

**Promoting functional diversity of
flower-feeding insects**

Yolanda Marie Hanusch

Bachelor (Honours)

Supervisors: Ass. Prof. Tanya Latty
Dr. Ros Gloag, Dr. Thomas White

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Keywords

agricultural diversification, crop pollination, flower-feeding insects, insect-plant interactions, introduced bees, market-gardens, native bees, natural pest predators, orchards

Abstract

Understanding which flower-feeding insects are supported by specific flowering plants in agroecosystems is important for guiding land management practices. Flower-feeding insects supply our agricultural production with important ecosystem services, including crop pollination and natural control of crop pests. They are also a key component of biodiverse landscapes. While there has been increasing work dedicated to studying flower-feeding insects in agroecosystems, this work has had a regional biases, with most studies conducted in America and Europe. Data from other geographic regions, that comprise different insect communities, is important for informing local management recommendations and understanding which data trends are general across space and taxa.

In this thesis, I aim to better understand flower-feeding insect diversity in some Australian horticultural systems. I first investigated patterns in flower-feeding insect diversity in two spring-flowering perennial orchard systems in Tasmania (apple and blueberry) (Chapter 2). I then investigated flower-insect interactions in small-scale diverse cropping systems (market-gardens) in both Tasmania (Chapter 3) and south-east NSW (Chapter 4). Finally, I conducted an experimental study examining changes in foraging behaviour of potential crop pollinators in the presence of a highly attractive plant (Chapter 5).

Overall, my results show that: (i) a large proportion of crops in orchards and market-gardens in my study regions are visited mostly or exclusively by introduced bees, *Apis mellifera* and (Tasmania only) *Bombus terrestris*, (ii) some crops are visited more frequently by native insects than others (e.g. apple, blueberries, caneberries – raspberry/boysenberry/blackberry by native *Exoneura* bees), (iii) plant species richness and abundance did not affect either diversity or abundance of native insects. Rather, it appeared that key plant species may be more important for attracting insect diversity than overall plant diversity in these agroecosystems; and (iv) the different foraging behaviours of pollinating taxa may account for the variable impacts of non-crop floral resources on crop pollination.

My data gives insight into specific flower feeding insects supported in Australian horticultural systems and should aid local ecological land management decisions.

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Declaration of Originality

I hereby declare that to the best of my knowledge, the content present in this thesis is entirely my own work and that all material written by others has been acknowledged. I certify that this thesis has not been submitted, either in full or in part, for a degree at this, or any other institution.

Yolanda Marie Hanusch

February, 2023

Chapter 1: General introduction

1.1 BACKGROUND

Towards sustainable agriculture

Global demands for food-production are increasing, yet the world's ecosystems also face increasing parallel threats from intensive agricultural practices, climate change, pollution and biotic invasion (Reid *et al.*, 2005). We therefore need our agricultural practices to be more productive and more resilient, whilst at the same time reducing the negative impacts that agriculture is having on our environment (Tscharrntke *et al.*, 2005; Landis, 2017; Tscharrntke *et al.*, 2021). One of the major problems associated with industrial agricultural production is landscape simplification and loss of native vegetation (Tscharrntke *et al.*, 2005). Simplified agricultural landscapes today contain fewer crops and non-crop habitat, which intensifies biodiversity losses and reduces the very ecosystem services upon which agricultural production depends (Landis, 2017). These ecosystem services (i.e. services that contribute to human well-being (Reid and Raudsepp-Hearne, 2005) include supporting services such as soil formation, soil fertility, nutrient cycling and the availability of fresh water, along with regulating services delivered from insects and other animals, including pollination and pest control (Power, 2010).

With agricultural production today making up around 40% of the ice-free world's surface (Foley *et al.*, 2005) there is substantial opportunity to manage farming landscapes in a way that increases rather than depletes biodiversity and ecosystem values (Landis, 2017). By adopting agricultural management practices that focus on enhancing integral ecological services, we have the opportunity to sustain both healthy landscapes and crop productivity into the future (Reid and Raudsepp-Hearne, 2005; Reid *et al.*, 2005; Bommarco *et al.*, 2013; Lichtenberg *et al.*, 2017). This may require paradigm shifts away from our focus on intensive monocultural agricultural systems and towards more diversified agricultural landscapes (Gurr *et al.*, 2016; Landis, 2017; Kremen, 2020). Many possible actions can aid in the diversifying of our production systems. Some are broader landscape approaches, such as the restoration of degraded natural ecosystems (Ansell *et al.*, 2016). Others can be implemented at small-scales within localised settings, via changes in the management practices of individual farming systems. One such local approach focuses on the availability of flowering resources in agricultural land, which farmers can have direct control over through the ways they manage their land (Burkle *et al.*, 2017).

Flowering resources in agro-ecosystems

Flowering resources play an integral part in agriculture, due to the role they play in supporting different functional groups of insects, including those that directly contribute to agricultural production (e.g. pollination, pest control); Figure 1.1). Such resources also sustain a broader diversity of insects in modified landscapes (Losey and Vaughan, 2006; Kremen *et al.*, 2007). There is increasing evidence that vegetative diversity in agricultural landscapes, together with the restricted use of chemicals, are essential measures needed to conserve and promote beneficial insects in our landscapes (Tscharntke *et al.*, 2005; Winfree *et al.*, 2009; Potts *et al.*, 2016). For example, land-use changes and simplification that alter floral and nesting resources also lead to changes in individual behaviour, population dynamics and community composition of pollinators (Tscharntke *et al.*, 2005; Kremen *et al.*, 2007; Ricketts *et al.*, 2008; Joshi *et al.*, 2016). Low heterogeneity and high disturbance in some cropping systems further make them less favourable to support natural pest enemies (Landis *et al.*, 2000). Instead, non-crop habitat around production areas is needed to sustain and support populations of natural pest enemies, which provides them with shelter and can act as source habitat from which insects then move into cropping areas to prey on pests, along with providing them with alternative prey (Landis *et al.*, 2000; Gurr *et al.*, 2004; Gagic *et al.*, 2018).

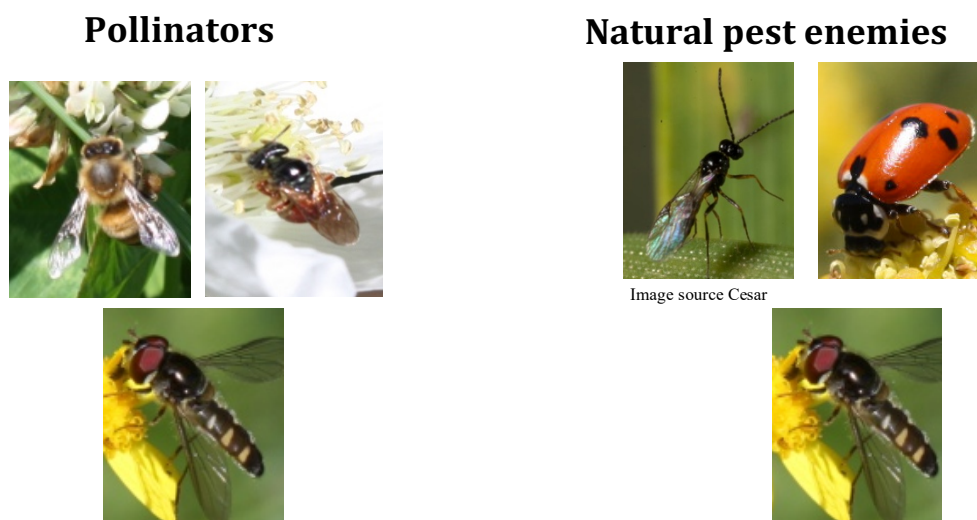


Figure 1.1. Beneficial flower-feeding insects in agroecosystems

However, the responses of flower-feeding insects to land-use changes can be highly context-specific and vary by region, depending on the community composition of insects present (De Palma *et al.*, 2016).

Thus, while some practices may be equally effective in a wide range of landscapes, other will be only locally effective. Identifying which aspects of floral resource management are cross-regional therefore remains problematic. To date, most work is regionally and taxonomically biased toward data from Europe and North America. Broadening the geographic areas of data collection is important for two reasons: (1) to better identify which macro-ecological trends in the relationship between land use and biodiversity are truly universal (Gemmill-Herren, 2016) and (2) to gain insight into the unique localised composition of insects and the floral resources that sustain them, so that we can then translate this information into specific management recommendations for farming in a given region (García and Minarro, 2014; Landis, 2017; Howlett *et al.*, 2021). Without sufficient localised insights into which flowers are most suitable to enhance particular beneficial insects we may run the risk of agricultural areas primarily supporting a small number of highly generalist species (Kleijn *et al.*, 2015), and potentially limiting the delivery of ecosystem services (Landis, 2017).

General insights into best practice for floral resource management also requires knowledge of diverse kinds of agricultural systems, including understudied small-scale and urban farms (Altieri, 2004; Lin *et al.*, 2015).

Crop pollinators

Animal-pollination is a crucial process in most productive terrestrial ecosystems around the world (Kevan 1999; Lomov *et al.* 2010). Insect pollinators play a vital role in sustaining ecosystem health and function, through underpinning the reproduction of many wild plants (Ollerton *et al.*, 2011) and by supporting pollination of our crops (Kleijn *et al.* 2015, Potts *et al.* 2016). More than half of crops for human consumption rely on pollination services provided by animals (Klein *et al.* 2007), and the market demand of crops that either highly benefit from and/or depend on insect pollination (e.g. nuts, fruit) is increasing (Aizen *et al.*, 2009).

Several insects contribute to the pollination of crops, including managed bees and wild insects (mainly bees, flies) (Klein *et al.*, 2007; Rader *et al.*, 2016). The most widespread managed bee species is the Western honeybee (*Apis mellifera*), which is native to Europe and Africa but has since been introduced to nearly all parts of the world to aid with crop pollination services, along with honey production. Honeybees have been the focus of much past research though the role of native bees and other pollinators is increasingly acknowledged (Potts *et al.*, 2016; Rader *et al.*, 2016). Such work has highlighted that conserving and enhancing pollinator diversity within natural and agricultural areas, in general, enriches and safeguards our food production, as diversity ensures the presence of species with different functional traits that exhibit different pollination services (Blüthgen and Klein, 2011). For

example, enhanced fruit set is achieved through more diverse pollinators visiting flowering crops (Martins *et al.*, 2015; Demestihis *et al.*, 2017). Also, native bees are more effective than honeybees at pollination of some crops (Ricketts *et al.*, 2008; Garibaldi *et al.*, 2013b). Importantly pollinator systems with diverse species are more likely to include species that can tolerate changes in climate, along with losses or decline of certain species, compared to pollinator systems that strongly rely on certain species (Lentini *et al.*, 2012; Garibaldi *et al.*, 2013b).

Crop pollinators in Australia

Apis mellifera was introduced to Australia in the 1860s and today is found as widespread feral and managed populations throughout the continent (Paton, 1993), with particularly high densities in the more temperate southern regions (Cunningham *et al.*, 2022). This species is recognised as an important pollinator of varied crops grown in Australia including apple, broad-beans, cucurbits (Cunningham *et al.*, 2002; Cunningham and Le Feuvre, 2013; Bernauer *et al.*, 2022; Gilpin *et al.*, 2022; Subasinghe Arachchige *et al.*, 2022). However, the future of honeybee pollination services in Australia is uncertain. In recent decades, a unique aspect of Australia is that feral (wild) *A. mellifera* populations have thrived, unlike many other parts of the world where a decline of honey bee populations has been observed (Dennis and Kemp, 2016). A key reason for these geographic differences has been the absence of the Varroa mite (*Varroa destructor*) in Australia. This parasitic mite feeds on developing honey bee larva and pupa, transmitting viruses in the process and often triggering colony death (Flores *et al.*, 2021). It has spread globally, with only Australia (until very recently) managing to remain Varroa-free (Lentini *et al.*, 2012; Dennis and Kemp, 2016). The 2022 Varroa mite incursion in New South Wales (DPI, 2022) has the potential to rapidly change the status quo for honey bee populations in Australia, and the ‘free’ pollination services they provide. This is because the establishment and potential spread of varroa mites throughout the Australian landscape could lead to substantial decline of feral alongside managed hives observed in other parts of the world, as seen for example in New Zealand (Iwasaki *et al.*, 2015).

Australia is also home, however, to a diverse assemblage of native bees. Australia-wide, there are an estimated 2000 native bees, though many species remain undescribed (Batley and Hogendoorn, 2009). Some (though not all) of these bees will forage on and pollinate crops in Australian landscapes (Cunningham *et al.*, 2002); along with other non-bees insects (mainly certain flies) (Cook *et al.*, 2020). For example, native eusocial stingless bees (*Tetragonula* spp.) have been shown to be effective pollinators of blueberry, watermelon (Kendall *et al.*, 2020; Subasinghe Arachchige *et al.*, 2022) and reed bees (*Exoneura* spp.) of apple and blackberry (Bernauer *et al.*, 2022; Coates *et al.*, 2022). The conservation and promotion of native bees and other pollinating insects in Australia should be viewed therefore as an insurance policy offering an alternative to the European honeybees as crop pollinators

(Cunningham *et al.*, 2002; Lentini *et al.*, 2012; Bernauer *et al.*, 2022). However, insight into diverse insect communities around the world (including Australia), their pollination services along with the pollination requirements of various crops are insufficient (Klein *et al.*, 2007). The Australian bee fauna is quite distinctive to other parts of the world in many ways, including the absence of native bees in the *Apis* or *Bombus* genera (Batley and Hogendoorn, 2009). Further plants grown within Australian agricultural system are mainly introduced (non-native) plant species (Cunningham *et al.*, 2002), which may lead to a lower contribution of native insects to crop pollination, compared to crops grown in their region of origin (Brown and Cunningham, 2019).

Other beneficial insects in agroecosystems

Australia further has a vast variety of non-bee insects feed on flowers, including 23% of the beetle families, and 51% of fly families, along with a high proportion of wasps (Armstrong, 1979). This includes several insects which are known to predate or parasitize agricultural pests, several of which further rely on flowering resources (hoverflies, wasps, beetles), in particular in their adult stage (Gurr *et al.*, 2003). Extensive research has highlighted that performance, fitness and population dynamics of natural enemies, can be enhanced when insects are supplied with suitable flowering resources (Landis *et al.*, 2000). Hoverflies for example rely on nectar as an energy source and pollen to complete their reproductive cycle (Mishra, 2016; Dunn *et al.*, 2020). Research within Australia has highlighted some natural pest enemies feed on certain introduced plant species (Robertson *et al.*, 2020; Tasker *et al.*, 2020), however other work further highlights the potentially important role of native vegetation in sustaining them (Gagic *et al.*, 2018; Pandey and Gurr, 2019).

1.2 AIMS OF THIS THESIS

The overarching aim of this thesis was to gather baseline data on, and new insights into, the flowering resources available in Australian horticultural systems and the types of insects they sustain. This aim encompasses both identifying the insects that are potentially contributing to the pollination of crops and examining which non-crop flowers and management approaches may be most useful for enhancing flower-feeding insect biodiversity and key ecosystem services such as pollination and pest control.

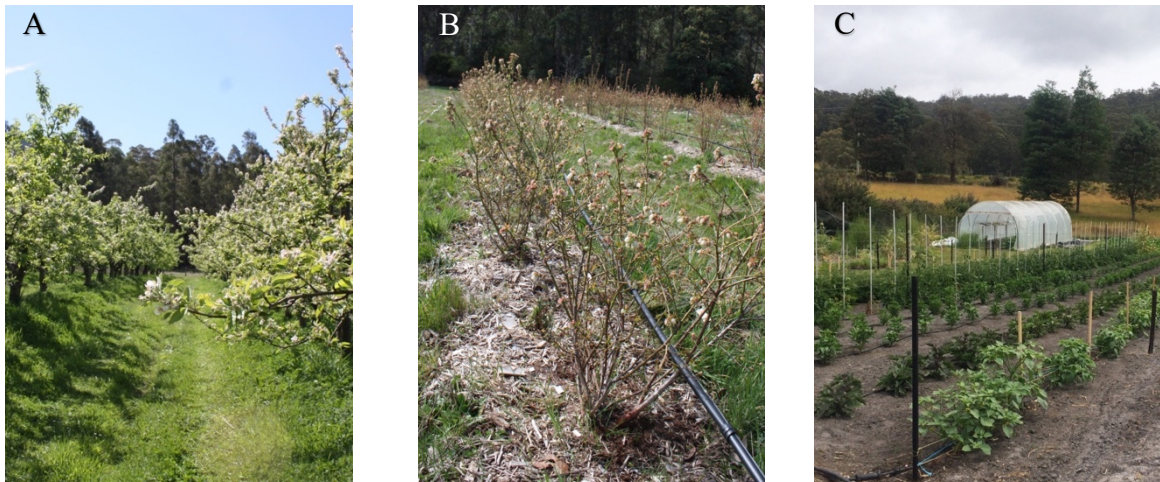


Figure 1.2 Agricultural systems examined in this study. A- Orchards, B- Blueberry, C- Market-gardens.

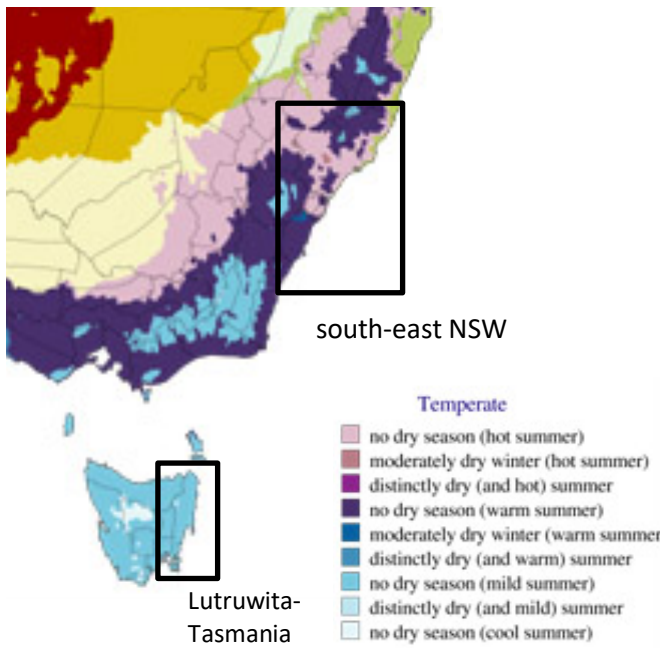


Figure 1.3 Regions of field-sites including Orchards and market-gardens in Lutruwita – Tasmania and market-gardens in south-east NSW. Map source BOM.

I focused my data collection on systems that grew insect-pollination-dependent crops, including orchards of two spring-flowering crops (apple and blueberry) in Lutruwita/Tasmania (Chapter 2); and small-scale diverse cropping systems (market-gardens) in Lutruwita/Tasmania (Chapter 3 and 5) and in South-East NSW (Chapter 4); (Figure 1.3).

Each study system offered different opportunities to study specific insect-plant interactions. The orchards were permanent agricultural systems embedded within semi-natural landscapes, with some production rows bordering directly onto remnant native vegetation. The small-scale market-gardens on the other hand offered unique opportunity to study agroecosystem which whilst offering high flower richness of several crops alongside diverse non-crop plants, consist of a plant composition with mainly introduced plant species

The different farming systems further varied in the potential management actions that can be implemented to promote beneficial insects via managing floral resources. My goal therefore was to gain an understanding of which specific flowering plants were found within each type of system and which insects they sustained, so as to then guide management recommendations for growers.

Specifically, I aimed to address the following three key questions across my study systems:

- Are crop pollination services potentially at risk because crops are mainly visited by a single pollinator species (*A. mellifera*)?
- Are introduced (non-native) plants of high value in sustaining a diverse native insect community, or do they mainly support a few highly generalist species?
- Are there key plant species that could be used to promote varied or specific ecosystem services and/or overall biodiversity?

1.3 STRUCTURE OF THIS THESIS

Each chapter of this thesis is written as a standalone manuscript. This means that there will be some repetition across chapters, especially in the discussions, background materials and methodological details. Where a chapter is referenced within another section of this thesis it will be referenced in text.

The original plan of my thesis was to focus only on flower visiting insects in Tasmanian agroecosystems, however the Covid-19 border restrictions prevented me from access to Tasmanian field sites in 2021-22. Instead, the opportunity was used to examine some of my research aims in a second location (NSW), and see if key patterns of insect-flower associations found within Tasmanian market-gardens would also be found within the type of agricultural systems in a different geographical and climatic areas. The community composition of insects differs in the two areas, with a highly abundant introduced bee (*Bombus terrestris*) found in Tasmania only, while South-East NSW has native eusocial stingless bees (*Tetragonula carbonaria*) and larger bodied native bees (e.g. *Amegilla* spp.) not found in Tasmania. Tasmania and NSW are also different climatic zones (Figure 1.2).

In **Chapter 2**, I investigate floral visitors in Tasmanian orchards to:

- (i) identify pollinating insects visiting two-spring flowering fruit crops (apple/blueberry), and
- (ii) examine if plant type (crop, non-crop introduced/native) influenced insect visitor assemblages

In **Chapter 3**, I investigate floral visitors in Tasmanian market-gardens to:

- i) examine the composition of flowering resources (crop and non-crop) within market-gardens
- (ii) examine insect-plant interactions to both crop and non-crop flowers to identify which beneficial and pest insects were visiting different flowering plants found in market-gardens
- (iii) identify which plant species attracted the highest diversity of flower-feeding insects, and which plants supported more specialised insect-plant interactions.

In **Chapter 4**, I investigate floral visitors in NSW market-gardens to:

- (i) examine the richness and abundance of flowering resources found in market-gardens impacted diversity and abundance of native and introduced flower-feeding insects

along with address addressing aims from Chapter 3 in a different geographical and climatic area:

- (ii) examine if local composition of plants influences the diversity of insects, and
- (iii) examine insect-plant interactions to both crop and non-crop flowers to identify which beneficial and pest insects were visiting different flowering plants found in market-gardens
- iv) identify which plant species attracted the highest diversity of flower-feeding insects, and which plants supported more specialised insect-plant interactions.

In **Chapter 5**, I used the experimental addition of a flowering plant to market-gardens to:

- (i) determine which insects integrated a novel plant into their foraging during short-term exposure
- (ii) test if exposure to a highly attractive plant changes visitation rates to adjacent flowering crops during and after exposure
- (iii) determine if insects switched feeding between plant species

The data in this chapter was impacted by Covid-19 border restrictions.

Clarification of terms used in this thesis

Some terms that reappear throughout this thesis are worth clarifying. I use ‘introduced’ to refer to insects that were purposefully brought to, or accidentally arrived in, Australia since European colonization from 1788 onwards. Whilst all crops surveyed were also introduced, such plants are referred to simply as ‘crops’, where crops describe plants that are sold post their flowering stage (fruit, vegetables etc.). I use the term ‘non-crop’ for flowering plants that were not crops, Here, each of the chapters further has some distinct groupings of non-crop flowers which are outlined in those chapters.

It is further important to note that this thesis does not examine the service delivery of insects (pollination, pest control) instead focuses on examining floral-usage of ‘potential’ ecosystem providers (Shackelford *et al.*, 2013) which are also referred to as ‘beneficial insects’ (Hogg *et al.*, 2011).

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Chapter 2: Both native and introduced non-crop flowering plants around orchards support potential crop pollinators and other beneficial insects

2.1 ABSTRACT

Non-crop floral resources in agricultural areas play an important role in supporting crop pollinating taxa and increasing biodiversity. We studied flower-insect interactions to two spring flowering crops and accompanying non-crop flowering resources (introduced/native) in apple and blueberry orchards in southern Tasmania, Australia, to (i) identify the important crop pollinating taxa in this region, and (ii) examine if crop and non-crop introduced and native flowering plants within orchards supported different community assemblages of flower feeding insects. We found a high overall contribution to crop visitation by introduced honeybees (*A. mellifera*), which dominated visitation to apple (91% of total visits) and blueberry (76% total visits). A second introduced bee, the earth bumblebee (*B. terrestris*), made up 19% of total visits to blueberry, yet rarely visited flowering apple. Reed bees (*Exoneura*) were the most frequent native bee visitor to both apple 2.5% and blueberry 4%. Non crop flowering plants around orchards showed significantly different community assemblages of flower-feeding insects in comparison to flowering crops. These differences were shaped by high association of insects with certain vegetation types, including *A. mellifera* with flowering apple, *B. terrestris* with flowering blueberries, native reed bees (*Exoneura*) with flowering apple and natives, soil nesting halictid bees (*Lasioglossum*) with introduced and natives and hoverflies with flowering apple and introduced forbs.

