridging the worlds of natural science and economics, conservation and development, and public and private policy. *Ecosystem Services*, 1(1), 4-15.
- Burkle, L. A., Marlin, J. C., & Knight, T. M. (2013). Plant-pollinator interactions over 120 years: loss of species, co-occurrence, and function. *Science*, 339(6127), 1611-1615.
- Burrill, R. M., & Dietz, A. (1981). The response of honey bees to variations in solar radiation and temperature. *Apidologie*, 12(4), 319-328.
- Butz Huryn, V. M. (1997). Ecological impacts of introduced honey bees. *The Quarterly Review of Biology*, 72(3), 275-297.
- Corbet, S. A., Fussell, M., Ake, R., Fraser, A., Gunson, C., Savage, A., & Smith, K. (1993). Temperature and the pollinating activity of social bees. *Ecological Entomology*, 18(1), 17-30.
- Costanza, R., d'Arge, R., De Groot, R., Farber, S., Grasso, M., Hannon, B., . . . Paruelo, J. (1997). The value of the world's ecosystem services and natural capital. *Nature*, 387(6630), 253-260.
- Danforth, B. N. (1999). Phylogeny of the bee genus *Lasioglossum* (Hymenoptera: Halictidae) based on mitochondrial COI sequence data. *Systematic Entomology*, 24(4), 377-393.
- Davis, E. S., Reid, N., & Paxton, R. J. (2012). Quantifying forage specialisation in polyphagous insects: the polylectic and rare solitary bee, *Colletes floralis* (Hymenoptera: Colletidae). *Insect Conservation and Diversity*, 5(4), 289-297.
- de Lange, P. J., & Rolfe, J. R. (2010). New Zealand Indigenous Vascular Plant Checklist 2010. Retrieved from http://nzpcn.org.nz/publications/de_Lange_PJ_and_Rolfe_J_2010.pdf
- Donovan, B. J. (1980). Interactions between native and introduced bees in New Zealand. *New Zealand Journal of Entomology*, 3(1), 104-116.
- Donovan, B. J. (2007). Apoidea (Insecta: Hymenoptera). *Fauna of New Zealand*, 57, 295.
- Donovan, B. J. (2017). [Personal Communication].
- Donovan, B. J., Howlett, B. G., & Walker, M. K. (2010). Relocation and establishment of nesting populations of the native bee *Leioproctus huakiwi* Donovan (Hymenoptera: Colletidae). *New Zealand Entomologist*, 33(1), 109-113.
- Elmqvist, T., Folke, C., Nyström, M., Peterson, G., Bengtsson, J., Walker, B., & Norberg, J. (2003). Response diversity, ecosystem change, and resilience. *Frontiers in Ecology and the Environment*, 1(9), 488-494.
- Fisher, B., Turner, R. K., & Morling, P. (2009). Defining and classifying ecosystem services for decision making. *Ecological Economics*, 68(3), 643-653.
- Garibaldi, L. A., Steffan-Dewenter, I., Winfree, R., Aizen, M. A., Bommarco, R., Cunningham, S. A., . . . Afik, O. (2013). Wild pollinators enhance fruit set of crops regardless of honey bee abundance. *Science*, 339(6127), 1608-1611.