2.2 INTRODUCTION

Safe-guarding insect pollinator populations is essential to agricultural production, with around one-third of all crops grown globally requiring or benefiting from insect pollination (Klein *et al.*, 2007). Global demand for crops which require pollination, particularly fruit, is also increasing globally (Aizen *et al.*, 2009; Demestihis *et al.*, 2017; Aizen *et al.*, 2019). Yet where natural ecosystems are replaced with monocultural cropping systems, there is typically a loss of insect biodiversity (Tscharntke *et al.*, 2005; Sánchez-Bayo and Wyckhuys, 2019; Harvey *et al.*, 2020). This includes a loss in pollinating insects, thereby threatening both natural ecosystems (Ollerton *et al.*, 2011) and pollination of the crop itself (Garibaldi *et al.*, 2017b).

The impacts of monoculture agriculture on pollinators include changes in individual behaviour, population dynamics and community composition of pollinators (Kremen *et al.*, 2007; Ricketts *et al.*, 2008; Joshi *et al.*, 2016; Brown *et al.*, 2022; Coates *et al.*, 2022). Key to protecting pollinator diversity and securing crop pollination services is the preservation and enhancement of native vegetation. Natural vegetation offers essential floral and nesting resources to a wide variety of bees and other insects (Ricketts *et al.*, 2008; Carvalheiro *et al.*, 2010; Joshi *et al.*, 2016). For example, wild bee visitation to crops declines with distance from native vegetation (Ricketts *et al.*, 2008). Thus, patches of native vegetation provide important resource heterogeneity for pollinators in agricultural landscapes.

Floral heterogeneity in agroecosystems is also shaped by edge vegetation (plants at the edge of production areas) (Kammerer *et al.*, 2015) and ground-cover (plants underneath crop, between crop rows) (García and Minarro, 2014; Saunders *et al.*, 2015; Norfolk *et al.*, 2016). Relative to native vegetation patches, however, the effect of these other types of non-crop vegetation on pollinator diversity remains understudied (Winfree *et al.*, 2011). Association with ground-cover varies between farming practices, industry recommendations and localized settings such that plants seen as effective cover plants in some circumstances may be classified as weeds in another (Ferree and Warrington, 2003). Generally, weeds are associated with having a negative impact on agricultural production (Oerke, 2006), due to competition for soil and water resources, hosting of diseases and their invasiveness. Yet emerging studies are also highlighting that weeds deliver important ecosystem values (Petit *et al.*, 2011), including food resources to native bees (Requier *et al.*, 2015; Rollin *et al.*, 2016) and other insects (Herz *et al.*, 2019).

Assessing insect floral feeding patterns at the plant species level allows for the identification of plants species which could be retained or selected for floral plantings to enhance crop pollination along with overall biodiversity services (Sutter *et al.*, 2017). Co-flowering vegetation within orchard rows have in the past been associated with a potential competitive effect for flower-visitors with crops (Somerville, 1994), which contributed to recommendations of ‘weed-free’ ryegrass dominated or bare orchard-inter-rows (Saunders *et al.*, 2013). Yet increasing evidence is highlighting facilitative effects of co-flowering vegetation within and on the edge of production areas (Klein *et al.*, 2007; Simba *et al.*, 2018), by increasing abundance and diversity of visitors (Norfolk *et al.*, 2016; Alomar *et al.*, 2018; Samnegård *et al.*, 2019), and having neutral or positive impact on managed honeybees (Földesi *et al.*, 2016). Non-crop flowering resources during and outside of crop bloom have further been linked with having a critical role for their conservation value, by sustaining insects not active during, or not attracted to, flowering crops (Mandelik and Roll, 2009; García and Minarro, 2014; Gilpin *et al.*, 2022b).

In this study, we investigated the visitation profiles of flower feeding insects to different vegetation types (crops and non-crops) in an agricultural setting in Tasmania, Australia. We examined two main questions *i) which potential pollinating insects visited flowering crops?*, and *ii) does plant type (crop, introduced, native) influence insect visitor assemblages?*

We focused on insect visitation to two economically important spring flowering orchard crops (apple – *Malus domestica* and blueberry – *Vaccinium corybosum*) and non-crop vegetation found within (ground-cover, orchard rows) and adjacent to production areas (edge-vegetation). Apple and blueberry are both widely grown fruit crops around the world, whose insect visitors have been well-documented. In northern America and northern Europe, both honeybees (*A. mellifera*) and non-apis pollinators (mainly native bees and hoverflies) are equally important to apple pollination (Pardo and Borges, 2020). Similarly, native bees have been found to be important to blueberry pollination in northern America (Jones *et al.*, 2014). In contrast, current evidence from southern Australia indicates that the introduced honeybee (*A. mellifera*), substantially dominates the visitation to apple and blueberries in Victoria (Brown *et al.*, 2020) and to apple in Tasmania (Prendergast *et al.*, 2021).

2.3 METHODS

Field sites and focal crops

This study was conducted on the traditional land of the Mouheneener, Mellukerdee and Lyluequonny people in south-east Lutruwita/Tasmania, Australia. Tasmania has a temperate oceanic climate (Cfb Koeppen climate classification), with an average annual rainfall of 730mm and an average temperature during the month of orchard bloom period (October, spring) of 17-19 deg. C. (Australian Bureau of Meteorology, 2021). The vegetation communities found in south-east Tasmania are mainly dry and wet eucalyptus forest, alongside agricultural, urban and introduced vegetation. Tasmania has two introduced bees, *A. mellifera*, which was introduced to Australia from the 1830s onwards (Hopkins 1886) and *Bombus terrestris*, which was accidentally or illegally introduced to Tasmania from New Zealand in the early 1990s (Semmens *et al.*, 1993; Buttermore, 1997; Schmid-Hempel *et al.*, 2007). Tasmania further has around 120 species of native bee (Hingston, 1999), all of which are solitary or non-eusocial (e.g. subsocial) (Armstrong, 1979; Houston, 2018) together with various other native flower-feeding insects (i.e. beetles, butterflies, waps) (Hingston and Mc Quillan, 2000).

We assessed floral visitors at 11 orchards (Table S2.1, Map Fig. S2.1) which were nearly exclusively managed organically (with the exception of one apple farm with conventional management). This included six orchards (4-70ha in size, detail Supplementary material Table S2.1) growing apple (*Malus domestica*; variety surveyed ‘Gala’) and five orchards (0.2-20 ha, detail Supplementary material Table S2.1) growing high-bush blueberries (*Vaccinium corymbosum*, varieties surveyed ‘Blue rose’, ‘Brigitta’, ‘Denise’).

Apple originated in central Asia and belongs to the Rosaceae family. Apple trees have flat or shallow cup-shaped flowers. Most apple cultivars, including ‘gala’ are self-incompatible and require cross-pollination (Free, 1970; McGregor, 1976). The Huon Valley is one of Australia’s major apple producing areas (45 million annual gross value 2019-20 south-east Tasmania, Hort Innovation, 2018), with Tasmanian apple production making up 9% of Australia’s total apple production (Hort Innovation, 2018).

Highbush blueberry (*Vaccinium corymbosum*,) originated in North America and belongs to the Ericaceae family. The flowers are bell-shaped and self-fertile yet cross pollination has been found to increase fruit set and leads to larger berries with more seeds (Jones *et al.*, 2014). Insect pollination

requires sonication (buzz pollination) for sufficient pollen release (Javorek *et al.*, 2002). Blueberries in Tasmania makes up 7% of blueberry production in Australia and allows for an extended growing period outside the major mainland production areas in NSW (Hort Innovation, 2018).

One apple and two blueberry farms had *A. mellifera* hives delivered to them during crop bloom and one blueberry farm had their own *A. mellifera* hives kept permanently on their farm.

The non-crop vegetation communities at our study sites consisted of accidental introduced vegetation (introduced to Australia), along with some orchards bordering onto remnant vegetation in which mainly native shrubs and trees were flowering. Plants were identified to species level using (Howells, 2012; Richardson *et al.*, 2016).

Floral visitation surveys

We collected data on insect visitation to both crop and non-crop flowers during bloom (Spring; October) and post-bloom (Summer; December) in each of two years 2018-2019. We defined floral visitation as an insect touching the reproductive parts of a flower for nectar feeding and/or pollen collection.

i) Which potential pollinating insects visited flowering crops?

To maximise the sampling of flowering crop we used standardized sampling protocols (transect sampling) based on existing protocols tailored to each crop type (Kendall *et al.*, 2020). In apple orchards, we surveyed insect visitation to fifteen trees in a randomly chosen row, with each tree surveyed for 1 min twice per day (9:00-10:00, 15:00-16:00). In blueberry, we surveyed a randomly chosen transect row for 50 meters by walking along it slowly for approximately 10 mins, three times per day (10:00, 12:00, 14:00).

ii) Does plant type (crop, introduced, native) influence insect visitor assemblages?

Flower-insect interactions at both flowering crops and non-crop flowering plants in orchards were assessed in circular sampling plots of 50m radius. Each sampling plot comprised of half flowering fruit-tree rows and half adjacent non-crop vegetation (Fig. 2.1).

Sampling plots were chosen to represent floristic composition around orchards, and when possible included areas with flowering native vegetation and/or flower patches. Three larger apple orchards had

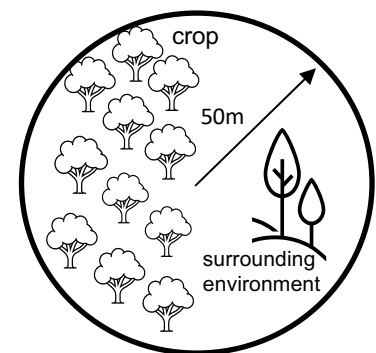


Figure 2.1 schematic representation of 50m radius circular sampling areas in each orchard. Half rows of flowering fruit trees half adjacent vegetation

two sampling areas to capture varied non-crop vegetation types (introduced/native) found within farms, whilst smaller orchards, or those with homogeneity of adjacent vegetation types, had one sampling area (see Table S2.1 for site descriptions).

Within each sampling plot we then used timed observations to observe visitation frequency to individual plant species. A small patch or area (~0.7m²) of a single plant species was monitored for 5-min at a randomly chosen location (using random number calculator from the total number of patches, tree or rows) within the sampling area. Flowering fruit trees were surveyed at four different randomly chosen trees, each non-crop flowering plant species was surveyed at two different patches or trees, unless only occurring once (one tree or patch). Plant species that only occurred in a very small patches (less than 0.2m²) were excluded. We chose timed observation of each plant species, rather than transect walks, so as to have the same amount of sampling effort per plant species.

Identification of flower-visitors

During survey observations, bees were identified to one of the following morphospecies: (1) honeybee (*Apis mellifera*: Apidae), (2) bumblebee (*Bombus terrestris*: Apidae), (3) reed bee (Exoneura, sub-genus Exoneura: Apidae), (4) Lasioglossum brown-red (Lasioglossum, sub-genus Paraphcodes: Halictidae), (5) other native bees. White banded Lasioglossum (6) (Lasioglossum sub-genus Chilactis: Halictidae) were separated into two sizes in the field, larger white banded lasioglossum and smaller white banded Lasioglossum.

Flies were identified to morphospecies as: (1) slim syrphids (genus Melangyna and Simosyrphus), (2) drone flies – *Eristalis tenax*, (2) house or bushflies (Muscidae) and (3) ‘other flies’. All other flower-feeding insects were identified to the lowest taxonomic level possible. Very small flies (<1mm) were not recorded.

To further identify native bees to species we collected at-least one individual per bee morphospecies per site. Bees were collected whilst feeding on flowers using a 120ml specimen container. Bees were then identified with dissection microscope to lowest taxonomic level possible using references keys (Walker, 1986; Walker, 1995; Smith, 2018), electronic data-base of Australian Pollinators (PaDIL) and further cross-referenced with taxonomist Michael Batley from the Sydney Museum. As the taxonomy of Tasmanian Exoneura is currently not resolved, identification was only possible to sub-genus for this group (Brown *et al.*, 2020, personal communication M. Batley).

Data analysis

i) which potential pollinating insects visited flowering crops?

To determine which insects are likely important pollinators for apple and blueberry crops in our study area, we calculated total visitation rates of each insect taxa using data collected during transect walks. Insect visitation does not equate to successful crop pollination in all cases, but visitation rates by major pollinating taxa (bees, hoverflies) is a typically a suitable proxy (Garibaldi *et al.*, 2013a; Fijen and Kleijn, 2017).

Next, we calculated pollinator richness and Shannon index using (R package, “vegan”) for each crop type (apple, blueberry), to allow comparison we used data collected during 50m plot sampling and not transect sampling to allow comparison. We ran analysis of variance model (ANOVA) to test if there were significant differences in richness and diversity between the vegetation types (crop, introduced, native) with (R Package, “lme4”).

ii) does plant type (crop, introduced, native) influence insect visitor assemblages?

We again calculated pollinator richness and Shannon index this time for each of the three vegetation types – crop (apple/blueberry) non-crop (introduced and native) for each orchard type. We ran analysis of variance to test for significant variation in richness/diversity between the groups and further ran post hoc comparison using Tukey method to compare the tree vegetation types against each other.

To visualize flower-insect interactions we constructed visitation networks using bipartite interaction networks (plotting insects and plant species as a two-dimensional matrix) and adjacency matrix (plotting interactions as a matrix) (R package “bipartite”, Dormann *et al.* 2019). We constructed two networks (bloom, post-bloom) for each orchard type and combined flowering species based on broader vegetation types (introduced, native) to examine which vegetation type the visitors were associated with. We further constructed bipartite networks including all plant species to examine interactions at the plant species level. To gain insight on specific floral usage of the most dominant visitors (observed at least five times) we constructed a visitation adjacency matrix. Here we only included plant species observed at least three times per season within each orchard type.

To test if each insect taxa was more frequently feeding on particular vegetation types we used an extension of the traditional indicator value (IndVal) index (Dufrêne and Legendre, 1997) to test group associations. The Indicator value index method calculates connection among each species and group, looking for combinations with the highest association with IndVal ranging from 0 (no association) to 1

(complete association). Significance of indicator value was then tested using 999- permutation test and Sidak's correction for multiple testing (Dufrene and Legendre, 1997). We used the 'multipatt' function (R package *indicpecies*, (De Cáceres *et al.*, 2016) as this gives index of frequency of interactions both to each individual group (as in traditional IndVal index) and combination of groups (extension) (De Cáceres *et al.*, 2012) .

We then tested if there was overall variation in the community assemblages of insects between each of the vegetation types at apple and blueberry orchards (crop, native, introduced), using multivariate generalized linear model fits for abundance data (package 'mvabund', (Wang *et al.*, 2012). We established models using 'manyglm' function and tested model assumption by visually inspecting residuals. We specified negative binomial distribution in our model to account for our insect visitation data being zero-inflated count data (Warton *et al.*, 2012). We then tested the multivariate hypothesis that species varied between vegetation types using 'anova.manyglm' function and adjusted univariate P-values, using step-down resampling procedure to test the variation between each vegetation types.

To examine further if certain insect species were more likely to be found visiting a particular vegetation type, we used the 'p.uni' adjusted argument in the anova function. The 'adjusted' part of the argument refers to the resampling method used to compute p values, taking into account family-wise error rates across species, univariate 'species-by-species results use resampling-based application of Holm's step-down multiple testing procedure (Westfall and Young, 1993; Wang *et al.*, 2012).

For both multivariate generalized linear model (manyglm) and indicator species analysis (IndVAL) we only included insects (morphospecies) observed at least five times per orchard type (apple/blueberry). To determine if key plant species strongly contribute to variation between vegetation types (crops, weeds, introduced), we visually inspected visitation networks at the plant species level. Here we found that one ornamental hedge (*Hebe* spp.), found only in one blueberry orchard during one season showed substantially high visitation by *A. mellifera*. We therefore ran the multivariate glm and IndVal analysis both including and excluding this plant species to account for its possible effect on our results; we found changes only for the overall floral associations of *A. mellifera* (IndVal), (Supplementary Table S3.).

2.4 RESULTS

i) which potential pollinating insects visited flowering crops

During transect walks we, combined overall all orchards, recorded 10 different morphospecies visiting apple and 6 visiting blueberry. Both visitor richness (F:22.4, p:<0.0001) and diversity (F:4.293, p:0.04) were significantly different between the two crop types (note: data from 50m plot survey used to allow comparison between apple and blueberry data using same method).

A large majority of visitation to apple was by introduced honeybees (*A. mellifera* n=1460, 91% of visits). Visitation to blueberry was also dominated by *A. mellifera* (n=812, 76% of total visits), yet flowering blueberry also received numerous visits by invasive bumblebees (nearly exclusively spring emerging queens) *B. terrestris* (n=202, 19%). *Bombus terrestris* visitation to apple flowers, on the other hand, was very low (9 total, <1%).

Native bee visitation to both crop types was mainly by *Exoneura* which contributed similar to apple (n=37, 2.5%, with 24 occurring at a single site) and blueberry (n=39, 4%; with 33 occurring at a site). Soil nesting halictid bees showed little contribution to apple (n=10, <1%, *Lasioglossum mundulum*, *L. clelandi*, *L. sulthicum*, and *Homalictus specodoides*) and blueberry (n=7, <1%, *L. clelandi*, *L. mundulum*, *L. hilactum*). Flies showed much higher visitation to apple, slim syrphids (n=48, 3%, genus *Melangyna* and *Simosyrphus*) other flies (mainly muscidae, n=32, 2.5%), and only low visitation to blueberry, slim syrphids (n=8, <1%, genus *Melangyna* and *Simosyrphus*).

ii) does plant type (crop, introduced, native) influence insect visitor assemblages?

Apple bloom

During the crop bloom at apple orchards, we recorded 36 non-crop flowering plant species. We recorded a higher number of introduced flowering plants (28 species, 11 never visited) compared to native plant species (8 species with 5 never visited). We recorded 10 different morphospecies visiting apple, 11 on introduced and 4 on natives. Both richness and diversity were significantly different between vegetation types (F: 23.4, p:<0.0001) and diversity (F:6.7, p:0.0015), post hoc comparison using tukey method found significant differences between richness and diversity for apple-introduced (richness= t.ratio:7.9, p: <0.001, diversity= t.ratio:3.2, p:0.004) and apple-native (richness=t.ratio: 4.6, p:<0.001, diversity= t.ratio:2.7, p.value:0.02) yet no significant differences between the two non-crop vegetation types (richness= t.ratio:0.07, p:0.99, diversity= t.ratio:0.8, p.value:0.69).

Examining visitation profiles highlights that *A. mellifera* substantially dominated visitation to apple (85% of all visits), whilst non-crop vegetation types showed overall lesser dominance of visitation by only *A. mellifera* (introduced: 46%, natives, 46%; Fig. 2.2).

Insect community assemblages between vegetation types showed significant differences (GLM, Table 1.; Table 2). Pairwise comparison showed that the significant variation existed between each of the three vegetation types (anova pairwise comparison, Table 2.1). Adjusting p-values to identify which insects were contributing the most to the variation in community assemblages shows that *A. mellifera* and two native bee taxa, larger white banded *Lasioglossum* and *Exoneura*, all significantly contributed to the variation between vegetation types. Examining the bipartite graph and indicator species analysis (Table 2) shows that *A. mellifera* and *Exoneura* were most highly (Fig. 2.2) and significantly (IndVal, Table 2) associated with flowering apple during bloom, whilst larger white banded *Lasioglossum* were significantly associated with non-crop native and introduced flowers (Table 2.2). Slim syrphid showed a significant association with crop and introduced flowers (Table 2.2).

Apple post-bloom

During post-bloom at apple orchards, we recorded 27 non-crop flowering species dominated by introduced (19 species, 6 never visited) with fewer natives (8 species, 3 never visited). We recorded 18 different morphospecies visiting introduced flowering plants and 14 different insects on natives. There were significant differences in richness between introduced and natives (F:22.4, p:>0.0001), yet non sign differences in diversity (F:3.1, p:0.076). *Apis mellifera* were not found to dominate visitation to either introduced (33%) or native (15%) flowering plants, instead high contribution by slim syrphids to introduced (33%) and native (40%) plants (Fig. 2.2.) and *Exoneura* to native plants (24%) (Fig. 2.2)

There was a significant difference in community assemblages between non-crop introduced and native flowering plants post-bloom (GLM, p=0.026), adjusting p-values found no significant contribution of a particular insects (Table 2.1.). Indicator species analysis on the other hand showed a significant association of *Exoneura* and larger white banded *Lasioglossum* visiting native flowers post bloom (Table 2.2).

Blueberry bloom

At blueberry orchards during bloom, we recorded 30 non-crop flowering species with more native plants (21 with 5 never visited) and fewer introduced plant species (9 species, 3 never visited).

We recorded 6 different morphospecies visiting blueberry, 5 visiting introduced and 14 visiting native flowering plants. No significant differences in richness and diversity were found between vegetation types at blueberry orchards during bloom (richness= F:1.3, p:0.27, diversity:1.602, p:0.205).

Flowering blueberry flowers received most visits by *A. mellifera* (58%) and further by *B. terrestris* (16%) (Fig.3). Visitation to non-crop introduced flowers on the other hand was highly dominated by *A. mellifera* (91%), whilst native flowers received high visits by *A. mellifera* (39%) along with native bees, *Exoneura* (30%) and *Lasioglossum* (15%) (Fig. 2.2).

Consistent with our findings in apple orchards, the multivariate generalised linear model found significant variation in insect visitation assemblages between blueberry and non-crop vegetation. Pairwise comparison showed that the significant variation existed again between each of the three vegetation types (anova pairwise comparison, Table 1). Adjusting p-values to identify which insects contributed the most to variation in the model shows that *B. terrestris* and *Exoneura* significantly contributed to the variation in community assemblages between vegetation types. Examining bipartite graph and indicator species analysis highlight that *B. terrestris* were most strongly (Fig. 2.2) and significantly (Table 2.2) associated with visiting blueberry flowers and *Exoneura* were most strongly and significantly associated with native flowers.

Table 2.1. Analysis of deviance for multivariate glm (anova.manyglm) results comparing crop (apple, blueberry) and non-crop vegetation types (introduced, native).

Test	Res.Df	Df. diff	dev	Pr(>Dev)	p.adjusted (i.)
Apple bloom					
visitors ~ vegetation type apple, introduced, native	321	2	213.8	0.001***	<i>A.mellifera</i> - 134.55dev, 0.01 Pr(>Dev)*** <i>Exoneura</i> - 41.464, 0.001*** <i>Lasio. larger</i> - 21.813, 0.001***
pairwise comparison: apple vs. introduced apple vs. native introduced vs. native				0.001*** 0.001*** 0.043*	
Apple post bloom					
visitors ~ vegetation type introduced, native	162	1	17.93	0.026*	all p>0.05
Blueberry bloom					
visitors ~ vegetation type blueberry, introduced, native	132	2	53.23	0.002**	<i>B.terrestris</i> -15.721dev,0.006 Pr(>Dev)** <i>Exoneura</i> - 12.839, 0.014*
pairwise comparison: blueberry vs. introduced blueberry vs. native blueberry vs. native				0.007** 0.031* 0.083*	
Blueberry post bloom					
visitors ~ vegetation type introduced, native	70	1	14.7	0.265	all p>0.05

Note: Only significant values are shown ***p≥0.001, **p≥0.01, *≥0.05.

i. univariate p values adjusted for multiple testing, using step-down resampling procedure

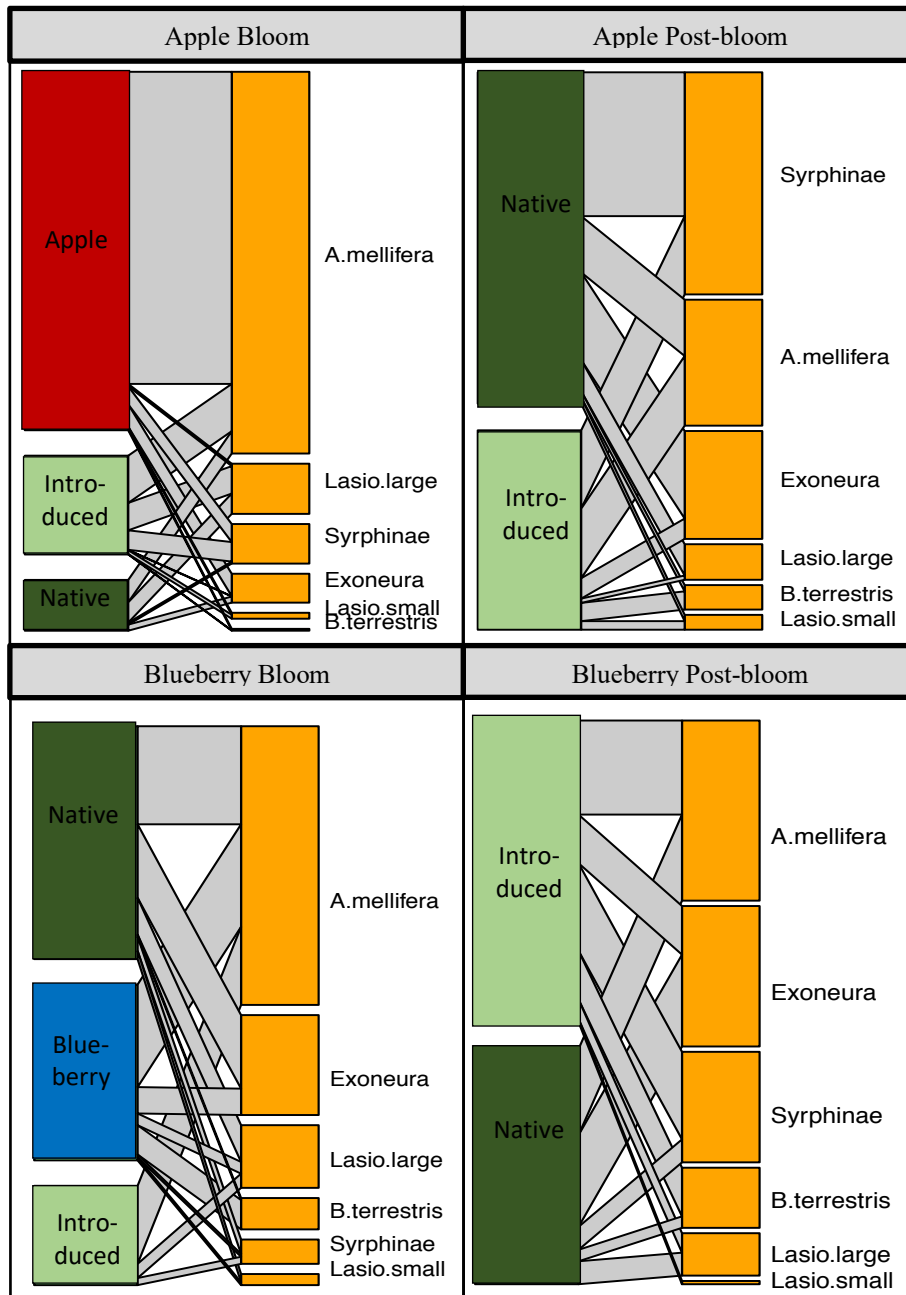


Figure 2.2 bipartite-NW of abundance each visiting taxa on vegetation type, higher bar width representing higher interaction frequency. For each vegetation type the mean value of all plant species within vegetation type was calculated for each crop type (apple, blueberry), during and post-bloom.

Blueberry post bloom

At blueberry orchards post-bloom, we recorded 22 non-crop flowering species: introduced (11 species, 5 never visited) and natives (11 species, 3 never visited). We recorded 13 different morphospecies visiting introduced flowering plants and 12 visiting natives.

Richness and diversity between introduced and native flowers at blueberry orchards post-bloom were not significantly different (richness: $F:0.57$, $p:0.45$, diversity= $F:1.1$, $p:0.29$). Visitation to non-crop vegetation post-bloom showed no distinct domination by one species. Introduced forbs were overall equally visited by *A. mellifera* (30%), and slim syrphids (30%) and native flowers similar visits by *A. mellifera* (40%) and *Exoneura* (35%) (Fig.2.2).

Multivariate models showed no significant differences in insect visitation assemblages between introduced and native flowers post-bloom. The indicator species analysis on the other hand showed a significant association between slim syrphids and introduced flowers (Fig. 2.2).

Table 2.2. Indicator species analysis (IndVal) of floral group associations between each crop type (apple - bloom/post-bloom, blueberry - bloom/post-bloom) and insect morphospecies.

	Apple		Blueberry	
	bloom	post-bloom	bloom	post-bloom
<i>A. mellifera</i>	apple IndVal=0.673, $p=0.001$ ***			
<i>B. terrestris</i>			blueberry IndVal=0.34, $p=0.0018$ **	
<i>Exoneura</i>	apple IndVal=0.248, $p=0.0005$ ***	native IndVal=0.196, $p=0.0193$ *	native IndVal=0.22, $p=0.0371$ *	
<i>Lasioglossum</i>	introduced and native IndVal=0.162, $p=0.0229$ *	native IndVal=0.235, $p=0.0092$ **		
<i>Syrphids</i>	introduced and apple IndVal=0.187, $p=0.016$ *			introduced IndVal=0.261, $p=0.0337$ *

Note: Only significant results included *** $p \geq 0.001$, ** $p \geq 0.01$, * $p \geq 0.05$. Note: This table shows results excluding single, to *A. mellifera* highly attractive plant species (*Hebe* sp.) see supplementary Table S3. for results including *Hebe* sp.

Insect plant interactions at the plant species level

Introduced bees

Examining floral feeding at the plant species level highlights that whilst *A. mellifera* showed high visitation to apple they were also found foraging on a variety of introduced forbs and native shrubs both during and post-bloom. *B. terrestris* queens, which were active during spring, were primarily found foraging on blueberry flowers. *B. terrestris* queens were also found visiting one native shrub (*Melaleuca squarrosa*), which was flowering at two blueberry orchards. During warmer post-bloom sampling *B. terrestris* workers were found on number of introduced and some native plant species (Fig.2.3).

Commonly encountered native insects

Larger *Lasioglossum* visited a variety of introduced forbs and some native shrubs both during and post-bloom, with greatest visitation to wild mustard (*Brassica rapa*). Smaller *Lasioglossum* were mainly found foraging on different introduced forbs and some native shrubs both during and post bloom at both orchard types. Native reed bees (*Exoneura*), which were found visiting both orchard crops surveyed (apple/blueberry), were otherwise mainly observed visiting native shrubs during bloom. Post bloom *Exoneura* were found again visiting native shrubs along with high visits to introduced blackberry bushes (*Rubus fruticosus* agg.), which were only flowering during the post-bloom survey. Slim syrphids were found visiting a variety of plants, with high visitation to several introduced forbs and some native shrubs (Fig. 2.3).

Other less commonly observed insects

A small number of insects including native bees belonging to the genera *Megachile*, *Trichocolletes*, *Leioproctus*, *Euryglossinae* (mainly males) were only observed during post-bloom surveys visiting native shrubs and introduced blackberry bushes (Table S2.3). Further a small number other halictid bees (*Homalictus specoides*) both during bloom and post-bloom found visiting both introduced forbs and native shrub (Table S2.3). A small number of other flies (*Muscoidae*, unidentified taxa) were also recorded visiting several introduced and some native flowering plants (Table S2.3). Along with 10 different genera of beetle feeding on varied non-crop introduced forbs, blackberry bushes and native shrubs and three different wasps again on blackberry bushes and native shrubs (Table S2.3).

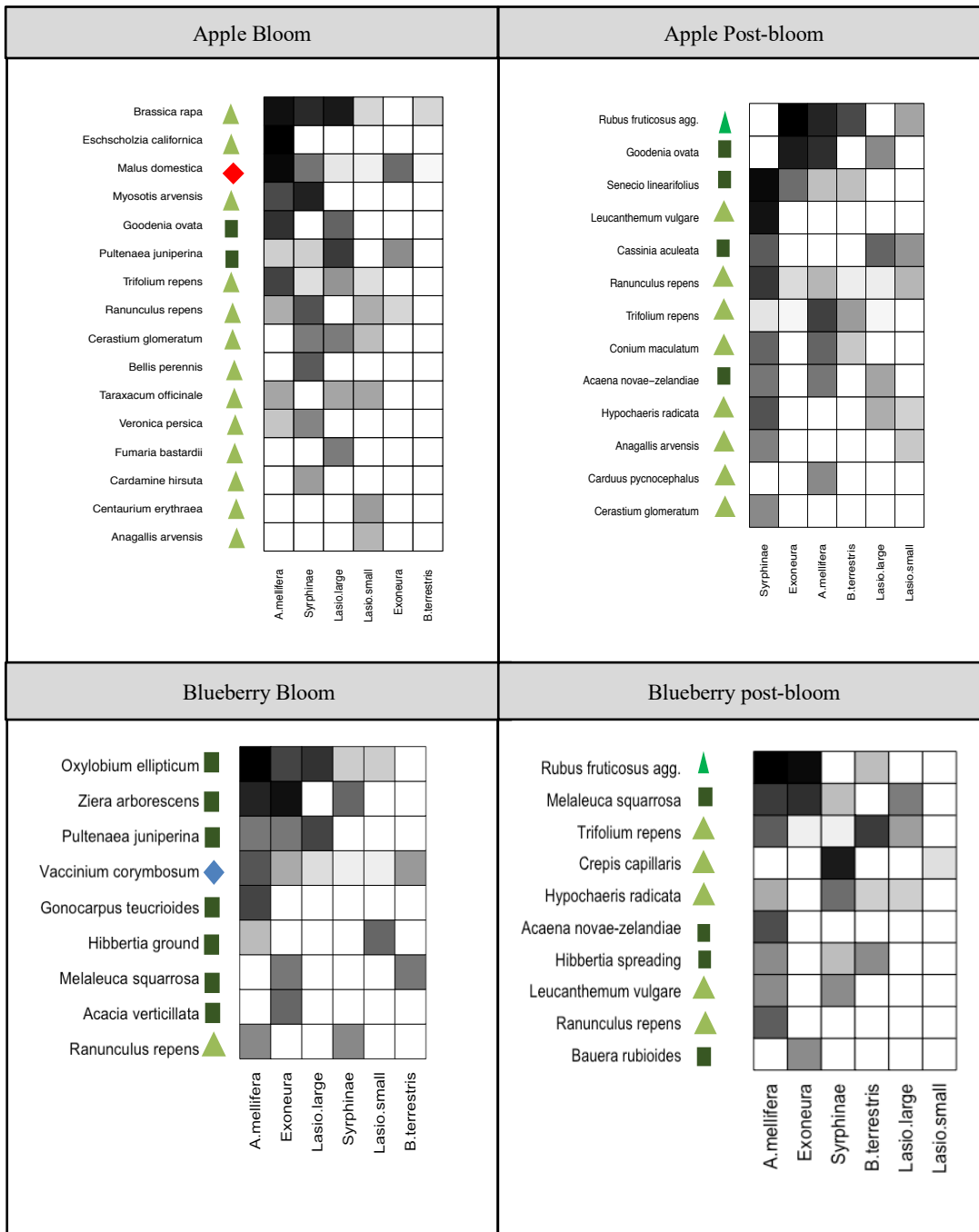


Figure 2.3. Visitation matrix with each cell showing interaction insect-plant species, darker colouring indicating higher visitation rates, matrix sorted by row/column(sum). Note= only plant spp. recorded at-least 3 times per orchard type/blooming-period included. ◆apple, ◆blueberry ▲ introduced forbs, ▲ introduced shrub, ■ natives.

2.5 DISCUSSION

Our study assessed visitation of flower-feeding insects to two spring flowering crops (apple and blueberries) and non-crop introduced and native floral resources in southern Tasmania. Our results show i) a high contribution of *A. mellifera* to both flowering crops and *B. terrestris* to blueberries only ii) an overall low contribution of other insects to crop visitation, with native reed bees (*Exoneura*) the most frequent visitor to both apple and blueberry flowers (apple 2.5% , blueberry 4% total visitation) and that iii) non-crop flowering plants during bloom and post-bloom were used as food sources by both the dominant crop pollinators and other insects, though with some discrete differences in floral association of agriculturally important taxa.

Introduced bees dominate visitation to apple and blueberry flowers

Our study adds to the growing evidence that in cooler southern regions of Australia, introduced honeybees (*A. mellifera*), dominate visitation to spring-flowering fruit trees (Goodman and Clayton-Greene, 1988; Brown *et al.*, 2020; Prendergast *et al.*, 2021; Bernauer *et al.*, 2022). We found *A. mellifera* to be the most frequent visitor to both apple and blueberry in southern Tasmania, yet with notably higher visitation of this taxa to apple flowers. In our study, only one apple grower had rented hives on their farm highlighting that the high presence of *A. mellifera* in the surveyed apple orchards was mainly from feral or managed hives on adjacent properties (Bernauer *et al.*, 2022). Visitation by the invasive bumblebee (*B. terrestris*), on the other hand, was much greater to blueberries than to apple. As with our data collected in southern Tasmania high visitation of primarily *B. terrestris* queens, as was also reported in related study conducted in Tasmanian (Kendall *et al.*, 2020). It has been documented elsewhere that *A. mellifera* forage on, but do not prefer blueberry flowers (Macfarlane, 1992; Batra, 1996), and that bumblebees are highly attracted to Ericacea pollen (Martins *et al.*, 2018). Worldwide *A. mellifera* contribute substantially to the pollination of most pollinator-dependent crops, often alongside other generalist-foraging social bee species, including *B. terrestris*, whilst the contribution of solitary native bees to crop pollination is understudied and undervalued (Klein *et al.*, 2007; Klein *et al.*, 2018).

Native reed bees potentially important crop pollinators

Currently Australia has not experienced a sharp decline of *A. mellifera* populations as observed in most other parts around the world (Lentini *et al.*, 2012; Garibaldi *et al.*, 2013b; Gemmill-Herren, 2016; Garibaldi *et al.*, 2017). Yet the introduction of severe Apis pests and diseases (i.e. Varroa mite), made more alarming due to the 2022 varroa incursion in NSW (DPI, 2022) could lead to a rapid decline of populations as seen in many other parts of the world (Cunningham *et al.*, 2002; Lentini *et al.*, 2012).

Hence, to safe-guard pollination security into the future, it would be cautious to support alternative non-apis flower visiting insects in Australian landscapes (Cunningham *et al.*, 2002; Bernauer *et al.*, 2022).

Our study found that the most common native insects foraging on both fruit trees were reed bees (*Exoneura* spp.), while hoverflies (syrphids) were abundant on apple only. These results are consistent with results from other studies in cooler south-east Australia, finding *Exoneura* to be among the most abundant native bee visitors to flowering fruit trees (Tasmania apple – Prendergast *et al.*, 2020; Victoria apple/blueberry - Brown *et al.*, 2020). Visitation of *Exoneura* was found to be slightly greater in our study, in particular at one site, compared to studies conducted in NSW, where *Exoneura* was more infrequent visitor (Bernauer *et al.*, 2022). Higher visits by *Exoneura* in Tasmania compared to NSW likely shaped by taxa being most prominent in southern parts of Australia, including Victoria and Tasmania. (Michener, 1965; Schwarz, 1986). Other commonly observed native bees during our surveys, *Lasioglossum* spp., were more infrequent visitors to apple and blueberry in our, and other studies (Prendergast *et al.*, 2021b; Brown *et al.*, 2022; Gilpin *et al.*, 2022a). Syrphids being frequently observed visiting apple flowers has also been reported in study from NSW, Australia (Robertson *et al.*, 2020) and outside of Australia (Pardo and Borges, 2020). However, as a study from the UK highlights hoverflies (genus *Episyrphus*) are less efficient compared to bumblebees and solitary bees in the pollination of apple (Garratt *et al.*, 2016).

A recent meta-analysis highlighted that several non-apis bees were more effective crop pollinators compared to honeybees, during single visit measurement, including studies examining apple and blueberry (Page *et al.*, 2021). Work by Bernauer *et al.*, 2022 in NSW, Australia, revealed that native bees in the genera *Exoneura* and *Lasioglossum* were more efficient at depositing pollen on apple flower stigmas compared to in NSW occurring social bees (*A. mellifera*, stingless bees - *Tetragonula carbonaria*). However, in Bernauer *et al.* 2022 overall visitation of *Lasioglossum* and *Exoneura* was lower than what was found in our study (>1% total visits), as in our study the visitation profile to apple was also dominated by social bees. It remains critical to highlight that even if solitary bees are at times more efficient crop pollinators, their low abundance, in particular in comparison to social bees, limits their overall contribution to crop pollination (Page *et al.*, 2021; Bernauer *et al.*, 2022). *Exoneura* being more prominent in southern parts of Australia (Michener, 1965; Schwarz, 1986), could make this taxa more suitable to enhance pollination of apple and blueberry when grown in Victoria and Tasmania compared to areas where *Exoneura* is less abundant. Both contribution of native bees along with their economic impact to crop pollination (Garratt *et al.*, 2016) is yet to be determined in many regional contexts, including south-east Australia.

Providing alternative floral resources

To support crop pollinating and other beneficial floral feeding insects, it is essential to prolong and diversify the availability of floral resources outside of short-term flowering of crops (Carvalho *et al.*, 2011; Holzschuh *et al.*, 2012). Non-crop flowering plants can facilitate crop pollination, by increasing visitation abundance and richness, via attracting insects into an area (Molina-Montenegro *et al.*, 2008). Along with adding nutritional values to insects (Woodard and Jha, 2017). Yet for facilitation to occur the non-crop foraging resources need to share visitors with those of flowering crops (Sardiñas and Kremen, 2015).

Observations from non-crop floral usage in our study highlights that whilst both introduced and native vegetation around orchards were included in the diet of several insects also found visiting crops, there were some notable differences in the likely agriculturally important taxa each vegetation type, and certain plant species, supported.

Introduced honeybees exploit variety of non-crop flowers

Specifically, we found that *A. mellifera* foraged on a variety of introduced and native flowering plants both during and outside of fruit-tree flowering. This comes as no surprise as *A. mellifera* are well known to be ‘super-generalists’ (Geslin *et al.*, 2017), including to introduced and natives flowering crops and other plants in Australia (Goulson *et al.*, 2002; Elliott *et al.*, 2021). High floral usage of non-crop flowers within and around orchards by *A. mellifera* as further been noted in studies from NSW, Australia (apple- Gilpin *et al.*, 2022a; cherry Gilpin *et al.*, 2022b). Visitation of *A. mellifera* to non-crop flowers within and adjacent to orchards does not need to translate into a competitive effect, instead as findings from Gilpin *et al.* (2022a) outline richness in non-crop flowers can increase *A. mellifera* visits to apple flowers.

The other introduced bees in our study region, *B. terrestris* is also a highly generalist bee taxa (Acosta *et al.*, 2016). We found that queens (spring) nearly exclusively visited flowering blueberry crops, while *B. terrestris* workers, which became more active during warmer post-bloom, visited more varied flowering plants, with highest abundance on introduced forbs and blackberries. Variation of diet-breadth and foraging preferences between queens and workers of *B. terrestris* have to our knowledge not been examined, or at least not published, and our data highlights the potential of exploring this further.

Semi-natural habitat important in sustaining native crop visiting reed bees

Our data further highlights a variation in floral usage of non-crop flowers between the most common native bees in our study. We found *Lasioglossum* spp., visiting several introduced forbs, in particular wild mustard, along with native shrubs, yet infrequently feeding on surveyed crops. *Exoneura* on the other hand, which were native bees most frequently visiting both apple and blueberry crops, were otherwise mainly found visiting different native shrubs, and post bloom also weedy blackberry bushes (found in remnant forest and riparian zones). Our findings of these floral associations of *Lasioglossum* and *Exoneura* are similar as reported from Victoria, Australia (Brown *et al.*, 2022).

Based on our findings, we conclude that introduced forbs around orchards may not be particularly useful to enhance native bee visitation to apple and blueberry in our study region. We see that the high association of *Exoneura* with plants flowering in semi-natural habitats highlights the likely importance of conserving and enhancing semi-natural vegetation around orchards as a mean of sustaining particular native crop pollinators (Garibaldi *et al.*, 2011; Watson *et al.*, 2011; Martins *et al.*, 2015). Ecological plantings could be added around orchards (i.e. hedgerows, shelterbelts), or riparian areas, to enhance floral resources for *Exoneura* along with other insects. Some of the local native plants we can recommend based on our visitation data include *Goodenia ovata*, *Melaleuca squarrosa*, *Oxylobium ellipticum*, *Pultenaea juniperina* and *Ziera arborescence*. Enhancing native plants around agricultural areas further plays a critical value to rarer native bees in our study region (Hingston, 1998; Hingston, 1999), including native bees with high specialisation to older plant lineages (Brown and Cunningham, 2022b).

The benefit of particular non-crop vegetation within and around agricultural production areas is however context-dependent and can vary between different landscapes and cropping systems (Sardiñas and Kremen, 2015). Findings from apple orchards in NSW, (Gilpin *et al.*, 2022a) highlight that co-flowering plant richness increased pollinator richness and *A. mellifera* abundance to apple flowers. We see that further work is needed to test the effect of flower richness on pollinator visitation to fruit trees in more southern areas of Australia, and specifically test effect of introduced v. native non-crop flowers.

It is also important to highlight that the floral association of native bees we observed in our study was potentially influenced by the availability of nesting substrates around the orchards, which can greatly influence bee community composition (Kremen *et al.*, 2004; Tschardtke *et al.*, 2005; Kremen *et al.*, 2007). Proximity to suitable nesting material can play a critical role in contribution of wild bees to crop pollination (Ricketts *et al.*, 2006), and potentially contributed to the high presence of *Exoneura* at some sites only.

Exoneura require pithy stems as nesting material, which they are not be able to attain from hardwooded fruit trees (Brown *et al.*, 2020), and instead rely on specific native vegetation (e.g., tree ferns and sedges, Schwarz, 1986) and certain introduced plants (e.g., canbeberries - blackberry, raspberry Coates *et al.*, 2022). The commonly encountered halictid bees in our study (*Lasioglossum clelandi*, *L.mundulum*) on the other hand, are known to survive and thrive in agricultural environments (Lentini *et al.*, 2012), which may arise from their adaptation to open (non-closed canopy) environments (Brown *et al.*, 2020), as found found around orchards.

We recommend further investigating proximity to semi-natural habitat along with testing the effect of installing artificial nesting material (i.e. bamboo and pithy stem bundles, Dollin *et al.*, 2016) to increase stem-nesting Exoneura abundance around orchards Tasmania and other southern parts of Australia. In the United States and Canada, the abundance of solitary leafcutter Osmia bees has been enhanced with the addition of artificial nesting boxes leading to increased pollination services to apple (Gruber *et al.*, 2011; Sheffield, 2014).

Introduced forbs sustaining hoverflies

Our data further highlights the role non-crop flowering plants, including introduced forbs around orchards play in sustaining non-bee flower-feeding insects. We found aphid-feeding syrphids (hoverflies) frequently visiting introduced forbs, with highest visits to wild mustard, yer also found frequently on some native Asteraceae herb - *Senecia linerifolis*. Hoverfly frequently feeding on introduced forbs around apple orchards overlaps with results by Robertson *et al.*, 2020 NSW, Australia).

Aphid-feeding hoverflies can play dual function in agricultural systems, with adult syrphids feeding on nectar and pollen (can contribute to crop pollination), whilst their larvae prey on soft bodied insects, including several agricultural pests (Dunn *et al.*, 2020). To support hoverflies around orchards, growers could increase availability of floral resources by adjusting mowing regimes and weed management to toleratable levels (Herz *et al.*, 2019; Robertson *et al.*, 2020). However, adopting management regimes that include introduced forbs needs to carefully identify what level of plant establishment is tolerable, taking into consideration aspects including competition for water and nutrition of plants and the spread of problematic weeds (Nicholls and Altieri, 2013), along with plants not harbouring pest and diseases. In our study we found that syrphids were the dominant visitors to some problematic agricultural weeds (*Conium maculatum*, *Leucanthem vulgare* secondary weed status), both of which are insect pollinated; hence syrphids could increase their establishment.