- Ghazoul, J. (2005). Buzziness as usual? Questioning the global pollination crisis. *Trends in Ecology & Evolution*, 20(7), 367-373.
- Google Inc. (2018). Google Earth Pro (Version 7.3.1).
- Goulson, D. (2003). Effects of introduced bees on native ecosystems. *Annual Review of Ecology, Evolution, and Systematics*, 34(1), 1-26.
- Greenleaf, S. S., & Kremen, C. (2006a). Wild bee species increase tomato production and respond differently to surrounding land use in Northern California. *Biological Conservation*, 133(1), 81-87.
- Greenleaf, S. S., & Kremen, C. (2006b). Wild bees enhance honey bees' pollination of hybrid sunflower. *Proceedings of the National Academy of Sciences*, 103(37), 13890-13895.
- Hart, N. (2007). *Industrious Native Bees: A Case Study in Whangarei*. (Environmental Science), Auckland University of Technology, Auckland.
- Heard, T. A., & Hendrikz, J. K. (1993). Factors influencing flight activity of colonies of the stingless bee *Trigona carbonaria* (Hymenoptera, Apidae). *Australian Journal of Zoology*, 41(4), 343-353.
- Hickey, L. J., & Doyle, J. A. (1977). Early Cretaceous fossil evidence for angiosperm evolution. *The Botanical Review*, 43(1), 3-104.
- Holden, C. (2006). Report warns of looming pollination crisis in North America. *Science*, 314(5798), 397-397.
- Holt, K. (2017). [Personal Communication].
- Howell, C., & Sawyer, J. W. D. (2006). New Zealand Naturalised Vascular Plant Checklist. Retrieved from <http://www.nzpcn.org.nz/publications/Naturalised-list-06-new.pdf>
- Howlett, B. G., Lankin-Vega, G. O., & Pattermore, D. E. (2015). Native and introduced bee abundances on carrot seed crops in New Zealand. *New Zealand Plant Protection*, 68(1), 373-379.
- Iwasaki, J. (2017). *Interactions Between Bee Species in Relation to Floral Resources*. (Doctor of Philosophy), University of Otago, Dunedin.
- Kayaalp, P., Schwarz, M. P., & Stevens, M. I. (2013). Rapid diversification in Australia and two dispersals out of Australia in the globally distributed bee genus, *Hylaeus* (Colletidae: Hylaeinae). *Molecular Phylogenetics and Evolution*, 66(3), 668-678.
- Kearns, C. A., Inouye, D. W., & Waser, N. M. (1998). Endangered mutualisms: the conservation of plant-pollinator interactions. *Annual Review of Ecology and Systematics*, 29(1), 83-112.
- Kevan, P. (1990). *Pollination: keystone process in sustainable global productivity*. Paper presented at the VI International Symposium on Pollination 288.
- Klein, A., Steffan-Dewenter, I., Buchori, D., & Tschardtke, T. (2002). Effects of land-use intensity in tropical agroforestry systems on coffee flower-visiting and trap-nesting bees and wasps. *Conservation Biology*, 16(4), 1003-1014.
- Klein, A., Vaissiere, B. E., Cane, J. H., Steffan-Dewenter, I., Cunningham, S. A., Kremen, C., & Tschardtke, T. (2007). Importance of pollinators in changing landscapes for world crops. *Proceedings of The Royal Society B*, 274(1608), 303-313.
- Kremen, C., Williams, N. M., Aizen, M. A., Gemmill-Herren, B., LeBuhn, G., Minckley, R., . . . Vazquez, D. P. (2007). Pollination and other ecosystem services produced by mobile organisms: a conceptual framework for the effects of land-use change. *Ecology Letters*, 10(4), 299-314.
- Kremen, C., Williams, N. M., & Thorp, R. W. (2002). Crop pollination from native bees at risk from agricultural intensification. *PNAS*, 99(26), 16812-16816.
- Landcare Research. (2015). New Zealand Land Cover Database version 4.1.
- Larsen, N. J., Minor, M. A., Cruickshank, R. H., & Robertson, A. W. (2014). Optimising methods for collecting Hymenoptera, including parasitoids and Halictidae bees, in New Zealand apple orchards. *Journal of Asia-Pacific Entomology*, 17(3), 375-381.
- Le Conte, Y., Ellis, M., & Ritter, W. (2010). *Varroa* mites and honey bee health: can *Varroa* explain part of the colony losses? *Apidologie*, 41(3), 353-363.
- Luck, G. W., Daily, G. C., & Ehrlich, P. R. (2003). Population diversity and ecosystem services. *Trends in Ecology & Evolution*, 18(7), 331-336.