Our data, together with work elsewhere, highlights the importance flower diversity around orchards to sustain multiple functional groups of insects including natural pest enemies (Lucas *et al.*, 2017; Santos *et al.*, 2018; Saunders and Luck, 2018) and crop pollinators. However, in respect to floral usage of natural pest enemies in orchards, our study only offers limited detail, as smaller wasps were potentially missed during visual observations, and flies other than hoverflies were not identified to a level that allows insight into their functional group. Flowering ground-cover is likely to sustain a greater number of other natural pest enemies for which our data only gives limited insight to. A study from south-east Australia (using pan traps not visual observation) for example found positive responses of flowering ground cover (similar composition of introduced forbs) to the abundance of natural pest enemies, mainly hoverflies and wasps (Saunders and Luck, 2018), in-line with similar findings outside of Australia (Lucas *et al.*, 2017; Santos *et al.*, 2018). Taken together these studies highlight that flowering ground-cover may sustain a greater number of other natural pest enemies for which our data only gives limited insight to. Our study does however give a detailed account of varied insect groups attracted to particular flowering plants around orchards in southern Tasmania, we see that further work is now needed to measure the impact of floristic compositions around orchards on yield, measuring both effect on pollination-success (fruit-set) and pest damage (Demestihis *et al.*, 2017; Albrecht *et al.*, 2020).

2.6 CONCLUSION

The scope of our two-year study gives insight into key insect floral associations in southern Tasmanian fruit orchards, and the insect visitors to non-crop vegetation. Future research could investigate the impact of different management and floral-enhancements practices (i.e. cover-crops, native vegetation) have on production and conservation values. As this requires longer-term evaluation (Blaauw and Isaacs, 2014; Campbell *et al.*, 2017) future work on floral resource provisioning for beneficial insects would greatly benefit from a strong collaboration between growers and researchers (Lichtenberg *et al.*, 2017). In particular, our findings highlight that exploring ways to enhance native bee visitation to fruit trees (e.g. artificial nesting materials, targeted floral resource augmentation), along with examining the values of increasing floral resources for pest predators (i.e. syrphids), as key avenues to safeguard both production and biodiversity values of agricultural land (Wade *et al.*, 2008).

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2.7 REFERENCES

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Chapter 3: Examining flower-insect interactions in small-scale diverse fruit and vegetable farms (market-garden)

3.1 INTRODUCTION

Agricultural production is intrinsically linked with the ecosystem services that support it (Dale and Polasky, 2007). The management practices used in agricultural systems thus influence associated ecosystem processes (Requier *et al.*, 2015; Burkle *et al.*, 2017; Kovacs-Hostyanszki *et al.*, 2017; St Clair *et al.*, 2022). This includes both the supporting ecosystem services, such as soil structure, soil fertility, nutrient cycling and water provision, and the regulating ecosystem services, such as soil retention, pollination and pest control (Zhang *et al.*, 2007; Power, 2010). Understanding how different management practices affect ecological process and key services in agro-ecosystems is an essential element in developing agricultural practices that are both profitable and sustainable (Bommarco *et al.*, 2013; Kovacs-Hostyanszki *et al.*, 2017)

One important measure of ecosystem services in agricultural systems is the abundance and diversity of beneficial insects (Fountain, 2022), including pollinating insects and insects that are ‘natural pest enemies’ (i.e. predators or parasites of crop pests (Dale and Polasky, 2007)). Pollinating insects play an essential role for successful fruit and seed development of many of our agricultural crops (Klein *et al.*, 2007) and in the reproduction of wild plants (Ollerton *et al.*, 2011). Crop pollination services globally are predominantly delivered by managed bees (e.g. honeybees *A. mellifera*) and some wild insects (mainly bees and flies, Rader *et al.*, 2009).

Further crop productivity warrants management of varied agricultural pests, including a variety of insects and mites (Sharma *et al.*, 2017). Overreliance on chemical pesticides to manage agricultural pests can lead to resistance in insect pests along with adverse effects on beneficial insects (pollinator, natural pest enemies) and our environment (e.g., water contamination, harmful effects to wildlife) (Pimentel, 2005). Supporting naturally occurring pest enemies to limit damage from agricultural pests is therefore of key economic and ecological importance (Lewis *et al.*, 1997; Losey and Vaughan, 2006).

Both pollinators (Hicks *et al.*, 2016) and many natural pest enemies (Landis *et al.*, 2000), rely on nectar and pollen for all or part of their life-cycles. Thus the availability of flowering resources in agricultural landscapes can influence the richness and abundance of pollinating insects (Haaland *et al.*, 2011;

Kennedy *et al.*, 2013; Norfolk *et al.*, 2016; Venturini *et al.*, 2017; Guzman *et al.*, 2019) and natural pest enemies (wasps, hoverflies, predatory beetles) (Landis *et al.*, 2000; Campbell *et al.*, 2017a).

Floral availability in agricultural landscapes can be managed, increased and diversified in varied ways that in turn impact the biodiversity of beneficial insects. This includes varying the crops that are grown (e.g. monocultures versus polyculture systems), allowing the growth of agricultural weeds and other wild flowering plants within the crop, and actively adding non-crop plant diversity (e.g. planting cover-crops, wildflower strips or hedgerows) (Burkle *et al.*, 2017). Plants vary in their suitability to enhance certain taxa and functional groups of insects, as insects show variation in what flowers they choose to, or are able to, feed on (Carrié *et al.*, 2012; Howlett *et al.*, 2021). For example, previous studies examining floral use by different functional groups of flower-feeding insects (Wood *et al.*, 2015; Campbell *et al.*, 2017a; Campbell *et al.*, 2017b), found that many natural enemies (e.g. hoverflies, parasitic wasps) only feed on open flowers, a flower-shape that requires no highly specialized floral feeding mouthparts (Landis *et al.*, 2000; Gurr *et al.*, 2003). Bees and other insects with more specialised floral feeding mouthparts (e.g. suctorial proboscides), are able to feed on flowers with more hidden nectaries (e.g. fabaceae) (Campbell *et al.*, 2017b). In these cases, the length of the bee tongue relative to flower corolla length determines accessibility (Krenn *et al.*, 2005). In addition to insect morphology, both inter and intra- guild variation in floral use has been found to be affected by a range of interacting factors (Lundin *et al.*, 2019) including floral design (colour, shape, display), chemical composition of plant and nutritional requirements of insects, localised floral abundance and availability, resource competition and partitioning between insects (Fründ *et al.*, 2010; Carvalheiro *et al.*, 2012; Carvalheiro *et al.*, 2014; Jeavons *et al.*, 2020).

To date, efforts to understand how the management of floral resources impacts the abundance and diversity of beneficial insects in agricultural landscapes has focused on large-scale cropping systems. There is currently a limited understanding, however, of how floral resources impact insect diversity in small-scale polyculture systems (Lin *et al.*, 2015; Aerts *et al.*, 2016; Garibaldi *et al.*, 2017a). Small-scale polyculture systems are still operated within many more ‘traditional’ farming systems around the world (Altieri, 2004) along with being embedded in more recently emerging alternative and urban farming movements in developed countries (Mougeot, 2000). An example of a small-scale polyculture system, which is gaining increasing popularity in Europe, North America and Australia, is the market-garden (also sometimes called microfarms) (Lin *et al.*, 2015; Morel and Léger, 2016). These are commercial production systems (>1.5ha), growing a variety of different crops (vegetable, herbs, fruit) outdoors and in tunnels, with produce sold directly to consumers via short supply chains (Morel and Léger, 2016). Farming practices associated with these emerging forms of market-gardening are inspired from alternative and traditional farming practices and philosophies, with growers typically endorsing organic and biointensive farming practises (Morell and Leger, 2016).

Market-gardens present distinct opportunities for understanding insect-flower interactions, relative to other agricultural systems. Unlike industrial farming systems, that focus on monocultural cropping regimes, market-gardens resemble more ‘traditional’ farming systems (Foley *et al.*, 2005), where a variety of different crops (polycultures) are grown on the same parcel of land. Small-scale polyculture systems offer high availability and variability of floral resources from co- and sequentially flowering crops and other plant species (Norfolk *et al.*, 2016). Market-gardens allow us to determine which insects are potentially contributing to the pollination of multiple crops grown in the same localised environment. They are further suitable to investigate whether crop diversification is an effective way to support diverse insect communities (St. Clair *et al.*, 2020; St Clair *et al.*, 2022), or if the presence of certain non-crop flowering resources is more important in sustaining insect diversity in agricultural settings (Kleijn *et al.*, 2015).

In this study, we assessed species-level interactions between flower-feeding insects and flowers in small-scale fruit and vegetable farming systems (market-gardens) in Tasmania, Australia. Examining interactions between insects and flowering plants at the plant species level can guide farming strategies aimed at either enhancing overall beneficial insect diversity, or enhancing particular ecological and agricultural functions provided by insects, via the targeted selection of certain plants (Garibaldi *et al.*, 2017b; Lundin *et al.*, 2019; Howlett *et al.*, 2021). Specifically, we aimed to identify i) what kind of crops and other plants were in flower around market-gardens during spring and summer, further to ii) examine insect-plant interactions to both crop and non-crop flowers to identify which beneficial and pest insects were visiting flowering different flowering plants found in market-gardens; and to iii) identify which plant species attracted highest diversity of flower-feeding insects, and which plants supported more specialised insect-plant interactions.

3.2 METHODS

Study sites

This study was conducted in on the lands of the lands of Mouheneener, Mellukerdee and Lyluequonny, Tommeginne, Pyemmailrener in Lutrawita - Tasmania, Australia during two sampling periods: spring (October-November 2019) and summer (January-February 2020). The climate of Tasmania is temperate oceanic climate (Cfb Koeppen climate classification) average temperate during January-February (max mean 22-24 degree °C) and October-November (max mean 17-19 degree °C) (Grove Research Station, Australian Bureau of Meterology, 2022).

The wildflower-visiting insect community in Tasmania consists of native bees, two introduced bees, and various other flower-feeding insects (beetles, wasps, flies, butterflies) (Hingston and Mc Quillan, 2000). Feral honeybees (*A. mellifera*) have been widespread across Australia (Hinson *et al.*, 2015) since their introduction from the 1830s (Hopkins, 1886) onwards for honey production and to aid in crop pollination. Feral bumblebees (*Bombus terrestris*) were either accidentally or illegally introduced from New Zealand in the early 1990s (Buttermore, 1997; Schmid-Hempel *et al.*, 2007) and are now found throughout Tasmania (Kingston *et al.*, 2002). Native flower feeding insects in Tasmania span various guilds, including around 120 native bee species (Hingston, 1998), all of which are solitary or non-eusocial (e.g. subsocial) (Armstrong, 1979; Houston, 2018). Australia further has the same groups of natural enemies as those found to be important worldwide, including wasps, beetles (carabid, coccinellid and staphylinid), lacewings and syrphid flies (Gagic *et al.*, 2018).

We assessed flower-insect interactions at 14 farms, located mainly in the Huon and Channel region (N=9), with the remaining sites in Hobart (N=1), Tasman (N=1), Coal Valley (N=1), Tamar Valley (N=1) and Cradle Mountain regions (N=1). All farms were small-scale ranging from approximately 0.1-1 hectare in size, used no synthetic fertilisers, pesticides or insecticides, and sold their produce locally to Hobart, Launceston and nearby towns via vegetable box schemes, road-side stores and restaurants. Two farms also used their produce directly in on-site restaurants. A variety of crops were grown at each farm, including salad greens, varied brassicas, cucurbits, legumes, nightshades and culinary herbs along with non-crop flowers at some farms. Weeds were managed mechanically (hand-weeding, flame-weeding), with a number of growers letting unused production spaces go fallow.

Data collection

The boundary of each market-garden was defined by fence-lines around the production areas. We first identified all plant species in flower within the market-garden, including flowering crops and non-crop plants. We then surveyed each of the flowering plant species at two randomly chosen patches or production rows. To choose patches or rows of flowering plants for surveys, we first counted the total number of patches or rows at the site that contained the plant, allocated a number to each, and then used a random number generator to select two survey locations per plant species. For crops only found in one production row or patch, we surveyed the flowering crop at opposite sides of the row or patch. For flowers that only occurred in a single location in the market-garden (e.g. a single shrub or tree) we surveyed only the one location for that species. During each survey we monitored a $\sim 0.6 \text{ m}^2$ patch of a plant species for 3 minutes. We recorded all insects visiting flowers for food in that interval, where floral visitation was defined as an insect touching the reproductive parts of a flower for nectar feeding and/or pollen collection.

All surveys occurred during 10:00 and 16:00 hr when temperatures were above 18 °C, with no high cloud cover or strong winds. Bushfires occurred in the study region in Summer 2019, but we did not sample during days of heavy smoke from bushfires.

Insect identification

We defined floral visitation as an insect touching the reproductive parts of a flower for nectar feeding and/or pollen collection. During survey observations, bees were identified to one of the following morphospecies: (1) honeybee (*Apis mellifera*: Apidae), (2) bumblebee (*Bombus terrestris*: Apidae), (3) reed bee (Exoneura, sub-genus Exoneura: Apidae), (4) Lasioglossum sub-genus Chilalictus: Halictidae). We further subdivided Lasioglossum subgenus Chiliaticus into three categories based on their sizes (small/medium/large), (5) Lasioglossum subgenus Paraphecodes: Halictidae), (6) Megachilidae, (7) 'other' native bees. To identify native bees to species we aimed to collect at-least one individual per bee morphospecies per site. Bees were collected whilst feeding on flowers using a 120ml specimen container. Bees were then identified with dissection microscope to lowest taxonomic level possible using references keys (Smith, 2018) and further cross-referenced with taxonomist Michael Batley from the Sydney Museum. As the taxonomy of Tasmanian Exoneura is currently not resolved, identification was only possible to sub-genus for this group (Brown *et al.*, 2020) personal communication M. Batley).

Flies were classified into 6 different morphospecies, slim hoverflies (Syrphinae), drone flies (*Eristalis tenax*), slim Muscoidea, other Muscoidea, bee flies (Bombyliidae), and other flies.

Other insects (eg. beetles, wasps and butterflies) were either identified to lowest taxonomic grouping (at least family) out in the field, for those insects not able to easily identifiable on wing we either took collections back to the lab or took photographs with Canon EOS 450D during surveys.

Plant group classification

We classified flowering plants monitored at market-gardens into four broad management groups.

Crops: flowering crops prior to their harvestable state, including insect-pollination dependent and independent crops. Based on literature (Free, 1970a; McGregor, 1976b; González-Pérez and Guerrero-Beltrán, 2021) crops were further classified as those that require insect-pollination for successful fruit or seed development and those that are non-insect pollinated.

Post harvest crops and culinary herbs: flowering of crops post their harvestable state that remained within market-gardens and left to go to flower, this included crops such as brassicas (e.g., broccoli, kale), root-vegetables (e.g., carrot) along with culinary herbs (e.g. basil, coriander).

Purposeful: flowering plants that were purposefully planted or sown yet of little or no direct market value, including medicinal herbs, ornamental plants, cover-crops and planted natives

Incidental: flowering plants that were not purposefully planted and a number of which can be broadly categorised as weeds in southern-Australia (Richardson *et al.*, 2016)

Data analysis

All analysis was performed in R-studio Version 1.4.1106.

To determine which insects were the most frequent visitors of flowering crops in our market-gardens, we calculated the proportion of visits per insect morphospecies to each flowering crop during each of our two sampling periods (spring and summer). To examine the overall flower-insect interactions to crop and non-crop flowering plants at market-gardens, and examine if insects showed potential preferences towards particular plant families and or species (Fründ *et al.*, 2010) we constructed visitation networks using the ‘bipartite’ package in R Studio (Dormann *et al.*, 2008). We used mean number of visits to a plant species per site and season, to account for plant species being measured twice per site. We chose the ‘visweb’ function which visualises the grid plot of the quantitative interactions between flower-feeding insects and plants. We constructed combined networks with the sum of interactions of plant families, and plant species, using data obtained from all sites and both sampling periods (spring and summer). For individual flowering plant species (N=175) we constructed networks for each insect orders separately (e.g., bees, flies, beetles, wasps, butterflies).

As there were a large number of plant species only occurring at one site (N=117 plants) we further constructed graphs that included plants found at two or more sites only (N=58 plants) this allowed us to examine plant species that offered some spatial repetition in observations.

To calculate network metrics for each plant and insect species we further constructed networks for each individual site/season including all plant species and insect morphospecies found at a site, again using mean number of visits to account for plant species measured twice per visit. We choose to use individual site networks, rather than combined networks so we can calculate unique localised metrics for each insect and plant species and examine mean values, rather than combined metrics from the sum of all sites. For each individual network we calculated network metrics for each plant and insect species using the ‘specieslevel’ function (Dormann *et al.*, 2009; Dormann, 2020). We calculated two network metrics for each insect: one metric to examine how many different plants each insect was visiting at the site (degree), and one metric to determine how many plants a given insect visited from all possible unique insect-plant interactions at a site (given in percentage; normalised degree). We then examined mean values of insect network metrics for most common insects (i.e. those with <20 observations across all sites).

For plant species we calculated three network metrics to identify key plant species within market-gardens, again using the individual site/season networks for calculations and mean number of visits to account to account for plant species measured twice per visit. This included examining how many unique visitors a plant species received (degree), determining the percentage of unique visitors a plant received from all possible interactions at a site (normalised degree), and calculating the sum of dependencies of each species (species strength) (Bascompte *et al.*, 2006). Species-strength provided a measure of how much each insect ‘depended’ on a given plant species among the set of observed plants. That is, plants with high “species-strength” values were those supporting insects in the market-garden that were never or rarely observed to feed on other plant species (Dormann, 2011). We then calculated mean values for each of the metrics and used the ‘cor’ function in the ‘hmisc’ package to examine if the each of the calculated metrics were correlated. To identify plant species with highest values of each metrics, we further ranked plant species for each network metrics separately (degree/normalised degree/species strength) for this we further only included plant species found at atleast two sites (N=58).

3.3 RESULTS

Flowering resources found at market-gardens

In total 175 flowering plant species were surveyed across all market-gardens. During spring we surveyed 67 different plant species that were in flower across all market-gardens, (9-27 spp per site) belonging to 19 plant families. During summer, flowering plant richness increased with 155 different flowering plant species recorded across all market-gardens (9-57 plant spp per site), belonging to 33 plant families.

The surveyed plant species across the four categories included: crops (N=28; 1-13 spp per site/season), post-harvest crops and culinary herbs (N=38; 1-14 spp per site/season), intentionally planted non-crops (non-native: N=50, natives: N=10; 1-20 different plant species per site/season,) and incidental plants (non-native:N=49; 2-16 spp per site/season).

The flowering crops belonged to eight plant families, with Curcubitaceae (5 spp summer only), Fabaceae (7 spp), Solanaceae (8 spp summer only) and Rosaceae (3 spp) most represented (Figure 2.). In each season, around half of all flowering crops were ones that required insect pollination for successful fruit production (spring: 4 of 6; summer: 12 of 24); (Fig.3.1).

Post harvest crops and culinary herbs belonged to 10 plant families, with Brassicaceae (10 spp), Apiaceae (5 spp) and Lamiaceae (8 spp) the most represented plant families. Personal communication with market-gardeners (Hanusch) highlighted that these were at times intentionally left within production areas to increase flower availability, for seed saving or protect soil, or accidentally left to go fallow.

The majority of purposefully planted non-crop species were not native to Australia (50 non-native plants belonging to 17 plant families; 1-17 different plant species per site/season) with Asteraceae (14 spp) and Lamiaceae (9 spp) the most represented. Only six of the fourteen market-gardeners had planted Australian natives around their production areas (10 species belonging to eight plant families; 1-3 spp per site/season), with Myrtaceae (4 spp) most represented, though only (N=6) species were native to Tasmania. Intentionally planted non-crops had no direct market-value to growers (personal communication, Hanusch), but had been included in the garden for aesthetic values or other benefits (e.g. soil enhancement, companion plants, medicinal).

Incidental plant species belonged to 17 plant families, with Asteraceae (12 spp), Brassicaceae (8 spp), Fabaceae (4 spp), and Lamiaceae (4 spp) the most represented incidental plant families. Plant species

recorded included white clover (*Trifolium repens*) which may also be seen as a beneficial, nitrogen fixing ground cover. We observed several plants that can be broadly defined as weeds in south-east Australia (Richardson *et al.*, 2016), including one declared weed (Californian thistle – *Cirsium arvense*) and two other non-declared agricultural weeds (capeweed- *Arctotheca calendula*, Scotch Thistle- *Cirsium vulgare*) (NRE, Tasmania).

Insect visitation to flowering crops

The two introduced bee species (*A. mellifera* and *B. terrestris*) were the dominant visitors to almost every flowering crop surveyed, including those that require insect pollination for successful fruit production (Fig.3.1). During spring *A. mellifera* were the most abundant visitors making up 66% of total visits to flowering crops, whilst *B. terrestris* only made up 10% of total visits. During summer, both introduced bees were similarly abundant (*A. mellifera*: 45.5% and *B. terrestris*: 48% of all visitors to flowering crops).

Two of the Fabaceae crops (broad beans – *Vicia faba*, scarlett runner beans – *Phaseolus coccineus*), which are pollinator-dependent, attracted mostly *A. mellifera* and *B. terrestris* in both spring and summer (Fig.3.1). Cucurbitacea crops, which only flowered during summer, were predominately visited by *A. mellifera* and *B. terrestris* (Fig 3.1). Smaller-flowered Cucurbitaceae (cucumber- *Cucumis sativus* and rockmelon -*Cucumis melo*) were primarily visited by *A. mellifera*, whilst larger-flowered cucurbits (pumpkin, zucchini and squash) were visited by both *A. mellifera* and *B. terrestris* equally (Fig.2). Solanaceae crops, which only flowered during summer, were more frequently visited by *B. terrestris* compared to *A. mellifera* (Fig. 3.1). High number of visits by the two introduced bees were recorded to one insect-pollinator dependent Solanaceae crop (Tomatillo - *Physalis philadelphica*) (Fig.3.1).

Fragaria x ananassa - Strawberries (Rosaceae) were the only crop for which the most abundant visitors were flies, with Syrphinae the most abundant visitors during spring (62.5% total visits) and during summer slim Muscoidea (75% total visits). *Rubus spp.* Raspberry/Boysenberry (Rosaceae) were the only crop to receive frequent visits by native bees (21 % *Exoneura sp.* reed bees, during summer only) although *A. mellifera* and *B. terrestris* were nevertheless the more common visitors to this crop (Fig.3.1).

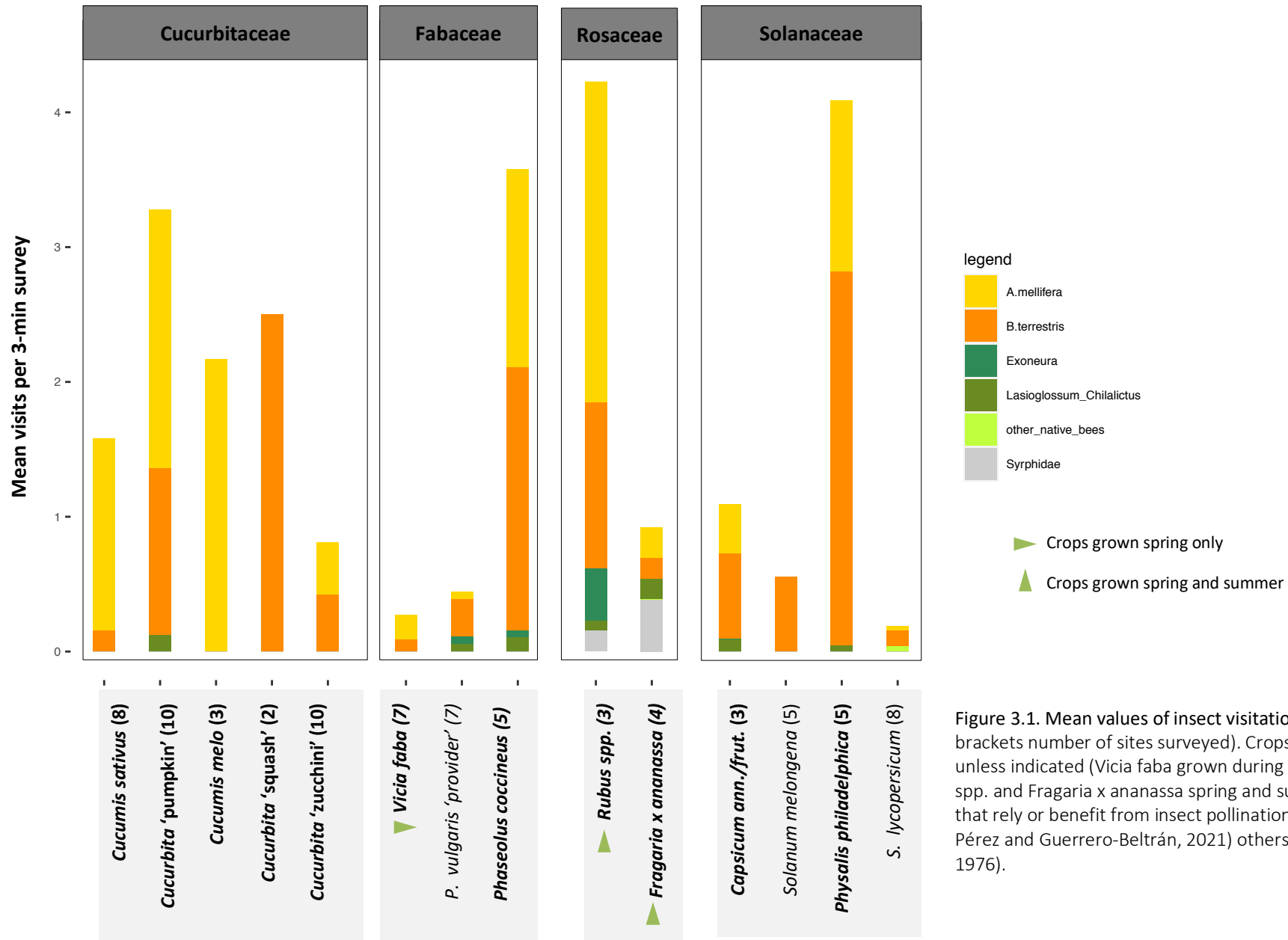


Figure 3.1. Mean values of insect visitation to flowering crops (in brackets number of sites surveyed). Crops surveyed summer only unless indicated (*Vicia faba* grown during spring only, both *Rubus spp.* and *Fragaria x ananassa* spring and summer). In bold plants that rely or benefit from insect pollination tomatillo (González-Pérez and Guerrero-Beltrán, 2021) others (Free, 1970; McGregor, 1976).

Patterns in floral usage by different insect groups

During spring, we recorded 4-9 (mean = 6) different morphospecies of insects per market-garden site, increasing to 7-25 (mean = 14) morphospecies in summer. This included 12 different morphospecies which potentially provide ecosystem services to agricultural production (Table 3.1.) and 1 agricultural pest species (Table 3.1.), and 23 other morphospecies for which no direct impact to agricultural production is known (Table 3.2.)

Potential pollinators

Introduced bees: The two most abundant visitors to crop flowers at market-gardens in our study, *A. mellifera* and *B. terrestris*, were also the most abundant flower-feeding insects at market-gardens when all flowering plants were considered (Figure 3.3.) *Apis mellifera* showed high activity in both spring (n=244, 38 % of total insect visits) and summer (n=759, 35.6 % total insect visits). *B. terrestris* (mainly workers) were found in lower frequency during spring (n=65, 10.5% total insect visits) then summer (n=567, 26.7% total insect visits). On average, *A. mellifera* and *B. terrestris* were observed visiting half of all available plants at a site (normalised degree: *A.mellifera* nd-mean per site=0.47 spring/summer and *B. terrestris* nd-mean= 0.35 spring, 0.6 summer). Both bee species showed high diet-breadth, visiting diverse plant families (Table 3.1, Fig.3.2, Fig.3.3). Certain plant families were nearly exclusively visited by introduced bees, including Boragaceae, Verbenaceae (mainly *B. terrestris*), along with the plant families which had several flowering crops (Curcubitaceae and Solanaceae; the later mainly visited by *B. terrestris*) (Fig.3.2).

Native bees: The two most commonly observed native bee genera, *Lasioglossum* and *Exoneura* showed low visitation frequency to crops in our study (Table 3.1).

We found Halictid bees in the genus *Lasioglossum* (subgenus *Chilalictus*) to be the most frequently observed native bees recorded in our study, making up nearly all native bee visits during spring (96%) and a large proportion (59.4 %) during summer. *Lasioglossum* visited a variety of plant species (Table 3.1., Fig. 3.2), with high abundance recorded on different Brassicaceae and Asteraceae (Fig. 3.3).

We classified *Lasioglossum* visits into three sized-based morphospecies, but subsequent inspection of collected specimens indicated that only our “small” size group was likely to represent a single species (*L. mundulum*; based on n= 23 spring, n= 43 summer specimens).

While our “medium” and “large” morphospecies groups each comprised several distinct species (medium-size: *L. clelandi* 86% of collected specimens, *L. sculperatum* 7%, *L. litovillum* 7%; n=28 spring, n=90 summer, and large-sized *L. brazieri* 55% of specimens, *L. repraesentans* 27%, *L. tamburinei* 18%; n=6 spring, n=22 summer; Table A1). As we only collected one individual of each morphospecies per site direct insight on foraging of each species could not be made instead floral associations based on morphospecies. On average *Lasioglossum* visited around 25% of available flowering plants at a site: medium *L.*(*Chilalictus*) (nd-mean= 0.24 spring, 0.22 summer), small *L.*(*chilalictus*) (nd-mean= 0.29 spring, 0.22 summer), large *L.*(*Chilalictus*) (nd-mean= 0.25 spring, 0.1 summer).

The second most abundant native bees were reed bees, *Exoneura* spp., which were active mainly during summer only, were they were found at around half of all market-gardens (Table 3.1.) (spring: N=1, summer: N=83 though 46 observations were recorded at a single site post-fire). *Exoneura* were found visiting several different plants and plant families (Table 3.1., Fig.3.2, Fig.3.3). Most frequently visited plant families during summer includeing Brassiceae (*B. oleraceae* (white), *Capsella bursa-pastoris*, *Diplotaxis tenuifolia*), Asteraceae (mainly *Cirsium arvense*, single site with high abundance of *Exoneura*), Lamiaceae (*Ocimum basilicum*, *Origanum vulgare*, *Thymus vulgaris*) (Fig. 3.2, Fig. 3.3). On average *Exoneura* visited 17% of available flowering plants at a site (normalised degree mean= 0.17 summer).

Drone hoverflies: Drone flies can be important to agricultural production, yet mainly found to aid in seed crop pollination (Table 1), and were not found visiting any of the flowering crops in our study. All drone flies recorded in our study belonged to one species *Eristalis tenax* and showed higher activity in summer (n=61, 21.2% total fly visits) compared to spring (n=11 spring, 3.5% total fly visits). *E. tenax* were also found visiting several different plants and plant families (Table 3.1., Fig. 3.2, Fig.3.3), with high visitation recorded to post harvest crops (*Brassica rapa mizuna*, *Diplotaxis tenuifolia*) and, incidental wild mustart (*B.rapa silv*) in the Brassicaceae family, and one weedy Asteraceae (*Cirsium arvense*, subfamily Carduoideae) along with several post-harvest crops and culinary herbs in the Apiaceae family (Fig.4) and some Lamiaceae (*O. vulgare*, *T. vulgaris*). On average *E. tenax* visited less than one quarter of plant species per site (nd-mean= 0.31 spring, 0.16 summer).

Beetle: Scarab beetles (*Phyllotocus rufipennis*) have been found to be effective pollinators of carrot seed in Tasmania (Gaffney *et al.*, 2018) and were the most active beetles during summer in our study (*Phyllotocus rufipennis*, n=48 summer). They were only found on a very small number of plants (nd-mean= 0.07), and mainly found feeding on Apiaceae.

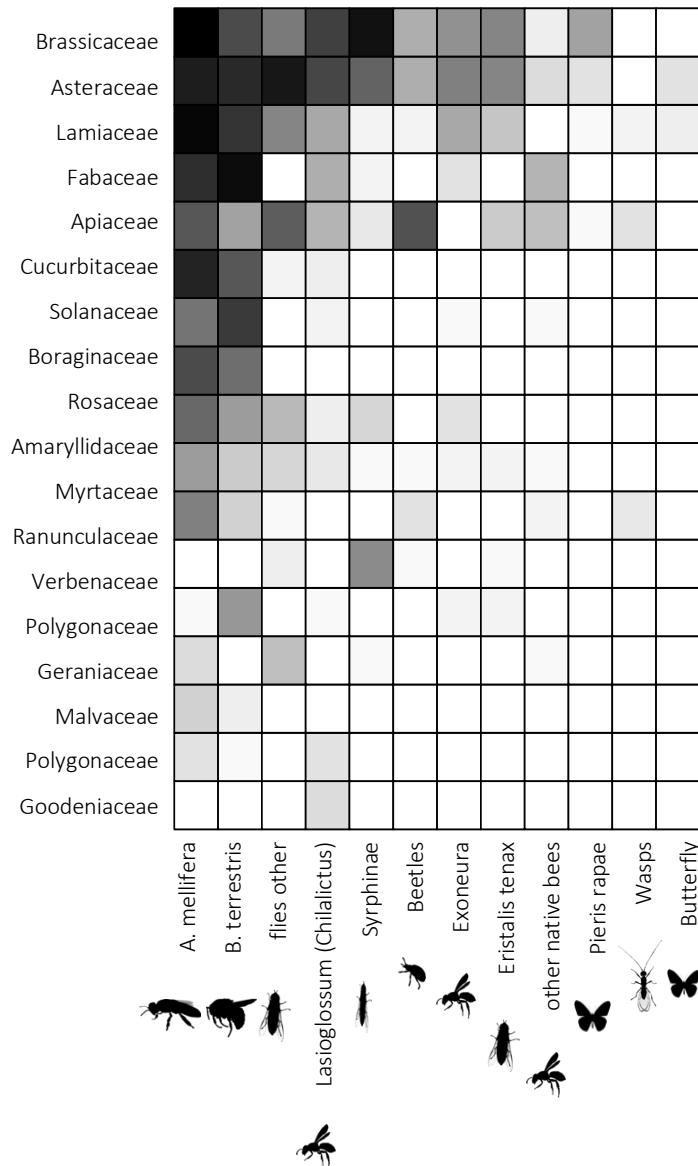


Figure 3.2 Visitation matrix of combined plant family network with sum values to each plant family, to aid visualisation we excluded plant families with only one plant species that received low visitation (Caryophyllaceae, Proteaceae, Portulacaceae, Rutaceae, Gentianaceae, Primulaceae) along with families not represented that received no visits (Amaranthaceae, Haemodoraceae, Orobanchaceae, Papveraceae, Scrophulariaceae). Each cell is showing interaction insect-plant species, darker colouring indicating higher visitation rates, matrix sorted by row/column(sum).

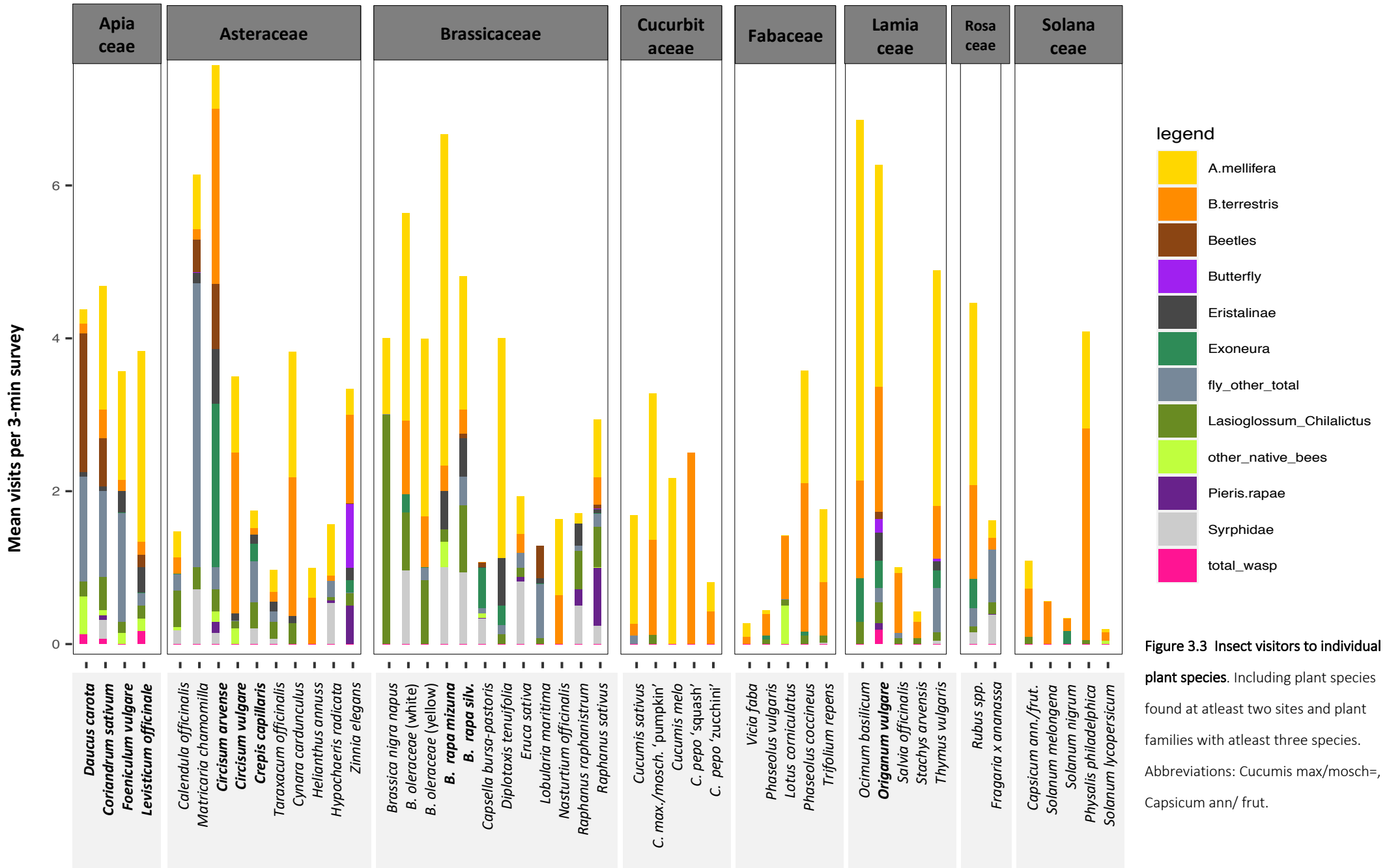


Table 3.1. Flower-feeding insects recorded at market-gardens that likely contribute to ecosystem services, disservices in agricultural production (<20 observations). We classified insects into specific ecosystem service groups (crop pollinators, pollinators, predators, pests) based on their potential role to agricultural production. Note: We defined the two major visitors of crops in this study as major crop pollinators, compared to others that have been found to be efficient pollinators of crops/seed crops elsewhere (crop pollinators, pollinators seed crops), predators were those known to act as natural pest enemies in agricultural productions, whilst pests those that are harmful to agricultural production. Predatory/Parasitoid wasps not included due to low observation (N=2).

Order	Morphospecies or Species	Potential ecosystem service	Visits to crop flowers in this study	Total plant species visited	Total plant families visited	Sites		average total abundance / site	
						spring 11	summer 13	spring	summer
Intro bees	<i>Apis mellifera</i>	major crop pollinator (a)	High several	94	22	11	13	22	57
	<i>Bombus terrestris</i>	major crop pollinator (a)	High several	91	22	10	13	6	43
Native bees	<i>Lasioglossum Chilalictus small L.mundulum</i>	crop pollinator (a)	low	32	10	7	10	2	3
	<i>L. Chilalictus med</i>	crop pollinator (a)	low	52	18	9	13	2.5	7
	<i>L. Chilalictus large</i>	crop pollinator (a)	very low	20	8	3	7	0.5	2
	<i>Exoneura</i>	crop pollinator (a)	med caneberries	25	11	1	8	0.1	6 ⁱ⁾
Hoverflies	<i>Eristalis tenax</i>	pollinator seed crops (c)	-	33	9	2	12	1	5
	<i>Slim Syrphinae</i>	predator pollinator crops/seed crops(d)	high strawberry med caneberries	35	14	10	7	16	2
Beetles	<i>Coccinellidae</i>	Predator (e)	-	9	3	0	4	0	2
	<i>Phyllotocus rufipennis</i>	pollinator seed crops (c)	-	9	4	0	6	0	2
Butterfly	<i>Pieris rapae</i>	pest (f)	-	9	6	0	5	0	2

a) *Apis mellifera*, *Bombus terrestris* found to be globally important pollinators (Klein *et al.*, 2018), including efficient pollinators of Blueberries in Tasmania (Kendall *et al.*, 2020), efficient pollinators cucurbits elsewhere (Knapp and Osborne, 2019)

b) *Exoneura* and *Lasioglossum* efficient pollinators of *Malus domestica* (Bernauer *et al.*, 2022)

c) *Exoneura* efficient pollinators of *Rubus* spp. (Coates *et al.*, 2022)

d) Efficient pollinators of seed crops; *Eristalis tenax*: *Daucus carota*, *Brassica rapa* subsp. *chinesis*, *D. carota* (Gaffney *et al.*, 2018; Cook *et al.*, 2020); and *Phyllotocus rufipennis* *D. carota* (Gaffney *et al.*, 2018)

f) *Syrphinae* can aid in pollination of some crops (*Fragaria x ananassa*, *D. carota*, *B. rapa* (Cook *et al.*, 2020)) and act as natural pest enemies, with larvae predating on aphids and other soft bodied pests (Cook *et al.*, 2020; Dunn *et al.*, 2020)

g) Cabbage white butterfly, *Pieris rapae* major introduced pest species on Brassicaceae crops (Sivapragasam *et al.*, 1997)

i) high abundance one site

Note: canberries include raspberry, blackberry boysenberry

Natural pest enemies

Hoverflies: Predatory hoverflies found in this study may deliver dual ecosystem services in terms of pollination (frequent visitors of strawberry, caneberries - raspberry/boysenberry/blackberry, in our study during summer) and in the predation of agricultural pests, in particular aphids. We recorded predatory slim hoverflies (Syrphinae, mainly *Melangyna* spp.) to be the most abundant flies recorded at market-gardens during spring (n=180, 70.8% all flies, 28.8 % total insect visits) with notably less activity during summer (n=28, 9.7% all flies). We found Syrphinae visiting several different plants and plant families (Table 3.1.), with most frequent visitation to several Brassicaceae (*B.oleraceae*, *B.rapa mizuna*, *B.rapa silv.*), several Asteraceae (*Hypochaeris radicata*, *Matricaria chamomilla*, *Crepis capillaris*, all subfamily Cichorioideae, Asteroideae) and one Ranunculaceae (*Ranunculus repens*) (Fig. 3.2, 3.3).

Beetles: We recorded two species of predatory Coccinellidae which were potentially important natural pest enemies to pests found in fruit and vegetable production systems (Table 3.1.). Predatory Coccinellidae recorded in our study were mainly introduced species (n=22 summer, Coccinellidae, introduced: *Hippodamia variegata*=16, native: *Coccinella transversalis* =6). On average Coccinellidae visited lesser than a quarter of all available plant species at a site (Coccinellidae: nd-mean=0.11). Coccinellidae as also found with other beetles were found visiting lesser plant families, compared to bees and hoverflies, and showed strong association with umbel shaped flowers in the Apiaceae family (Fig. 3.2, 3.3).

Wasps: We only recorded two potential natural pest enemies feeding on flowers at market-gardens, Chalcidoideae/Mymaromatidae (n=1 spring) and Incheumonoidae sp.1 (n=1 summer).

Agricultural Pests

Butterflies: We observed one introduced pest butterfly *Pieris rapae* (n= 24 summer) at market-gardens, these were found mainly feeding on Brassicaceae flowers (radish; *Raphanus* spp.) and one Asteraceae (*Zinnia elegans*) (Fig.3.3).

Other insects with un-known contribution to agricultural production

Native bees: Across all market-gardens and seasons, we overall observed seven genera of native bees belonging to four families: Halictidae (*Lasioglossum* spp., and *Homalictus* spp.), Apidae (*Exoneura* spp.), Colletidae (*Leioproctus* spp., *Hylaleus* spp., *Euryglossa* spp.) and Megachilidae (*Megachile* spp.).

Apart from *Lasioglossum* (*Chilalictus*) and *Exoneura* described above all other insects were observed less frequently (<10 per morphospecies) and during summer only (Table 3.2). One unique floral association was found for *Megachille* spp. with 7 out of 8 flower visits to yellow flowering incidental Fabaceae ground-cover (*Lotus corniculatus*) at four different sites, other native bees were found on some introduced (nearly exclusively non-crop flower) and others only on native plants (Table 3.2).

Flies: Out of the 6 different fly morphospecies recorded we only examined floral associations for hoverflies, as other morphospecies were very broad and included several different families and genera.

Beetles: We overall recorded 13 different morphospecies of flower-feeding beetles at market-gardens during our surveys, including soldier beetles which were most abundant beetles during spring (*Chauliognathus* spp, N=10 spring, N=37 summer, nd-mean=0.14 spring/summer) and false blister beetles (*Asclera* spp, n=32 summer, nd=0.06). Along with several other beetle genera in lower frequency (>1-11 per genera) mainly during summer only Table 3.2). Visitation patterns highlighted a strong association between beetles and umbell-shaped *Apiaceae* family (Fig.3.2, Fig. 3.3). Beetle visitation was also high to a ornamental Myrtaceaea native (non- native to Tasmania, *Sannantha similis*) found flowering at a single site. *S.similis* received visitation by *Asclera* spp., *Stenoderus suturalis* and only plant Buprestidae sp. were recorded on.

Other wasps: We further recorded three other genera of wasps all of which in low abundancy (Table 3.2) . Overall wasps were found on two introduced (*Apiaceae*, *Lamiaceae*) and one native (*Myrtaceae*) plant family (Fig. 3.2).

Other butterflies: A small number of native butterflies ‘browns’ Nymphalidae (n=8 summer all one site) were observed, mainly on *Z. elegans* and one *Lamiaceae* (*Origanum vulgare*).

Table. 3.2 Sum abundance of other flower-feeding insects recorded at market-gardens for which no direct contribution to agricultural production could be found in this study or literature (exception flies).

Order		Total observations	Subsequent species identification
other native Bees	Lasioglossum (Parasphcodes) spp.	7, summer	<i>Lasioglossum sulthicum</i> (N=2) Lasioglossum (Parasphcodes) sp.2
	Homalictus sp.	2, summer	<i>Homalictus sphecooides</i> (N=2)
	Leioproctus	8, summer, one site	<i>Leioproctus spatulatus</i> (N=1)
		1, summer	<i>Hylaeus nubilosus</i>
			<i>Hylaeus (Prosopisteron) asperithorax</i>
		2, summer	<i>Hyleoides concinna</i>
	Euryglossa	1, summer	<i>Euryglossa ephippiata</i>
			<i>Euhesma maculifera</i>
	Megachilidae	8, summer	<i>Megachile maculariformis</i> (N=1) <i>M. ordinaria</i> (N=1) <i>M. tasmanica</i> (N=1)
other beetles	Chauliognathus	10, spring 37, summer	
	Asclera	32, summer	
	Mordellidae	11, summer	
	<i>Stenderus</i>	11, summer	<i>Stenderus suturalis</i> (N=11)
	Eleale	1, spring 4, summer	
	Buprestidae	2, summer	
	Pentatomidae	1, summer	
	Adoxia	1, summer	<i>Adoxia femoralis</i>
	Pseudolytus	1, summer	
	Hesthesis	1, summer	
Other wasps	Rhagigastera	2, summer	<i>Rhagigastera scalae</i>
	Diamma	2, summer	<i>Diamma bicolor</i>
	Cyrtocheilus	3, summer	
Flies	slim Muscoidea	4, spring 126, summer 110 one site	
	other Muscoidea	8, spring 45, summer	
	Bombyllidae	4, summer	Geron sp.1 (2) Comptosia sp.1 (2)
	Other flies	51, spring 45, summer	

Plant species that attract high insect diversity or insects with floral specialisation

We calculated three network metrics for each individual site (and season per site) to determine key plant species contributing to flower feeding insect diversity within market-gardens. These three network metrics (degree, normalised degree and species strength) were positively correlated with one another (Pearsons correlation coefficient, degree-normalised degree $r=0.61$ $p\text{-value}=1.9e^{-39}$, degree – species strength $r=0.77$, $p=7.03e^{-67}$, normalised degree- species strength $r=0.59$ $p=2.01e^{-36}$). That is, plants with a high richness (degree) of insect visitors also tended to attract a high proportion of all possible visitors at a site (normalised degree), and be the plants that were visited by insects most ‘dependent’ on the plant (species strength). Among the plants ranked most highly for each metric (top 15, Table 3.3.), the majority belonged to four plant families: Asteraceae, Apiaceae, Brassicaceae and Lamiaceae. These included weedy Asteraceae species (thistle- *Cirsium arvense* smooth hawkbeard- *Crepis capillaris*) and more intentional planted species (chamomile – *Matricaria chamomilla*, zinnia- *Zinnia elegans*), it further included all species within the Apiaceae family (Fig 3.3), which were all post-harvest crops or culinary herbs, (e.g., carrot – *Daucus carota*, - coriander – *Coriandrum sativum*), along with a culinary herb in the Lamiaceae family (Oregano – *Origanum vulgare*), and some of the flowering Brassicaceae (mizuna post-harvest crop – *Brassica rapa mizuna*, wild mustard incidental – *B.rapa silv*).