- Malone, L., Aulsford, J., Howlett, B. G., Scott-Dupre, C., Bardol, N., & Donovan, B. J. (2010). Observations on bee species visiting white clover in New Zealand pastures. *Journal of Apicultural Research*, 49(3), 284-286.
- Memmott, J., Waser, N. M., & Price, M. V. (2004). Tolerance of pollination networks to species extinctions. *Proceedings of the Royal Society of London B: Biological Sciences*, 271(1557), 2605-2611.
- Meteorological Service of New Zealand. (2018). Rural - Taranaki. Retrieved from <http://www.metservice.com/rural/taranaki#!/new-plymouth>
- Michener, C. D. (2000). *The Bees of the World*. United States of America: The Johns Hopkins University Press.
- Michener, C. D., & Grimaldi, D. A. (1988). The oldest fossil bee: Apoid history, evolutionary stasis, and antiquity of social behavior. *Proceedings of the National Academy of Sciences*, 85(17), 6424-6426.
- Newstrom-Lloyd, L. E. (2013). Pollination in New Zealand. In J. R. Dymond (Ed.), *Ecosystem Services in New Zealand* (pp. 408-431). Lincoln: Manaaki Whenua Press.
- O'Toole, C. (2013). *Bees - A Natural History*. United States: Firefly Books Ltd.
- O'Toole, C. (2002). Those other bees: changing the funding culture. *Pollinating Bees-The Conservation Link Between Agriculture and Nature*, 37-40.
- Paini, D. (2004). Impact of the introduced honey bee (*Apis mellifera*)(Hymenoptera: Apidae) on native bees: a review. *Austral Ecology*, 29(4), 399-407.
- Papanikolaou, A. D., Kühn, I., Frenzel, M., & Schweiger, O. (2017). Semi-natural habitats mitigate the effects of temperature rise on wild bees. *Journal of Applied Ecology*, 54(2), 527-536.
- Peterson, G., Allen, C. R., & Holling, C. S. (1998). Ecological resilience, biodiversity, and scale. *Ecosystems*, 1(1), 6-18.
- Pettis, J. S., Lichtenberg, E. M., Andree, M., Stitzinger, J., & Rose, R. (2013). Crop pollination exposes honey bees to pesticides which alters their susceptibility to the gut pathogen *Nosema ceranae*. *PLoS ONE*, 8(7), e70182.
- Polgar, C. A., Primack, R. B., Williams, E. H., Stichter, S., & Hitchcock, C. (2013). Climate effects on the flight period of Lycaenid butterflies in Massachusetts. *Biological Conservation*, 160(1), 25-31.
- Potts, S. G., Biesmeijer, J. C., Kremen, C., Neumann, P., Schweiger, O., & Kunin, W. E. (2010). Global pollinator declines: trends, impacts and drivers. *Trends in Ecology & Evolution*, 25(6), 345-353.
- Potts, S. G., Petanidou, T., Roberts, S., O'Toole, C., Hulbert, A., & Willmer, P. (2006). Plant-pollinator biodiversity and pollination services in a complex mediterranean landscape. *Biological Conservation*, 29(4), 519-529.
- R Core Team. (2018). R: The R Project for Statistical Computing (Version 3.4.3).
- Rader, R., Howlett, B. G., Cunningham, S. A., Westcott, D. A., & Edwards, W. (2012). Spatial and temporal variation in pollinator effectiveness: do unmanaged insects provide consistent pollination services to mass flowering crops? *Journal of Applied Ecology*, 49(1), 126-134.
- Rader, R., Reilly, J., Bartomeus, I., & Winfree, R. (2013). Native bees buffer the negative impact of climate warming on honey bee pollination of watermelon crops. *Global Change Biology*, 19(10), 3103-3110.
- Ricketts, T. H. (2001). The matrix matters: effective isolation in fragmented landscapes. *The American Naturalist*, 158(1), 87-99.
- Roubik, D. W., Moreno, J. E., Vergara, C., & Wittmann, D. (1986). Sporadic food competition with the African honey bee: projected impact on neotropical social bees. *Journal of Tropical Ecology*, 2(02), 97-111.
- Schmidt-Adam, G., Murray, B. G., & Young, A. G. (2009). The relative importance of birds and bees in the pollination of *Metrosideros excelsa* (Myrtaceae). *Austral Ecology*, 34(5), 490-498.
- Sekercioglu, C. H. (2010). Ecosystem functions and services. In N. S. Sodhi & P. R. Ehrlich (Eds.), *Conservation Biology for All* (pp. 45-72): Oxford University Press.
- Southwick, E. E., & Southwick, L. (1992). Estimating the economic value of honey bees (Hymenoptera: Apidae) as agricultural pollinators in the United States. *Journal of Economic Entomology*, 85(3), 621-633.