Examining the visitation profile to those plants with high network metrics highlights that plants with high degree and normalised degree were all visited by the two introduced bees, several native bees and flies (hoverflies/other flies). Further, plants in the Apiaceae and some plants in the Asteraceae family (*M. chamomilla*, *C. arvense*) were also visited by several beetles and most plants in the Apiaceae family and one Lamiaceae (*O. vulgare*) by a small number of wasps (Figure 3.4).

High species strength values for plant species appeared to be shaped by their ability to attract insects that were found in low numbers overall (beetles, wasps, less common native bees). This included plants in the Apiaceae family, which all had high ‘species strength’ values (Table 3.3); and were all visited by several insects that were found visiting them nearly exclusively (including several which were single observations). Apiaceae were in particular all visited by beetles (up to seven different beetles recorded on *D. carota* at single site), small number of wasps (all single observations, *Ichneumon* sp., *Cyrtocheilus* sp., *Chalidoidea/Myrmarmorommatioidea* sp.) and less common native bees (*Leioproctus* sp., *Homaligus specoides*, *Lasioglossum* (para) sp.). For example, the high ‘species strength’ value for *C. arvense* (Asteraceae) stems from being visited by beetles and less common native bee species (*Leioproctus* sp.).

Likewise, *B. rapa mizuna* (Brassicaceae) in part due to being visited by less common native bees (Lasioglossum (para) sp.). Further *O. vulgare* (Lamiaceae) and *Z. elegans* (Asteraceae) were both visited by butterfly ‘browns’ (Nymphalidae), along with *O. vulgare* being visited by wasp (*Bembix furcata*), both insects were otherwise not found visiting other plant species.

High species strength was also found for *Lotus corniculatus* in the Fabaceae family, this plant received visit by less common native bees (Megachilidae spp.), which was nearly exclusively found visiting this plant, along introduced bees, hence not rated high for richness metrics. Species strength further shaped by being visited by other less common native insects (<20 observations in total) such native bees (Exoneura, Lasioglossum (chilalictus) larger), hoverflies (*Eristalinae tenax*, Syrphinae) and other flies visiting, explaining higher species strength in other plans in particular in the Asteraceae family (e.g. *C. capillaris*, *Calendula officinalis*, *M. chamomilla*).

Table 3.3 Mean values of network metrics from each site/season to determine key plant species within market-gardens. Values are ranked for each network metric: richness (degree), proportion of visits from all possible insect-plant interactions (normalised degree), insect dependency on plant (species strength). In bold plants that overlapped all three metrics. AS- Asteraceae, AP- Apiaceae, BR- Brassicaceae, LA- Lamiaceae, FA – Fabaceae.

Degree			Normalised degree			Species strength		
Plant	mean	Std Dev	Plant	mean	Std Dev	Plant	mean	Std dev
<i>Cirsium arvense</i> - AS	7.5	2.12	<i>Brassica rapa mizuna</i> - BR	0.51	0.49	<i>Daucus carota</i>- AP	3.79	2.64
<i>Daucus carota</i>- AP	6.75	3.5	<i>Cirsium arvense</i> - AS	0.45	0.13	<i>Cirsium arvense</i> - AS	2.52	1.22
<i>Matricaria chamomilla</i> - AS	6	2.83	<i>Coriandrum sativum</i> - AP	0.39	0.22	<i>Coriandrum sativum</i> - AP	1.86	1.55
<i>Zinnia elegans</i>- AS	6		<i>Daucus carota</i>- AP	0.37	0.08	<i>Levisticum officinale</i> - AP	1.85	1.86
<i>Coriandrum sativum</i> - AP	5	2.55	<i>Foeniculum vulgare</i>- AP	0.29		<i>Brassica rapa mizuna</i> - BR	1.60	1.55
<i>Foeniculum vulgare</i>-AP	4.33	0.58	<i>Zinnia elegans</i> - AS	0.27	0.18	<i>Brassica rapa silv</i> - BR	1.51	0.48
<i>Crepis capillaris</i> - AS	4.17	1.60	<i>Ocimum basilicum</i> - LA	0.27	0.10	<i>Foeniculum vulgare</i>-AP	1.31	0.68
<i>Brassica rapa mizuna</i> - BR	4	2.83	<i>Brassica rapa. Silv</i> - BR	0.27	0.13	<i>Matricaria chamomilla</i> - AS	1.26	0.35
<i>Levisticum officinale</i> - AP	3.67	2.52	<i>Matricaria chamomilla</i> - AS	0.27	0.06	<i>Origanum vulgare</i> - LA	0.96	1.13
<i>Origanum vulgare</i> - LA	3.6	3.13	<i>Cirsium vulgare</i>- AS	0.24	0.15	<i>Cirsium vulgare</i> - AP	0.92	0.91
<i>Cirsium vulgare</i> - AS	3.5	2.12	<i>Raphanus sativus</i> - BR	0.24	0.04	<i>Eruca sativa</i> - BR	0.83	0.53
<i>Thymus vulgaris</i> - LA	3.5	1.91	<i>Crepis capillaris</i> - AS	0.23	0.19	<i>Zinnia elegans</i> - AS	0.81	
<i>Brassica rapa. Silv</i> - BR	3.33	0.27	<i>Origanum vulgare</i> - LA	0.22	0.11	<i>Crepis capillaris</i> - AS	0.76	0.38
<i>Cynara cardunculus</i> - AS	3.25	0.17	<i>Calendula officinalis</i> - AS	0.19	0.10	<i>Calendula officinalis</i> - AS	0.75	0.50
<i>Ocimum basilicum</i> - LA	3	0.27	<i>Trifolium repens</i> - FA	0.18	0.4	<i>Lotus corniculatus</i> - FA	0.73	0.62

3.4 DISCUSSION

Introduced bees are the most frequent visitors to crops in Tasmanian market gardens

Our results indicate that the two introduced bees, *A. mellifera* and *B. terrestris* were the most abundant flower-feeding insects found in Tasmanian market-gardens, at both flowering crops and non-crops. A large proportion of flowering crops, including those that require insect pollination for successful fruit production, such as cucurbits (zucchini, pumpkin, melon, cucumber (Free, 1970a; McGregor, 1976b), certain legumes (broad-bean, scarlet runner (Free, 1970a; McGregor, 1976b) and nightshades (chilly, tomatillo- (González-Pérez and Guerrero-Beltrán, 2021), were nearly exclusively visited by the two introduced bees.

Our findings overlap with findings from the UK, where flowering cucurbits were also nearly exclusively visited by *A. mellifera* and *Bombus* spp. (Knapp and Osborne, 2017), and not solitary bees (Knapp *et al.*, 2019). Similar results were also reported for a diversified farm in Montana, USA, in which native bee visitation to squash flowers was low (Burkle *et al.*, 2017; Delphia *et al.*, 2022). Further, a study from South Australia also found very low numbers of solitary bees visiting broad beans; here, yield was instead increased from managed *A. mellifera* (there are no introduced bumblebees in this area of Australia) (Cunningham and Le Feuvre, 2013). Our data highlights that native bees, including *Lasioglossum* species were active when crops like broad beans and cucurbits were flowering. However despite their activity, native bees were rarely observed visiting crops. Instead, they were more often found visiting variety of other plant species in market gardens, suggesting low attraction to specific crop flowers, or difficulty accessing their nectar and pollen.

Globally, *A. mellifera* and *B. terrestris* substantially contribute to the pollination of many crops, whilst not always the most effective pollinators (Garibaldi *et al.*, 2013a; Woodcock *et al.*, 2013) they are super-generalist foragers, and have been found visiting a wide variety of flowering crops around the world (Klein *et al.*, 2007; Klein *et al.*, 2018). Higher visits of *B. terrestris* to nightshades (solanaceae) recorded in our study can be explained by their ability to vibrate ‘buzz’ flowers to release pollen (De Luca and Vallejo-Marín, 2013), which is needed to release pollen of solanaceae flowers (Cooley and Vallejo-Marín, 2021). Further, high association of *B. terrestris* with legumes (Fabacea) found in our study has also been reported elsewhere (Goulson and Darvill, 2004), including *B. terrestris* frequently visiting agricultural legumes in New Zealand, where this bumblebee was introduced in the late 19th century (Iwasaki *et al.*, 2018).

Native insects on Rosaceae crops

Two rosaceae crops grown in Tasmanian market-gardens received frequent visits by native insects: strawberries, with high visitation by hoverflies (Syrphinae) during spring, and caneberries (raspberry, blackberry, boysenberry), with frequent visits by native reed bees (*Exoneura*) during summer. Both Syrphinae and *Exoneura* may make important contributions to the pollination of these crops; studies have found hoverflies to be effective pollinators of strawberries (*Episyphus* spp., (Hodgkiss *et al.*, 2018; Cook *et al.*, 2020), and reed bees are effective pollinators of caneberries (Coates *et al.*, 2022). Hoverflies may also pollinate raspberry, though this warrants further research (Cook *et al.*, 2020).

Crops post harvest, culinary herbs and some weeds attracted pollinators and some natural pest enemies

Our study highlights that plants that are flowering incidentally within and around production areas may play an important role in sustaining beneficial flower-feeding insects (both pollinators and some natural pest enemies) (Bretagnolle and Gaba, 2015; Rollin *et al.*, 2016). Incidental flowering plants included weedy and ornamental plant species in the Asteraceae family, along with post market-value crops left to go to flower in the Brassicaceae and Apiaceae family, and flowering herbs in the Lamiaceae family. The latter were in some gardens left to go to flower purposefully (either to save seeds or increase flowering resources) and in other gardens accidentally (in fallow production areas) (personal communication, Hanusch).

In particular, our data highlights that several Brassicaceae and Asteraceae (in particular those in the subfamilies Asteroideae and Cichorioideae) were potentially useful food sources for common pollinating taxa, including native halictidae bees, *Lasioglossum* (chilictus) spp., along with common pest enemies (predatory hoverflies, Syrphinae). Our findings coincide with insight on floral usage from other studies in south-east Australia (Johanson *et al.*, 2018; Gilpin *et al.*, 2022) and New Zealand (Iwasaki *et al.*, 2018) in which weedy *Hypochaeris radicata* (Asteraceae), were frequently visited by *Lasioglossum*. Similarly, both common weedy dandelion (*Taraxacum officinale*) and weedy wild mustards (*Brassicas* spp.) were visited by predatory hoverflies in NSW apple orchards (Robertson *et al.*, 2020). Studies in the UK and Spain have also found that hoverflies and solitary bees preferentially visit Asteraceae and Brassicaceae in wildflower strips (Carreck and Williams, 2002; Barbir *et al.*, 2015). As outlined earlier Syrphidae hoverflies recorded in our study may be contributing to the pollination of some Rosaceae crops in market-gardens, whilst further acting as natural pest enemy as their larvae feed on soft-bodied agricultural pests such as aphids (Dunn *et al.*, 2020).

Other flower-feeding natural pest enemies found in our study were predatory ladybeetles (Coccinellidae), which as like Syrphinae can be important insects to aid in the control of aphids (Rizvi *et al.*, 2022). Findings on floral associations in our study highlight that both Coccinellidae and other beetles were mainly found foraging on introduced umbellifer flowers in the Apiaceae family. Apiaceae flowers being highly attractive to beetles has also been reported elsewhere (Lago and Mann, 1987), including different Apiaceae supporting high abundance and diversity of Coccinellidae (Balzan *et al.*, 2016). However findings from other studies have further shown high abundance of Coccinellidae on some Asteraceae (*Leucanthum vulgare*) (Hatt *et al.*, 2017).

Plants within the Apiaceae and Asteraceae family, are often integrated into wildflower strips throughout Europe, to support multiple functional groups of insects, including hoverflies, parasitoid wasps (predatory insects) and short-tongued bees (pollinators) (Balzan *et al.*, 2016; Scheper *et al.*, 2021). Apart from beetles we further found overall high visitor diversity of flower-feeding insects to flowering plants in the Apiaceae family, including carrots (*Daucus carota*), this included less common native bees, wasps. Insight of floral visitation in our study further highlights that plants known to enhance wide range of pollinators and natural pest enemies elsewhere, may also be useful to aid ecosystem and biodiversity services in Australian agricultural production systems (Huang *et al.*, 2011; Rizvi *et al.*, 2022).

Different flowering Lamiaceae (found mainly as culinary, ornamental herbs) on the other hand, whilst also attracting diverse visitors, were mainly visited by pollinating taxa including introduced and more common native bees (*Exoneura*, *Lasioglossum* (Chilalictus)). Flowers of the Apiaceae, Brassicaceae and Asteraceae family have open-shallow floral morphology, which makes them more suitable to flower-feeding insects with less modified mouthparts (Krenn *et al.*, 2005). Lamiaceae, on the other hand have restricted, deeper corollas (Jachula *et al.*, 2018). As in our study, Lamiaceae are often found to be highly attracted to honeybees, bumblebees and solitary bees (Jachula *et al.*, 2018). We further found drone hoverflies (*Eristalis tenax*) and some other flies feeding on some Lamiaceae, however not predatory hoverflies.

Our study also found a distinct floral association between native leaf-cutter bees (*Megachile* spp.), which, although only present in low numbers, nearly exclusively visited an introduced fabaceae – *Lotus corniculatus*. High association of *Megachile* with *L. corniculatus* has also been reported in another study in south-east Australia (Johanson *et al.*, 2018) and to the Australian native *Lotus australis* (Pandey and Gurr, 2019).

Implications for the management of floral resources in market-gardens

The low attraction of insects other than introduced bees to several flowering crops highlights that growing different crops per se may not be a useful measure to increase wild pollinators (St. Clair *et al.*, 2020). Instead leaving insect-attractive post-harvest crops (e.g., carrot, fennel, brassicas) and culinary herbs (e.g., coriander, thyme, oregano, basil) to go to flower could be a useful way to offer flowering resources to varied insects, along with having asteraceae (calendula, chamomile) flowering around production areas. With this growers could increase floral availability without additional cost, and promote flowering of plants that have economic (post market crops, culinary herbs) or aesthetic values (in particular for market-gardens open to public) (Barbir *et al.*, 2015; Christmann *et al.*, 2021; Sentil *et al.*, 2022).

However, some management approaches that increase the availability of floral resources for beneficial insects may also increase potential disservices to agricultural production (Carrié *et al.*, 2012; Howlett *et al.*, 2021). For example, in our study one pest butterfly (*Pieris rapae*) was also feeding on Brassicacea (in particular radish *Raphanus* spp.). Some market-gardeners surveyed in this study suggested that brassicas crops are particularly prone to pests in market-garden systems during summer. Leaving plants in the Brassicaceae family within production systems could potentially increase pest populations, including *Pieris rapae* and aphids (Sivapragasam *et al.*, 1997). Our study also found that a classified invasive weed, Californian thistle (*Cirsium arvense*), attracted high diversity of visitors. Whilst weeds can supply important diversity in food resources to beneficial insects (Bretagnolle and Gaba, 2015; Rollin *et al.*, 2016), cautions management is required as not to encourage invasive, problematic agricultural and environmental weeds. Hence we encourage management aimed at increasing flowering resources around agricultural production areas to further embed insight on pest monitoring and knowledge on weed status of plant species.

The potential missing role of native vegetation

Within surveyed small-scale market-gardens in our study, the plant community nearly exclusively consisted of introduced crop and non-crop flowering plants. Whilst they supported a variety of different flower-feeding insects, some native insects were notably absent. Among the native bees for example, there was a notable dominance of one native bee subgenera, *Lasioglossum chilicatus* spp (with *L.clelandi* and *L.mundulum* inferred as the most commonly observed taxa). Exoneura spp. were also common at one market-garden site. The relative abundances of different native bee taxa in Australian landscapes remains poorly documented (Lentini *et al.*, 2012). However, there is some evidence that certain ground-nesting halictid bees (including *Lasioglossum*, *Homalictus*) are the most abundant native bees found in agricultural (Lentini *et al.*, 2012) and urban (Threlfall *et al.*, 2015; Makinson *et al.*, 2017)

landscapes in south-east Australia. Other studies from south-east Australia suggest that *Exoneura* spp. are the most common native bees in studies monitoring natural (Johanson *et al.*, 2018) and varied types of landscapes (Goulson *et al.*, 2002; Johanson *et al.*, 2018). Agricultural landscapes are presumably more suitable for soil-nesting *Lasioglossum*, compared to those nesting in other types of substrates (e.g. pithy-stem nesting *Exoneura*) (Brown *et al.*, 2020).

It is likely that the low presence of native vegetation in our study contributed to low encounters of several native bee genera otherwise found in the area, in particular bees in the Colletidae, Megachilidae bee family observed more frequently in another Tasmanian study (Hingston, 1998; Hingston, 1999). Several other studies highlight that native bees encountered in low numbers in south-east Australia were found predominately feeding on natives (Stout and Goulson, 2000; Goulson *et al.*, 2002; Brown and Cunningham, 2022b).

The lack of native flowering plants around market-gardens may further explain low encounters of other natural pest enemies in our study. However our method of data collection using only visual observations, not traps, likely missed small parasitoid wasps.

Evidence from a literature review (Gagic *et al.*, 2018) suggests that introduced plants may not be less suitable compared to native plant species in supporting parasitic and predatory wasps in the Australian landscape. In a study comparing selected native and exotic interplantings in brassica production system a study found bush mint - *Mentha satureioides* to be most effective at promoting parasitism rate of diamondback moth (Pandey and Gurr, 2019). However, overall there is limited insight if the use of selective introduced plant species, found to be useful to promote natural pest enemies overseas, could be useful in Australia (Rizvi *et al.*, 2022).

We only found a small amount of native plants integrated within production systems in our study, to further enhance biodiversity along with ecosystem (pollination, pest control) services native flowering shrubs could be integrated as strips (e.g., windbreaks, hedgerows, insectary strips) around production areas. Enhancing native vegetation (*Goodenia ovata*, *Pultenaea juniperina*, Chapter 2), could be a measure to sustain crop pollinators, including native reed bees (*Exoneura*), that likely contribute to the pollination services of *Rubus* spp. (Coates *et al.*, 2022), and to increase natural pest enemies (*Mentha satureioides* - Pandey and Gurr, 2019, *Bursaria spinoza* - Retallack *et al.*, 2019). However adding native vegetation can come at high implementation costs (Sentil *et al.*, 2022) and may not be feasible on leased land often used by urban market-gardens (Lin *et al.*, 2015).

A cost-effective way for market-gardeners to enhance useful floral resources around their production areas could be letting some of the crops and culinary herbs in the ground to go to flower (Barbir *et al.*, 2015; Christmann *et al.*, 2021), in particular in the Apiaceae (e.g., carrots, coriander) and Lamiaceae (e.g., basil, oregano) families, along with low risk weeds and ornamentals in the Asteraceae families.

3.5 CONCLUSION

Findings from our study highlight that flowering crops, including those that depend on insect pollination, were nearly exclusively visited by introduced bees, with exception of two rosaceae crops. Diversity of flower-feeding insects, was however still promoted within market-gardens, including both varied pollinators (e.g., introduced and native bees, hoverflies) and some natural pest enemies (predatory hoverflies and ladybeetles). To better understand suitable native and exotic plants to enhance multiple functional groups of insects in fruit and vegetable production systems more work is warranted, both in terms of thorough review of literature and testing effectiveness of different plant species (Howlett *et al.*, 2021).

3.6 REFERENCE

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Chapter 4: Supporting beneficial insects in market-gardens – why plant choice matters

Covid 19 no longer allowed access to field-sites in Tasmania

All field-sites for the first two year of data collection (spring-Summer 2018-2019, spring-summer 2019-2020) were located in Lutruwita. However due to covid 19 border restrictions I was no longer able to continue data collection and undertake any further experimental studies planned within Tasmania.

In July 2020 the University of Sydney granted me permission to undertake fieldwork initially within a 100 km radius in greater-Sydney area, which after a few months got extended to other areas in NSW. As several market-gardens were found in the greater Sydney area I used this opportunity to assess if key findings of visitation patterns from flower-feeding insects to crops and non-crops within Tasmania would also be applicable within a different geographical region of Australia. As I was able to obtain a larger sample size of market-gardens within south-east NSW, compared to Tasmania, I further used this data-set to examine if particular local variables influenced the diversity of flower-feeding insects.

4.1 INTRODUCTION

Flower-feeding insects play a critical role in agricultural production, including the delivery of crop pollination services provided by managed bees (e.g., honeybees – *Apis mellifera*), and wild insects (mainly bees and hoverflies) (Rader *et al.*, 2009); along with control of agricultural pests (Gurr *et al.*, 2003) by ‘natural pest enemies’, such as predator/parasitoid wasps, beetles, and hoverflies. The reliance of pollinators and many natural pest enemies on floral resources for at least part of their lifecycle, makes the maintenance of heterogeneity in disturbed landscapes a key element in sustaining the diversity and abundance of beneficial insects (Landis *et al.*, 2000; Gurr *et al.*, 2003; Tschamntke *et al.*, 2005; Winfree *et al.*, 2009).

The diversification or ‘ecological intensification’ of agricultural production may help support multiple ecosystem and biodiversity services in disturbed landscapes (Bommarco *et al.*, 2013; Gurr *et al.*, 2016), including increased abundance and diversity of beneficial flower-feeding insects (Kovacs-Hostyanszki *et al.*, 2017). The aim of agricultural diversification is to move away from monocultural cropping regimes, instead growing varied crops (polycultures), diversifying non-crop vegetation through rotational (e.g., cover-crops) or more permanent plantings (e.g., wildflower strips, hedgerow) along with allowing greater establishment of ‘weedy’ plant species (Bretagnolle and Gaba, 2015; Kovacs-Hostyanszki *et al.*, 2017; Mallinger *et al.*, 2019). However, limited insight exists into if and how specific local-management actions within agricultural (Kremen *et al.*, 2002) and urban landscapes (Lin *et al.*, 2015) used for food production are supporting ecosystem and biodiversity services. This includes insufficient knowledge around the extent to which floral resources found in more diversified farms support beneficial insects (St. Clair *et al.*, 2020), natural pest enemies (Arnold *et al.*, 2019), or, counter productively, agricultural pests (Carrié *et al.*, 2012).

Greater vegetative diversity in disturbed agroecosystem is often linked with a higher abundance and richness of insect communities (Winfree *et al.*, 2009; Shackelford *et al.*, 2013). Including higher abundance and richness of pollinators in small-scale food production systems with greater plant diversity. Norfolk *et al.*, 2016 for example found that small-holder orchard systems in Spain, where a variety of other crops and herbaceous plants were grown amongst almond trees, supported a high diversity of pollinators and showed high contribution of native bees to crop pollination. High flower richness and flower availability in urban kitchen gardens (Egerer *et al.*, 2019) and community gardens (Bennett and Lovell, 2019) in the USA were found to support higher richness and abundance of certain pollinators. In disturbed agricultural landscapes, high flower diversity in ornamental gardens supported a high diversity of pollinators in Sweden (Samnegård *et al.*, 2011). However, other studies highlight the fact that higher diversity or availability of floral resources does not always support a greater insect

abundance. A study from Australia, for example, found no relationship between local variables in community gardens and bee diversity (Makinson *et al.*, 2017). Further, a study from the USA (St. Clair *et al.*, 2020) found that diverse fruit and vegetable farms did not support greater diversity of bees when compared to monocultural soybean farms. Floral diversity found within agricultural production systems, in particular of the new world, including Australia and the Americas, are often substantially dominated by introduced (non-native) plants species (Cunningham *et al.*, 2002; St Clair *et al.*, 2022). Diversity of introduced plants may have lesser impact on sustaining native insect community, if such instead, are more influenced by composition and availability of native plant species (Makinson *et al.*, 2017). There is some, yet inconclusive evidence that native bees prefer native species over introduced plants (Morandin and Kremen, 2013; Palmersheim *et al.*, 2022). There is further evidence from a global review that crops grown outside their geographical origin attract lower visitor diversity, in particular for crops belonging to introduced plant families (Brown and Cunningham, 2019).

Also, examining direct interactions between insect and flowering plants highlights that often only a subset of the whole plant community is exploited by particular insects, which can mean that diversity is less important than flower identity and thus, it may be more important to promote a set of highly attractive plant species in agroecosystems, rather than focusing on flower diversity per se (Sutter *et al.*, 2017). Makinson *et al.* (2017), for example, found that plant species richness did not affect bee diversity in community gardens in Australia, and suggested differences in insect diversity were likely shaped by only a few plant species being highly attractive to native bees. Similarly, (García and Minarro, 2014) found that from the total diversity of floral resources found within orchard ground-vegetation in Spain, only a subset of plants were important in attracting high diversity and abundance of native bees.

Having key floral resources available for beneficial insects has been found to promote functional diversity of flower feeding insects in agroecosystems. Flower-feeding natural pest enemies, including hoverflies, wasps, beetles, lack modified mouthparts, which restricts them to feeding on flowers with open nectaries (Campbell *et al.*, 2017a). In contrast, many pollinators can access floral resources from plants with restricted nectaries or long corollas (Krenn *et al.*, 2005). This makes the selection and promotion of suitable floral resources a critical component to enhancing natural pest enemies in agroecosystems (Landis *et al.*, 2000). Gaining insight into if and how agricultural management practices aimed at diversification are useful for enhancing natural pest enemies is important information to guide more cost-effective and ecologically sound management interventions to reduce crop damage (Arnold *et al.*, 2019).

In this study, we assessed flower-insect interactions in small-scale fruit and vegetable farming systems (market-gardens) in south-east NSW, Australia to explore the role of agricultural plant diversity in supporting insect communities. Specifically, we aimed to: (i) examine the composition of flowering

resources (crop and non-crop) in market-gardens; (ii) determine if the richness and abundance of flowering resources found in market-gardens impacted diversity and abundance of native and introduced flower-feeding insects; (iii) identify key plant species which attracted a high abundance and/or diversity of flower-feeding insects, and iv) determine if some flowers supporting more specialised insect-plant interactions.

4.2 METHODS

Study sites

This study was conducted on the traditional land of the Worimi, Awabakal, Kuring-gai, Eora, Dharug, Tharawal, Yuin nations in south-east NSW, Australia over two sampling periods in late spring (November 2020) and summer (January 2021 - March 2021). The climate of south-east NSW is humid subtropical (Cfa Koeppen climate classification) and the average maximum temperature during the study period 23 °C and the average min temperature was 18 °C (Australian Bureau of Meteorology, 2022).

The flower-visiting insect community in south-east NSW consists of around ~ 300 native bees, including one species of eusocial stingless bees (*Tetragonula carbonaria*), with the sampling location being at the southern end of *T. carbonaria*'s natural range (Dollin *et al.*, 2016). South-east NSW also has two introduced bee species: honeybees (*Apis mellifera*) and the African carder bee (*Pseudoanthidium (Immanthidium) repetitum*). Feral and managed honeybees (*A. mellifera*) have been widespread across Australia (Hinson *et al.*, 2015) since their introduction from the 1830s (Hopkins, 1886) onwards for honey production and to aid in crop pollination. The African carder bee is a non-eusocial bee first sighted in south-eastern Queensland in 2000 (Baumann *et al.*, 2016) and found to be abundant in Sydney in 2016 (Makinson *et al.*, 2017). Other common flower-feeding insects (include the same natural enemies found to be important worldwide, such as wasps, beetles (Carabid, Coccinellid and Staphylinid), lacewings and syrphid flies (Gagic *et al.*, 2018).

We assessed flower-insect interactions at 21 farms (Appendix C), 5 farms were assessed in both spring and summer while the remaining farms were sampled in summer only. Farms were small-scale systems ranging from approximately 0.1 to 1 hectare in size, used no synthetic fertilisers, pesticides or insecticides, and sold their produce locally to nearby cities and regional towns via vegetable box schemes, road-side stores and restaurants. A variety of crops were grown at each farm, including salad greens, varied brassicas, cucurbits, legumes, nightshades and culinary herbs along with non-crop flowers at some farms. Weeds were managed mechanically (hand-weeding, flame-weeding), several

producers let unused production areas go fallow, left some crops to go to flowers, along with having varied ornamental plants within their production systems.

Data collection

The boundary of each market-garden was defined by fence-lines around the production areas. We first identified all flowering plant species within the market-garden, including flowering crops and non-crop plants. We then surveyed each of the flowering plant species at two randomly chosen patches or production rows. To choose patches or rows of flowering plants for surveys, we first counted the total number of patches or rows at the site that contained the plant, allocated a number to each and then used a random number generator to select the survey locations per plant species. For crops only found in one production row or patch, we surveyed the flowering crop at opposite sides of the row or patch. For flowers that only occurred in a single location in the market-garden only (e.g., a single shrub or tree) we surveyed only the one location for that species. During each survey we monitored ~ 0.6 m² of a plant species for 3 minutes and roughly counted all open flower or flower heads (umbel flower, racemes) in this area. We recorded all insects visiting flowers for food in that interval, where flower visitation was defined as an insect touching the reproductive parts of a flower for nectar feeding and/or pollen collection. We further estimated the relative abundance of each plant species at the survey patch and across the whole site. All surveys occurred between 10:00 and 16:00 hr when temperatures were above 18 °C, with no high cloud cover or strong winds.

Insect identification

We defined flower visitation as an insect touching the reproductive parts of a flower for nectar feeding and/or pollen collection. During survey observations, bees and other insects were placed into their lowest taxonomic grouping identifiable on the wing. Large insects were photographed where possible using a Canon EOS 450D camera. In addition, we collected one of each bee morphospecies, using 120ml specimen containers. Smaller insects which could not be easily identified on the wing or photographed were also collected in 120 ml specimen containers. Collected insects were killed by placing them in a freezer and later pinned for identification. Bees were identified with a dissection microscope to the lowest taxonomic level possible using references keys (Smith, 2018), electronic database of Australian Pollinators (PaDIL). Other insect were identified using online references key ‘What bug is that’ (CSIRO) and guides (Daley, 2007; Farrow, 2016). As the taxonomy of Exoneura is currently not resolved, identification was only possible to sub-genus for this group (Brown *et al.*, 2020) personal communication M.Batley).

Plant group classification

We classified flowering plants in market-gardens into four broad management groups:

Crops: included flowering crops prior to their harvestable state crops. Crops were further classified into crops that require insect-pollination for successful fruit or seed development and those that are not insect pollinated based on literature (Free, 1970a; McGregor, 1976b; González-Pérez and Guerrero-Beltrán, 2021)

Post-harvest crops and culinary herbs: flowering crops post their harvestable state that were left to go to flower; this included crops such as brassicas (e.g., broccoli, kale), root-vegetables (e.g., carrot) along with culinary herbs (e.g., basil, coriander).

Intentional: flowering plants that were purposefully planted or sown yet of little or no direct market value, including medicinal herbs for personal use, ornamental plants, cover-crops and planted natives

Incidental: flowering plants that were not purposefully planted and a number of which can be broadly categorised as weeds in southern-Australia (add reference book).

Data analysis

Basic descriptive statistics were calculated in Excel Version 16.43, all statistical analysis was performed in R 4.05 GUI via R-studio (1.4.1106).

Floral abundance: To estimate the abundance of flowers per site (floral abundance) and between management groups (crops, others) we first calculated the overall relative abundance of a plant species at a site and then used data collected on the number of flowers in a patch (0.6 m²) and calculated the number of flowers for a plant species across site as;

*flower count plant species = relative abundance / 0.6 m² (patch) * mean amount of flowers patch (for plant species surveyed twice)*

Lastly, we summed up all values for crops and other plant species across a site.

Flower-feeding insect richness and diversity: We used the ‘vegan’ package to calculate insect richness and Shannon diversity for each site (separate for sites surveyed twice, in spring and summer) .

Next, we examined if floral-feeding insect diversity and abundance in market-gardens was affected by two local variables; flower richness and floral abundance. We included only data collected over the summer period as this is when all sites were surveyed. We tested the effect using generalized linear models (glm). To account for variation of sampling effort (since plant richness determined the duration of sampling per site) we standardized our response variables (insect diversity and abundance) measures per site, by dividing insect diversity by the number of plants surveyed at each site. For insect abundance we subset the total abundance data into *A. mellifera*, native bees, and other insects and ran separate models for each, as we predicted potential variation between different taxonomic groups' responses to local variables. We included floral richness and floral abundance as main effects in all models. We specified a 'Gaussian' family with Identity link function throughout to allow modelling of non-integer data, and tested model assumptions using the 'DHARMA' package (Hartig, 2020).

To examine if overall flower richness and floral abundance effect abundance and diversity of insects we ran model including all market-gardens surveyed (N = 21). As three gardens were not actively growing crops (instead had cover-crops and fellow production areas), we further ran models excluding the three sites to test if this changed our results.

To determine which insects were the most frequent visitors of flowering crops in our market-gardens, we calculated the proportion of visits per insect morphospecies to each flowering crop during each of our two sampling periods (spring and summer). To examine the overall flower-insect interactions to crop and non-crop flowering plants at market-gardens, and examine if insects showed preferences towards particular plant families and or species (Fründ *et al.*, 2010), we constructed visitation networks using the 'bipartite' package in R Studio (Dormann *et al.*, 2008). We chose the 'visweb' function which visualises the grid plot of the quantitative interactions between flower-feeding insects and plants. We constructed combined networks with the sum of interactions of plant families, and plant species, using data obtained from all sites and both sampling periods (spring and summer). For individual flowering plant species (N = 201) we constructed networks for each insect order separately (e.g., bees, flies, beetles, wasps, butterflies). As there were a large number of plant species only occurring between sites (N = 119 plants) we further constructed graphs that included plants found at two or more sites only (N = 77 plants) this allowed to examine plant species that offered some spatial repetition in observations.

To calculate network metrics for each plant and insect species we constructed networks for each individual site/season including all plant species and insect morphospecies found at a site. We choose to use individual site networks, rather than combined networks so we can calculate unique localised metrics for each insect and plant species and examine mean values, rather than combined metrics from the sum of all sites. For each individual network we calculated network metrics for each plant

and insect species using the ‘specieslevel’ function (Dormann *et al.*, 2009; Dormann, 2020). We calculated two network metrics for each insect: one metric to examine how many different plants each insect was visiting at the site (degree), and one metric to determine how many plants a given insect visited from all possible unique insect-plant interactions at a site (given in percentage; normalised degree). We then calculated mean values of insect network metrics for the most common insects (i.e. those with > 15 observations across all sites).

For plant species we calculated three network metrics to identify key plant species within market-gardens, again using the individual site/season networks for calculations. This included determining how many unique visitors a plant species received (degree), determining the percentage of unique visitors a plant received from all possible interactions at a site (normalised degree), and calculating the sum of dependencies of each species (species strength) (Bascompte *et al.*, 2006). Species-strength provided a measure of how much each insect ‘depended’ on a given plant species among the set of observed plants. That is, plants with high “species-strength” values were those supporting insects in the market-garden that were never or rarely observed to feed on other plant species (Dormann, 2011). To identify plant species with highest values of each metrics, we further ranked plant species for each network metrics separately (degree/normalised degree/species strength) for this we further only included plant species found at least two sites (N = 77).

4.3 RESULTS

Composition of plant species

In total we surveyed 201 flowering plant species across all market-gardens: crops (19 flowering species, mean: 4 std: 3 per site), post-harvest crops and culinary herbs (29 flowering species, mean: 4 std: 2 per market-garden), intentional (i.e., ornamental, cover-crops) (68 plant species out of this 4 plant native species, mean: 6 std: 4), and incidental (i.e., weedy) plant species (75 plant species, mean: 3 std: 5).

The flowering crops belonged to 4 plant families, with Cucurbitaceae (8 spp), Solanaceae (6 spp) and Fabaceae (4 spp) and most represented plant families. The post-harvest crops and culinary herbs belonged to 6 plant families with Brassicaceae (12 spp), Lamiaceae (9 spp), Apiaceae (8 spp) and Amaryllidaceae (6 spp), most represented plant families. The intentional plant species belonged to 15 plant families, including 3 native plant families (Geraniaceae, Goodeniaceae, Myrtaceae), the most represented plant families were Asteraceae (17 spp), Lamiaceae (12 spp), Apiaceae (4 spp).

The incidental plant species belonging to 18 plant families, with Asteraceae (17 spp), Fabaceae (8 spp), Solanaceae (4 spp), Boraginaceae (4 spp) most represented plant families.

At market-gardens where crops were actively grown the flowering crops made up on average $13\% \pm 14$ of the total floral abundance at market-gardens, post-harvest crops and culinary herbs made up a mean: $13\% \pm 14$; and purposefully added plants mean: $25\% \pm 30$; and incidental plant species mean $42\% \pm 29$.

Effect of floral composition on insect diversity

The mean insect diversity (Shannon) at market-gardens was 1.32 ± 0.54 . Total flower richness at market-gardens did not affect the diversity of flower-feeding insects, nor the abundance of native bees (Table 4.1). It did, however, have a negative effect on the abundance of *A. mellifera*, and weakly positive but ultimately non-significant effect on the abundance of other insects (Table 4.1).

Table 4.1 Results generalized linear model testing effect of flower richness and floral abundance on diversity and abundance of different insect groups Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

N = 21 Market-gardens, all sites included				
	Estimate	Std. Error	t value.	Pr (> t)
Insect diversity / plants sampled per site ~				
Flower species richness	-0.0017103	0.001	-1.901	0.072632
Floral abundance	-6.082e-07	7.460e-07	-0.815	0.425
<i>A. mellifera</i> abundance / plants sampled per site				
Flower species richness	-0.043041	0.004248	-10.13	1.28e-08 ***
Floral abundance	-2.448e-06	3.157e-06	-0.775	0.449
Native bee abundance / plants sampled per site				
Flower species richness	0.008591	0.015936	0.539	0.597
Floral abundance	-5.565e-07	4.579e-06	-0.122	0.9047
Non-bee insects' abundance / plants sampled per site				
Flower species richness	0.02807	0.01427	1.968	0.0656 .
Floral abundance	-6.161e-07	4.504e-06	-0.137	0.892786

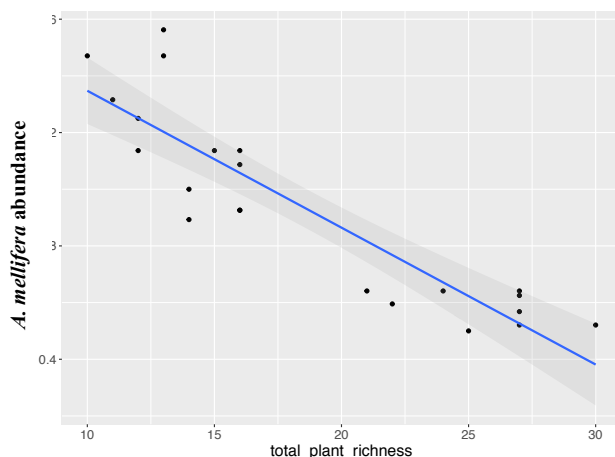


Figure 4.1 Relationship between flower richness at south-east NSW market-gardens and abundance of *A. mellifera*

Visitation to crops

Honeybee (*A. mellifera*) were the most abundant visitors to the majority of flowering crops surveyed (85.7% of total visits), including those that require or benefit from insect pollination (Fig. 4.2). Larger flowering Cucurbitaceae (pumpkin, squash, zucchini - *Curcubita maxima/pepo*) were nearly exclusively visited by *A. mellifera* (Fig 4.2). Native bees contributed 10.2% of visits to flowering crops, and included five different bee genera (Fig. 4.2, Table 4.3). *Lipotriches phanerura* were the most abundant native bees observed visiting mainly Tomato – *Solanum lycopersicum*. Native bees were found mainly on Solanaceae crop and small flowering Cucurbitaceae (honeymelon- *Cucumis melo*, watermelon- *Citrullus lanatus*, cucumber – *Cucumis sativus*) (Fig 4.2), however apart from *L. phanerura* – Tomato, all native bee visits were single observations. One introduced pest butterfly (*Pieris rapae*) was further visiting small flowering Cucurbitaceae (Fig. 4.2). Self-pollinating French-beans (*Phaseolus vulgaris*) were found flowering at four sites and were never found visited by any flower-feeding insects during our observations.

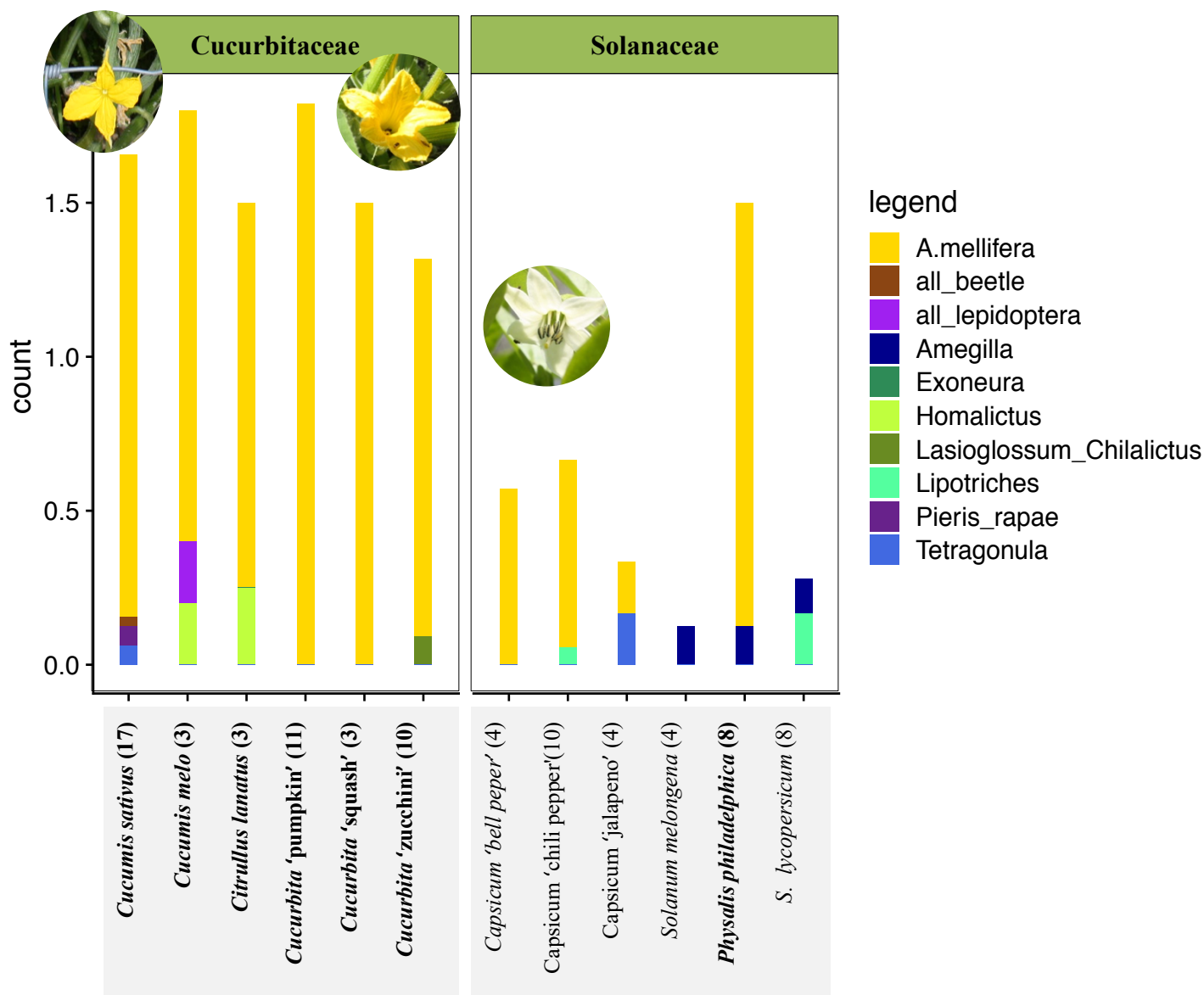


Figure 4.2 Flower-feeding insect visitation to the different flowering crops surveyed at south-east NSW market-gardens, in bold plants that are known to benefit from insect pollination

Patterns in floral usage by different insect groups

We overall recorded 48 different morphospecies of insects (Table 4.3). Honeybees (*A. mellifera* – 48.6%) and native bees - 18.1 % (52 % stingless bees, 64 % halictidae bees) were most abundant flower-feeding insects, followed by flies - 17.1 % (28 % predatory hoverflies), butterflies and moth - 9.1% (56 % introduced pest – *Pieris rapae*), beetles - 4.8% total visits (29 % natural pest enemies) and wasps - 2.1 % total visits (out of this 56 % likley natural pest enemies).

Pollinators

Honeybees: The most abundant visitor to crop flowers in this study, *Apis mellifera*, were also the most abundant visitor overall (N = 858). *Apis mellifera* visited a high proportion of plants at each site (mean normalised degree = 0.63) and they visited nearly half of all flowering plant species (99 out of 201 plants visited) across market-gardens. Visitation was high to several plant families (Fig. 4.3) with 17 plant families visited by *A. mellifera* in total.

Native bees: We recorded native bees belonging to four families and 10 genera; Apidae- Tetragonula, Exoneura, Amygilla, Halictidae - Homalictus, Lasioglossum (chilalictus), Lasioglossum (para.); Megachilidae - Megachile and Colletidae -Leioproctus, Hylaeinae, Hemirhiza. Five of the genera/subgenera were never found on crops, and instead were found on other introduced plant species, including Exoneura, (Lasioglossum (Paraphecodes), all bees in the Colletidae family.

The most abundant native bees were social stingless bees, *Tetragonula carbonaria* (N=168). *Tetragonula carbonaria* visited several plant species at a site (normalised-degree mean per site 0.24), and were found visiting 30 (out of 201) different plant species belonging to 8 plant families. They rarely visited crops (Fig.4.2). The highest abundance of *T. carbonaria* visits were recorded on *Rheum rhabarbarum*, and several plants in the Lamiaceae, Brassicaceae plant family (Fig., 4.3). Other frequently observed bees (> 15 total visits) included ground-nesting bees in the Halictidae family including *Lipotriches* (two species, Table 4.3) which were found visiting 11 plant species belonging to 7 plant families, with the highest visitation to crops (Tomato) and incidental Solanaceae. *Homalictus* (6 species, Table 4.3), were found visiting 10 different plant species belonging to 9 plant families. *Lasioglossum* (*Chilalictus*) were separated into three morphospecies based on their sizes (Table 4.3). Only two of these were found >15 times. Smaller *Lasioglossum* (*Chilalictus*) (n= 19, 3 spp) which were found visiting 16 plant species belonging to 8 plant families, and larger *Lasioglossum* (*Chilalictus*) (n= 17, 2 spp.), found visiting 14 plant species and 8 plant families. *Lasioglossum* (*Chilalictus*) spp. were overall most frequently observed visiting flowers in the Asteraceae plant family. Reed bees (*Exoneura*, n=27, not identified to species level), were found visiting 12 different plant species belonging to 6 plant families with the highest visitation was recorded on Brassicaceae, Asteraceae (Fig. 4.3, Fig. 4.4).

Natural pest enemies

Hoverflies: We recorded 4 different genera of predatory hoverflies (Table 4.3). The most abundant hoverflies were *Sphaerophoria* spp. (N=48) which were found visiting 34 different plant species belonging to 8 plant families, with the highest visitation recorded to plants in the Brassicaceae, Asteraceae and Apiaceae plant families (Fig. 4.3, Fig. 4.4). The second most abundant hoverflies were *Melangyna* spp. (N=32), which were found visiting 12 plant species belonging to 6 plant families, with the highest visitation recorded on plants in the Brassicaceae and Asteraceae families (Fig. 4.3, Fig. 4.4).