- Souza, B., Carvalho, C., & Alves, R. (2006). Flight activity of *Melipona asilvai moure* (Hymenoptera: Apidae). *Brazilian Journal of Biology*, 66(2B), 731-737.
- Stavert, J. R., Pattermore, D. E., Gaskett, A. C., Beggs, J. R., & Bartomeus, I. (2017). Exotic species enhance response diversity to land-use change but modify functional composition. *Proceedings of The Royal Society B*, 284(20170788), 1-10.
- Steffan-Dewenter, I., Potts, S. G., & Packer, L. (2005). Pollinator diversity and crop pollination services are at risk. *Trends in Ecology & Evolution*, 20(12), 651-652.
- Thompson, H. M. (2010). Risk assessment for honey bees and pesticides—recent developments and ‘new issues’. *Pest Management Science*, 66(11), 1157-1162.
- Tylianakis, J. M. (2013). The global plight of pollinators. *Science*, 339(6127), 1532-1533.
- Westerkamp, C., & Gottsberger, G. (2002). The costly crop pollination crisis. *Pollinating Bees-The Conservation Link between Agriculture and Nature*, P. Kevan and V. Imperatriz Fonseca, eds.(Brasilia: Ministry of Environment), 51-56.
- Winfree, R., Williams, N. M., Dushoff, J., & Kremen, C. (2007). Native bees provide insurance against ongoing honey bee losses. *Ecology Letters*, 10(11), 1105-1113.

Appendices

Table 1 Overview of native bees caught at each site during this study

Site	Coordinates	Farming Intensity	Bee Abundance	Species Diversity	<i>L. paahaumaa</i>	<i>L. huakiwi</i>	<i>L. pango</i>	<i>L. monticola</i>	<i>L. sordidum</i>	<i>L. cognatum</i>	<i>H. relegatus</i>
P1	-38.96525, 174.45006	MED	5	2	3	2	-	-	-	-	-
P2	-38.9615, 174.45118	HIGH	20	3	2	-	-	-	7	11	-
P3	-38.95015, 174.45602	HIGH	12	3	1	-	-	-	7	4	-
P4	-38.92485, 174.47861	MED	11	3	1	-	-	-	1	9	-
P5	-38.9214, 174.48254	MED	7	2	-	-	1	-	-	6	-
P6	-38.89508, 174.51398	MED	19	3	5	-	-	-	7	7	-
P7	-38.89481, 174.51563	MED	6	2	4	-	-	-	-	2	-
P8	-38.8926,	LOW	14	3	5	-	-	-	4	5	-

	17451918										
P9	-38.89094, 174.52233	LOW	10	4	5	-	1	-	-	1	3
P10	-38.89131, 174.52222	LOW	24	4	11	-	-	-	2	3	8
P Totals	-		128	6	37	2	2	0	28	48	11
U1	-38.94854, 174.5326	MED	1	1	-	-	-	-	-	1	-
U2	-38.94972, 174.53465	MED	-	-	-	-	-	-	-	-	-
U3	-38.96211, 174.55243	MED	7	2	3	-	-	-	-	4	-
U4	-38.96383, 174.5539	MED	15	2	9	-	-	-	6	-	-
U5	-38.97801, 174.55495	HIGH	7	3	5	-	-	-	1	1	-
U6	-38.9963, 174.55986	MED	-	-	-	-	-	-	-	-	-
U7	-39.00869, 174.56631	HIGH	1	1	-	-	-	-	1	-	-
U8	-39.01531, 174.57198	MED	-	-	-	-	-	-	-	-	-
U9	-39.01856, 174.56971	HIGH	7	2	6	-	-	-	1	-	-
U Totals	-		38	6	23	0	0	0	9	6	0

KU1	-39.05041, 174.3978	LOW	9	1	9	-	-	-	-	-	-
KU2	-39.04896, 174.4005	LOW	7	2	5	-	-	-	2	-	-
KU3	-39.04157, 174.4116	LOW	7	2	4	-	-	-	3	-	-
KU4	-39.04169, 174.41276	LOW	15	2	10	-	-	-	5	-	-
KU5	-39.03726, 174.41472	MED	13	2	12	-	-	-	1	-	-
KU6	-39.03321, 174.40755	MED	10	4	7	1	-	-	1	1	-
KU7	-39.03017, 174.40823	MED	7	1	7	-	-	-	-	-	-
KU8	-39.02643, 174.40743	HIGH	4	1	4	-	-	-	-	-	-
KU9	-39.02019, 174.40329	MED	7	1	7	-	-	-	-	-	-
KU10	-39.01386, 174.39877	MED	4	2	3	-	-	-	-	1	-
KU Totals	-	-	83	4	68	1	0	0	12	2	0
O1	-39.03111, 174.27341	HIGH	21	3	7	-	-	-	2	12	-
O2	-39.03515,	HIGH	6	2	1	-	-	-	5	-	-

	174.28239										
K5	-39.12371, 174.28578	LOW	3	1	-	-	-	-	3	-	-
K6	-39.12111, 174.28136	MED	-	-	-	-	-	-	-	-	-
K7	-39.09075, 174.28298	HIGH	7	1	7	-	-	-	-	-	-
K8	-39.07751, 174.26584	HIGH	6	1	6	-	-	-	-	-	-
K9	-39.04738, 174.25424	MED	2	1	-	-	-	-	-	2	-
K10	-39.04546, 174.26649	HIGH	3	2	2	-	-	-	1	-	-
K Totals	-		66	6	56	2	0	1	5	2	0
F1	-38.89437, 174.52658	LOW	-	-	-	-	-	-	-	-	-
F2	-38.89436, 174.5274	LOW	-	-	-	-	-	-	-	-	-
F3	-38.89348, 174.52512	LOW	-	-	-	-	-	-	-	-	-
F4	-38.89347, 174.52416	LOW	3	2	1	-	2	-	-	-	-
F5	-38.89589, 174.52454	LOW	-	-	-	-	-	-	-	-	-
F6	-38.89521,	LOW	3	2	2	-	-	-	-	-	1

	174.52404										
F7	-38.8964, 174.52275	MED	3	2	2	-	-	-	-	1	-
F8	-38.89511, 174.52201	MED	4	2	3	-	-	-	-	1	-
F9	-38.89276, 174.52245	LOW	1	1	1	-	-	-	-	-	-
F10	-38.89454, 174.52333	LOW	-	-	-	-	-	-	-	-	-
F Totals	-		14	4	9	0	2	0	0	2	1
L1	-39.02446, 174.21492	HIGH	1	1	1	-	-	-	-	-	-
L2	-39.07326, 174.22413	HIGH	10	2	9	-	-	-	1	-	-
L3	-39.08115, 174.22725	HIGH	8	1	8	-	-	-	-	-	-
L4	-39.09098, 174.23657	MED	12	1	12	-	-	-	-	-	-
L5	-39.06797, 174.23814	HGIH	12	3	6	-	-	-	5	1	-
L6	-39.05376, 174.22294	HIGH	5	2	4	-	-	-	1	-	-
L7	-39.04383, 174.23585	HIGH	9	1	9	-	-	-	-	-	-
L8	-39.02291,	HIGH	27	4	4	-	-	-	8	14	1

	174.22713										
L9	-39.01955, 174.23413	HIGH	11	3	6	-	-	-	2	3	-
L Totals	-		95	4	59	0	0	0	17	18	1
M1	-38.9714, 174.45102	HIGH	6	1	6	-	-	-	-	-	-
M2	-38.95918, 174.46371	HIGH	9	1	9	-	-	-	-	-	-
M3	-38.9534, 174.46768	MED	14	3	9	-	-	-	1	4	-
M4	-38.95343, 174.47012	MED	6	2	4	-	-	-	-	2	-
M5	-38.96359, 174.47404	MED	10	2	9	-	-	-	1	-	-
M6	-38.97007, 174.47151	MED	2	1	2	-	-	-	-	-	-
M7	-38.98133, 174.47603	MED	-	-	-	-	-	-	-	-	-
M8	-38.98158, 174.48379	LOW	9	2	8	-	-	-	-	1	-
M Totals	-		56	3	47	-	-	-	2	7	-
Total Bees			572	-	360	5	4	1	90	99	13

Table 2 Results of pollen analysis showing the number of bees caught carrying each pollen type. The bee species are ranked starting with most generalised at the top, to least at the bottom.

Bee Species	<i>Agapanthus</i> spp.	Apiaceae spp. 1	Apiaceae spp. 2	Apiaceae spp. 3	Asteraceae spp. 1	Asteraceae spp. 2	Asteraceae spp. 3	Asteraceae spp. 4	Asteraceae spp. 5	Asteraceae spp. 6	Asteraceae spp. 7	Brassic a spp. 1	Brassic a spp. 2	<i>Hoheria</i> spp.	<i>Hydrangea</i> spp.	<i>K.</i> <i>excelsa</i>	Myrtaceae spp.	<i>Phormium</i> spp.1	<i>Phormium</i> spp. 2	<i>Prunella</i> spp.	<i>Ranunculus</i> spp.	<i>Rubus</i> spp.
<i>L. paahaumaa</i>	0	8	1	31	2	148	138	0	20	25	1	1	1	3	2	1	4	0	1	0	5	0
<i>L. sordidum</i>	1	0	0	12	0	33	28	1	2	3	1	0	5	0	0	0	3	0	1	0	5	10
<i>L. cognatum</i>	0	0	0	5	0	49	38	0	1	4	0	3	1	0	0	1	3	0	0	1	10	2
<i>L. huakiwi</i>	1	1	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
<i>L. pango</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0
<i>L. monticola</i>	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1

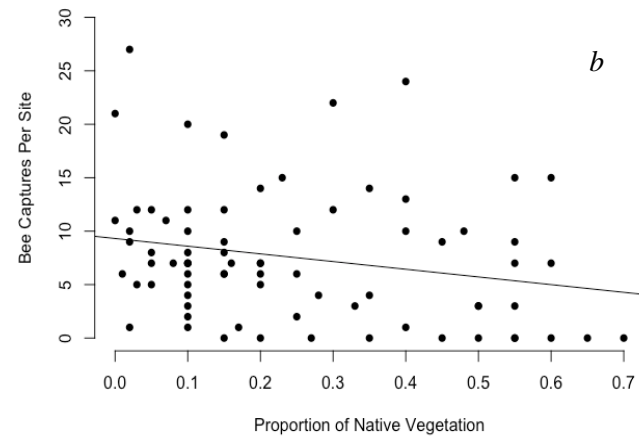
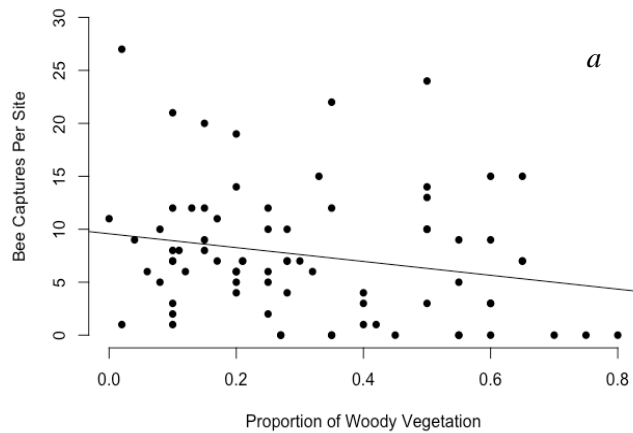


Figure 1 Bee captures per site vs. woody vegetation (a), and native vegetation (b).

Table 3 ANOVA of bee captures per site vs. woody vegetation.

	DF	Deviance Resid.	DF Resid.	Dev	Pr(>Chi)
Null			75	404.81	
Woody Veg	1	18.206	74	386.61	1.982e-05

Table 4 ANOVA of bee captures per site vs native vegetation.

	DF	Deviance Resid.	DF Resid.	Dev	Pr(>Chi)
Null			75	404.81	
Native Veg	1	20.465	74	384.35	6.075e-06

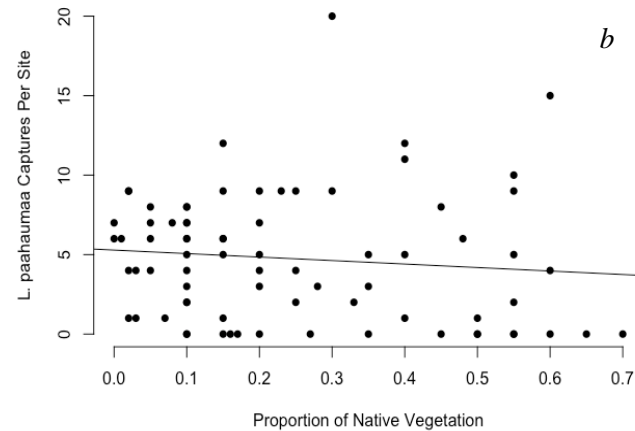
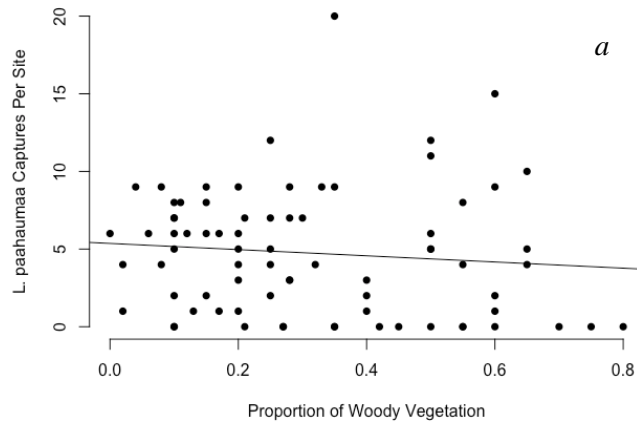
**Figure 2** *L. paahaumaa* captures per site vs. woody vegetation (a), and native vegetation (b).

Table 5 ANOVA of *L. paahaumaa* captures per site vs. woody vegetation.

	DF	Deviance Resid.	DF Resid.	Dev	Pr(>Chi)
Null			75	298.66	
Woody Veg	1	2.6595	74	296/00	0.1029

Table 6 ANOVA of *L. paahaumaa* captures per site vs. native vegetation.

	DF	Deviance Resid.	DF Resid.	Dev	Pr(>Chi)
Null			75	298.66	
Native Veg	1	2.9742	74	295.69	0.0846

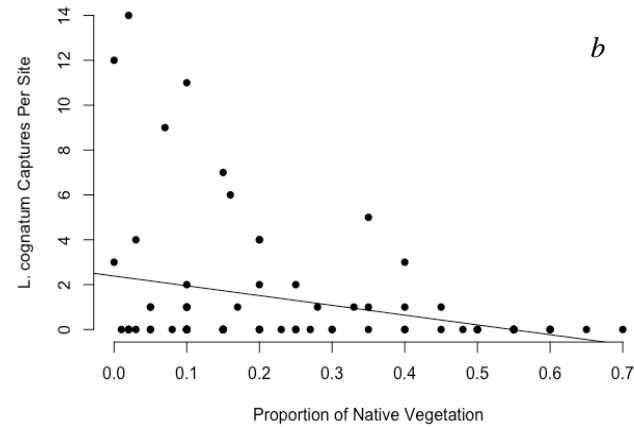
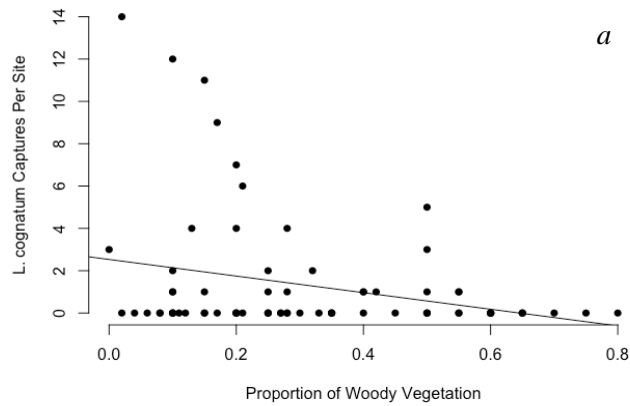
**Figure 3** *L. cognatum* captures per site vs. woody vegetation (a), and native vegetation (b).

Table 7 ANOVA of *L. cognatum* captures per site vs. woody vegetation.

	DF	Deviance Resid.	DF Resid.	Dev	Pr(>Chi)
Null			75	293.10	
Woody Veg	1	42.963	74	250.13	5.58e-11

Table 8 ANOVA of *L. cognatum* captures per site vs. native vegetation.

	DF	Deviance Resid.	DF Resid.	Dev	Pr(>Chi)
Null			75	293.10	
Native Veg	1	52.122	74	240.97	5.217e-13

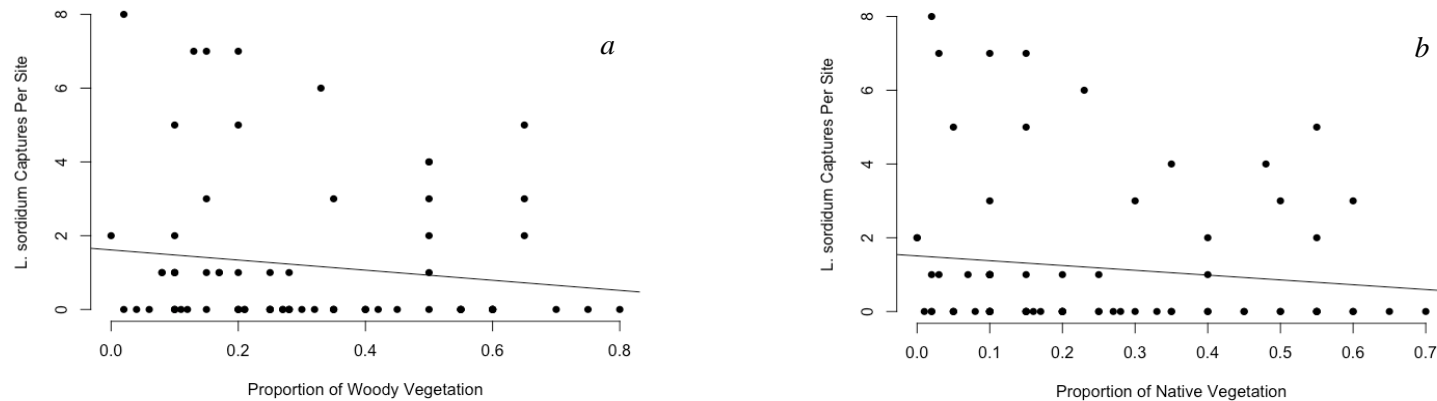


Figure 4 *L. sordidum* captures per site vs. woody vegetation (a), and native vegetation (b).

Table 9 ANOVA of *L. sordidum* captures per site vs. woody vegetation.

	DF	Deviance Resid.	DF Resid.	Dev	Pr(>Chi)
Null			75	213.99	
Woody Veg	1	5.1619	74	208.83	0.02309

Table 10 ANOVA of *L. sordidum* captures per site vs. native vegetation.

	DF	Deviance Resid.	DF Resid.	Dev	Pr(>Chi)
Null			75	213.99	
Native Veg	1	4.3028	74	209.69	0.03805