Beetles: The most abundant beetles were non-native predatory ladybeetles (Coccinellidae – *Hippodamia variegata*, N=23), which were found visiting 10 plant species belonging to 4 plant families. We further recorded 11 other genera of beetles, none of which are known to be natural pest enemies (Table 4.3). Coccinellidae along with other beetles were mainly found feeding on flowers in the Apiaceae family, apart from high visits of *Hippodamia variegata* to buckwheat – *Fagopyrum esculatum* in the Polygonaceae family.

Wasps: We recorded some (N=16) potential natural pest enemies (Table 4.3), which included an invasive generalist predatory wasp (*Polistes chinensis*). We recorded 9 other wasp families. Overall, wasps were mainly found feeding on flowers in the Apiaceae and Lamiaceae family (Fig. 4.3).

Agricultural Pests

Cabbage white butterflies: We found a high number of introduced cabbage white butterflies (*Pieris rapae* N = 96, nd-, plant species, plant families), which are major pest of Brassica crops (Sivapragasam *et al.*, 1997), high visits recorded to flowers in the Boraginaceae a, Brassicaceae, Astreaceae and Lamiaceae family (Fig. 4.3). We further recorded 4 other butterflies and moth (N=32, Table 4.3), however non of those are known to pose risk to agricultural production.

Harlequin bug: A second pest species recorded were native *Dindymus versicolour* (N=7), which can are minor pest in fruit and vegetable production, (Stahle, 1981). These were found mainly feeding on three plant species (*Daucus Carota*, *Aster amellus*, *Origanum vulgare*) in low numbers.

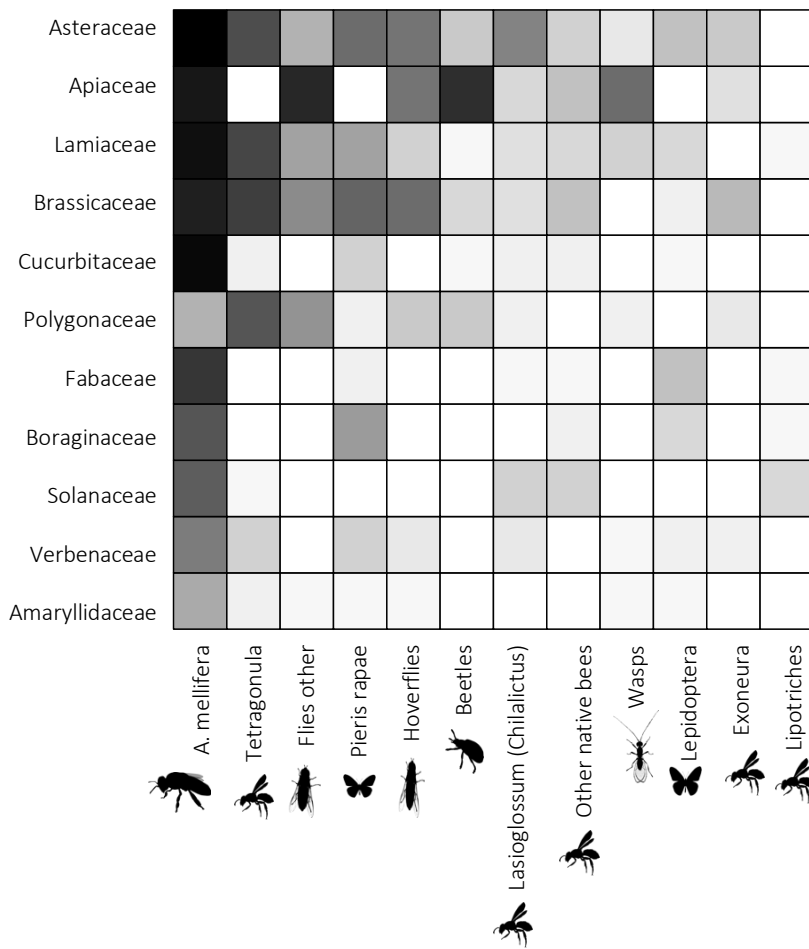


Figure 4.3 **Visitation matrix of combined plant family network** with sum values to each plant family. To aid visualisation plant families with only one plant species and for which no or low visitation data was recorded excluded (Primulaceae, Gentianaceae, Geraniaceae, Goodeniaceae, Malvaceae, Myrtaceae). Each cell is showing interaction insect-plant species, darker colouring indicating higher visitation rates, matrix sorted by row/column(sum). Images source PhyloPic.

Table 4.3 Flower-feeding insects recorded at all market-garden sites in south-east NSW, Australia.

	Potential agricultural service/disservice	Recorded	total visits	Species
Honeybee	Pollinators	<i>Apis mellifera</i>	858	
Native bees	Pollinators	<i>Tetragonula carbonaria</i>	168	
		Lipotriches	15	<i>L. australis</i> (1) <i>L.phanerura</i> (10)
		Lasioglossum (Chilalictus) small	19	<i>L. tridens</i> , <i>L.mundulum</i> , <i>L.pachycephalum</i>
		Lasiglossum (Chilalilctus) large	17	<i>L.lanarium</i> , <i>L.tamburinei</i>
		Homalictus	18	<i>H. sphecodoides</i> (6), <i>H.caloundrensis</i> (2), <i>H.bremerensis</i> (1), <i>H.urbanus</i> (2) <i>H.flindersi</i> (2) <i>H sp. 2</i> (1)
		Amygilla brown	4	<i>Amygilla bombiformis</i>
		Megachilid		
	Amygilla (blue)	7	<i>Amygilla pulchra</i>	
	Pollinators	Lasioglossum (Chilalictus) medium	14	
		Exoneura		
		Masked bees		<i>Hylaeinae euxanthus</i> <i>Hemirhiza sp.1</i>
		Leioproctus	7	<i>Leioproctus sp.1</i> <i>Leioproctus sp.2</i>
		Lasioglossum (para) larger	4	<i>Lasioglossum (para) sp.1</i> <i>Lasgioglossum(para) sp. 2</i> <i>L. para sp. 3</i>
	Lasioglossum (para) smaller	3	<i>L. para sp. 4</i>	
flies	Natural pest enemy	Sphaerophoria	32	
		Melangyna	42	
		Hoverflies other	5	
		<i>Eristalis tenax</i>	9	
		Rhinnidae	14	
		Bombyllidae	4	<i>Exechohypopion sp.1</i> (2)
		Muscoidea	53	
		unidentified flies	49	
Beetles	Natural pest enemy	Coccinellidae <i>Hippodamia variegata</i> (23) <i>Micraspis frenata</i> (1)	24	
		Mordellidae	10	
		<i>Chaulioghathus lugubris</i>	4	
	<i>Pentatomidae</i>	4		
	Lycidae	2		
	<i>Neorrhina punctatum</i>	6		

		<i>Glycyphana stolata</i>	2	
		<i>Phyllotocus rufipennis</i>	12	
		<i>Phyllotocus macleaya</i>	1	
		Amphrihoe	1	
		<i>Ardidaeus thoracicus</i>	1	
		<i>Melyridae</i>	1	
		<i>Aphanestes</i>	1	
Bug	Agricultural pest	<i>Dindymus versicolour</i>	7	
Lepti	Agricultural pest	<i>Pieris rapae</i>		
<i>Lepti.</i>		<i>Utetheisa</i>	7	
		<i>Zizina labradus</i>	10	
		Hesperiidae	15	Hesperiidae sp. 1 (13) Hesperiidae sp.2 (2)
<i>Wasps</i>	Natural pest enemy	Chalcidoidea/Myrmarommatoidea	4	
		Ichneumonidae	5	
		<i>Polistes chinensis</i> (introduced)	7	
		Sphecidae spp.	5	Sphecoidae sp.1 Sphecoidae sp.2, Sphecoidae sp.3
		Anthoboscinae	3	
		Turneromyidae	2	
		<i>Radumeris tasmaniensis</i>	1	
		Scollidae	3	
		Multillidae	1	
		Megaspilidae	1	
		Tippiidae	1	
		Peridae	1	
		Missed wasps	2	

Mean visits per 3-min survey

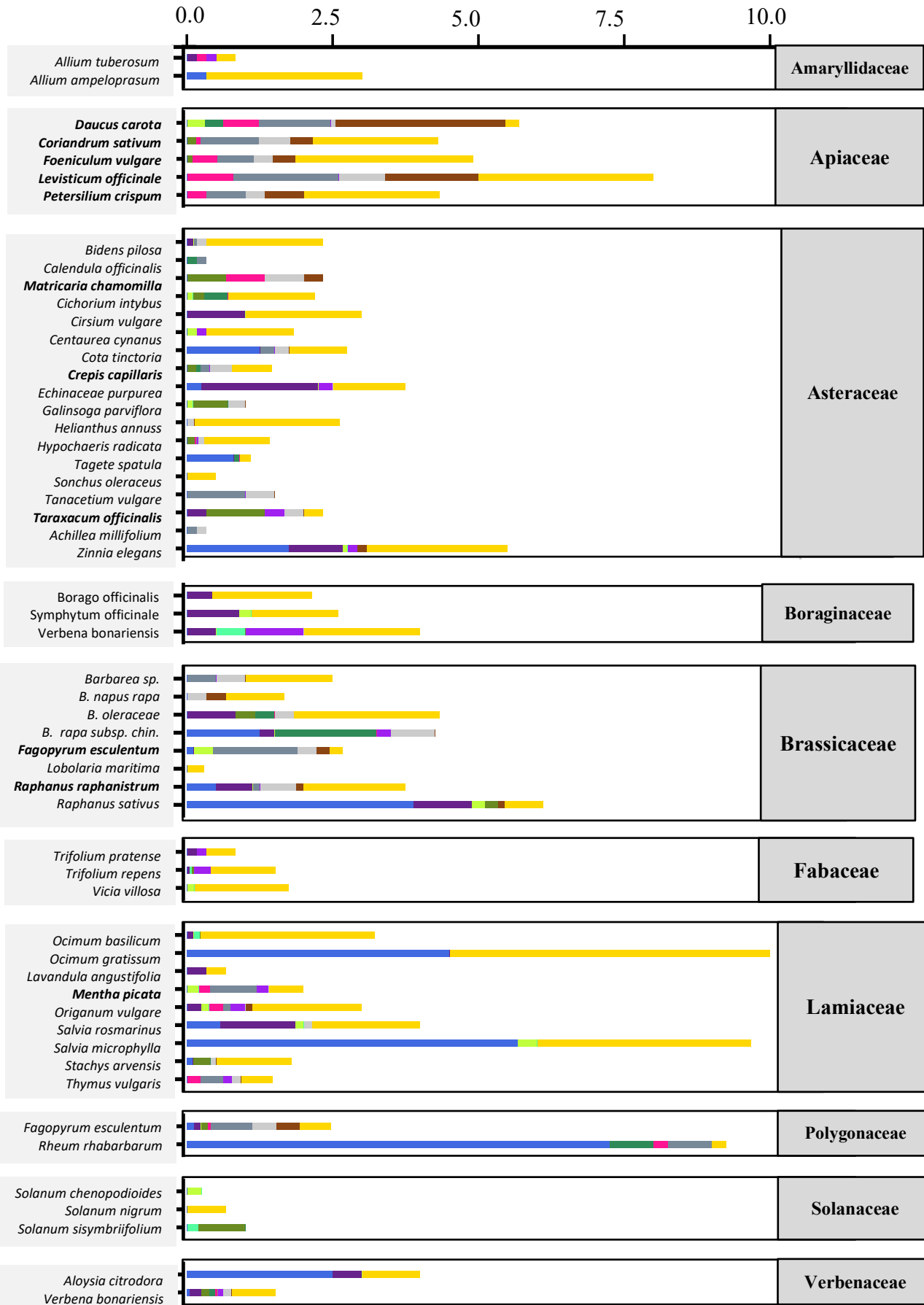


Figure 4.4 Insect visitors to other (non-crop) flowers. Including plant species found at at least two sites and plant families with at least three plant species. In bold plant species for which high network metrics were recorded.

Key plant species

We calculated three network metrics for each individual site (and season per site) to determine key plant species contributing to flower feeding insect diversity within market-gardens. Ranking the top 15 plant species for each network metrics shows that most plant species were ranked high for each measured network metrics (Table, 4.4). This means that plants that were visited by insects most ‘dependent’ on the plant (species strength) also attracted high visitor richness (degree, normalised degree). The majority of plants with the highest metric values belonged to four families Apiaceae, Asteraceae, Brassicaceae and Polygonaceae.

In the Apiaceae family, several plants were ranked high in all network metrics (Table 4.4), and were mainly culinary herbs (e.g., lovage- *Levisticum officinale*, coriander - *Coriandrum sativum*) or post-harvest crops (Carrott – *Daucus carota*). In the Asteraceae family two weedy plant species, smooth hawkbeard- *Crepis capillaris*, dandelion - *Taraxacum officinale*, and one purposefully added medicinal species, chamomile – *Matricaria chamomilla*, were ranked high for all network metrics. In the Brassicaceae family incidental wild radish - *Raphanus raphanistrum* and purposefully added alyssum- *Lobularia maritima*, had high network values. And in the Polygonaceae family a post-harvest crop, rhubarb- *Rheum rhabarbarum*, and purposefully added (cover-crop), buckwheat - *Fagopyrum esculatum* further were ranked high in all network metrics.

Examining visitation profile to those plants with high network metrics highlights that plants with high degree/normalised degree and species-strength were visited by several different orders of insects. This included visitation by bees (introduced and native) and flies (hoverflies, other flies) to all plants. Visits by wasps to plants with high network metrics in the Apiaceae and Lamiaceae family. Further some plants with network metrics were further visited by beetles, this were all plants in the Apiaceae family, along with *M. chamomilla* and *F. esculatum*. High network metrics, in particular species strength for plants was further shaped by insects found overall low, including single site encounters, with insects never found on other plants, which included all orders native bees, wasps, beetles, lepidopteran (excluding pest *Pieris rapae*).

Two smaller flowering Cucurbitaceae crops (melon- *Cucumis melo*, honeymelon- *Citrullus lanatus*) had a high normalised degree yet were not ranked high for any other network metrics. At the sites these network metrics were recorded at, *A. mellifera* and native bees visiting crops, were the only flower-feeding insects recorded at the sites.

Table 4.4. Mean values of network metrics from each site/season to determine key plant species within market-gardens. Values are ranked for each network metric: richness (degree), proportion of visits from all possible insect-plant interactions (normalised degree), insect dependency on plant (species strength). In bold plants that overlapped all three metrics. AP- Apiaceae, AS- Astereaceae, BR- Brassicaceae, CU- Cucurbitaceae, LA- Lamiaceae, PO- Polygonaceae.

Degree			Normalised degree			Species strength		
Plant	mean	Std Dev	Plant	mean	Std Dev	Plant	mean	Std dev
<i>Levisticum officinale</i> - AP	5	4.36	<i>Petroselinum crispum</i> - AP	0.46	0.48	<i>Daucus carota</i>- AP	3.73	5.03
<i>Daucus carota</i>- AP	4.6	5.5	<i>Levisticum officinale</i> - AP	0.38	0.08	<i>Levisticum officinale</i> - AP	3.61	3.24
<i>Rheum rhabarbarum</i> - PO	3.5	2.12	<i>Citrullus lanatus</i> - CU	0.38	0.17	<i>Rheum rhabarbarum</i> - PO	2.3	1.75
<i>Coriandrum sativum</i> - AP	3.3	1.37	<i>Cucumis melo</i> - CU	0.34	0.22	<i>Lobularia maritima</i> - BR	2.1	1.9
<i>Crepis capillaris</i> - AS	3.3	1.5	<i>Coriandrum sativum</i> - AP	0.34	0.16	<i>Matricaria chamomilla</i> - AS	2.02	0.68
<i>Lobularia maritima</i> - BR	3	2.88	<i>Rheum rhabarbarum</i> - PO	0.33	0.18	<i>Petroselinum crispum</i> - AP	1.86	2.08
<i>Brassica.rapa.subsp.chinensis</i> - BR	3	0	<i>Raphanus raphanistrum</i>	0.31	0.17	<i>Brassica.rapa.subsp.chinensis</i> - BR	1.82	1.24
<i>Matricaria chamomilla</i> - AS	3	0	<i>Daucus carota</i>- AP	0.29	0.19	<i>Coriandrum sativum</i> - AP	1.67	1.04
<i>Taraxacum officinale</i> - AS	3	2.8	<i>Lobularia maritima</i> - BR	0.28	0.33	<i>Mentha picata</i> - LA	1.5	1.08
<i>Foeniculum vulgare</i> - AP	2.7	1.1	<i>Mentha picata</i> - LA	0.28	0.19	<i>Taraxacum officinale</i> - AS	1.48	0.69
<i>Mentha picata</i> - LA	2.7	0.58	<i>Taraxacum officinale</i> - AS	0.28	0.24	<i>Raphanus raphanistrum</i>	1.46	0.69
<i>Petroselinum crispum</i> - AP	2.6	1.46	<i>Crepis capillaris</i> - AS	0.28	0.19	<i>Fagopyrum esculentum</i> - PO	1.45	0.9
<i>Fagopyrum esculentum</i> - PO	2.6	1.06	<i>Foeniculum vulgare</i> - AP	0.27	0.15	<i>Foeniculum vulgare</i> - AP	1.26	1.1
<i>Brassica oleracea</i> - BR	2.3	1.53	<i>Thymus vulgaris</i>- LA	0.26	0.17	<i>Thymus vulgaris</i>- LA	1.21	1.26
<i>Raphanus raphanistrum</i> - BR	2.3	1.5	<i>Fagopyrum esculentum</i> - PO	0.25	0.15	<i>Crepis capillaris</i> - AS	1.2	0.9

Discussion

Our findings are in line with other studies which found no relationships between plant species richness and pollinator communities when this was examined other diverse agroecosystems (community gardens) in Australia (Makinson *et al.*, 2017; Tasker *et al.*, 2020; McDougall *et al.*, 2022), and diverse cropping system in the US (St. Clair *et al.*, 2020). However are in contradiction with several other studies including in urban (Bennett and Gratton, 2012; Egerer *et al.*, 2017; Bennett and Lovell, 2019; Egerer *et al.*, 2019; Tasker *et al.*, 2020) and rural (Saunders *et al.*, 2013; Norfolk *et al.*, 2016; Alomar *et al.*, 2018) agroecosystems that found positive association with local plant composition and flower-feeding insect communities.

We also found that honeybee - *A.mellifera* abundance was negatively influenced by floral richness, potentially shaped by *A. mellifera* being attracted to large stands of flowers rather than plant richness per se (Grab *et al.*, 2017; Nicholson *et al.*, 2019). Native bee abundance on the other hand showed no effect.

Several factors may have influenced why local floral richness was not found to effect insect diversity or abundance of insects other than *A. mellifera* in our study. This includes the influence of broader landscapes variables, which were not examined in this study, however could have masked the effect of local variables (Kennedy *et al.*, 2013). High richness of plants further does not necessarily translate to a high presence of attractive plant species; instead, site flower richness may have been strongly influenced by plants that were unattractive or of low nutritional value to flower-feeding insects (García and Minarro, 2014; Sutter *et al.*, 2017; Woodard and Jha, 2017). Our findings highlight that further work is needed to examine if the presence and diversity of particular flowers are more important than overall plant richness (García and Minarro, 2014; Makinson *et al.*, 2017). And could further test if effects vary between urban and rural, small and larger agroecosystems (Arnold *et al.*, 2019).

Low overall native insect visits to crops

Findings from our study also highlight that crop diversity itself is not necessarily a useful measure to promote diversity of flower feeding insects (St. Clair *et al.*, 2020). Crops were mainly visited by *A. mellifera*, which resembles findings in community gardens (Makinson *et al.*, 2017) and our findings in market-gardens in Tasmania (Chapter 3).

Our study suggests that some crops were more attractive to native bees then others. Larger cucurbit crops (zucchini, squash, pumpkin) in particular appear to be unattractive to native bees, whilst smaller

flowered cucurbits (melon, watermelon and cucumber) appeared to show slightly higher attractiveness to native bees. Visit of native bees to smaller flowering cucurbit recorded in this study included stingless bees - *Tetragonula carbonaria* visiting cucumber and *Homalictus sphaecoides* visiting melon and watermelon. Other studies in Australia, looking at larger cucurbit fields, found Halictidae bees to be potentially important native pollinators of watermelon and cucumber (Nacko *et al.*, 2022; Subasinghe Arachchige *et al.*, 2022). We overall only encountered halictid bees in very low frequency visiting melon and never on cucumber, however our sampling effort to crops was much lower compared to that found by (Nacko *et al.*, 2022, Subasinghe Arachchige *et al.*, 2022). Stingless bee contribution to cucurbit pollination in Australia varies, with very low attraction to cucurbit flowers recorded for southern NSW - (Nacko *et al.*, 2022), yet higher contribution in warmer areas where stingless bees are naturally found in larger numbers (Subasinghe Arachchige *et al.*, 2022). However, it is important to note that as found in our study visits to cucurbits by native bees was also found to be dominated by *A. mellifera*, in studies looking at larger fields (Nacko *et al.*, 2022; Subasinghe Arachchige *et al.*, 2022).

We found several native bees, mainly in the genera *Amegilla* and *Lipotriches*, visiting Solanaceae crops in this study. Both *Lipotriches* and *Amegilla* are known to be buzz pollinators of native Solanaceae (Anderson and Symon, 1988). Some work conducted in Australia has found *Amegilla chlorocynanea* to be a potential candidate to aid in the pollination of Tomatoes grown in enclosures (Hogendoorn *et al.*, 2006). Whilst Solanaceae are commonly self-pollinated, mainly only requiring insect pollination when grown in enclosures, crops such as bell-peppers (*Capsicum annuum*) grown in open fields, show increased crop yield when visited certain bees (Pereira *et al.*, 2015). We see that our findings further highlight that further work could examine native bees' contribution to Solanaceae and Cucurbit crop pollination in Australia in general, including breeding of native bees to be used in enclosure, along with their contribution to crop production in the field.

Key non-crop plant species overlapped with findings in Tasmania

Our results highlight that key plant species identified in this study were visited by a very similar groups of insects as found when observing floral-associations in Tasmanian market-gardens (Chapter 3). Which included several post-harvest crops in the Apiaceae (e.g., carrot, coriander), *Brassica* spp. and culinary herbs in the Lamiace family (e.g., mint); along with ornamental and weedy Asteracea.

Further the key plant species found to attract highest diversity and greater specialisation, in south-east NSW and Tasmania (Chapter 3), also overlap with plant species found to be useful to support similar taxa elsewhere e.g., (Maingay *et al.*, 1991; Barbir *et al.*, 2015; Iwasaki *et al.*, 2018; Robertson *et al.*, 2020; Tasker *et al.*, 2020), suggesting that some plant species may be more universally suitable to enhance beneficial insects (Mallinger *et al.*, 2019).

Adopting particular management initiatives to promote key plant families and species

Specific management initiatives can be used to increase more suitable plant species and families, several of which were undertaken by farms surveyed in this study. This includes leaving some vegetable crops and culinary herbs, that are sold prior to their flowering stage to go to flower, e.g. carrots, brassicas, lovage, basil (Maingay *et al.*, 1991; Bugg *et al.*, 2008; Barbir *et al.*, 2015; Christmann *et al.*, 2021).

Plants in the open flowers in the Apiaceae and Asteraceae family may be more particularly useful to support natural pest enemies (Campbell *et al.*, 2017a). In our study Asteraceae flowers were frequently visited by hoverflies, and Apiaceae flowers further by ladybeetles and a few smaller wasps. Compared to herbs in the Lamiaceae family, which were mainly visited by bees and larger flower wasps. Nectar the Lamiaceae flowers can be less accessible to insects with simple flower-feeding mouthparts (Patt *et al.*, 1997), which makes them less suitable to enhance natural pest enemies but suitable to support varied pollinators (Tommasi *et al.*, 2004; Jachuła *et al.*, 2018)

Other management approach to integrating insect friendly plants includes cover-crops or as ornamental insect friendly flower strips (Mallinger *et al.*, 2019; Delphia *et al.*, 2022). Key plant species identified from this study include, buckwheat - *Fagopyrum esculatum* which can be used as a summer cover-crop (Bugg and Waddington, 1994). We found buckwheat to attracted high diversity of visitors, including hoverflies and predatory ladybeetles, and highlights its role in promoting natural pest enemies (Ambrosino *et al.*, 2006; Hogg *et al.*, 2011; Campbell *et al.*, 2016). We found often promoted plant species for natural pest enemies - alyssum – *Lobularia maritima* (Ambrosino *et al.*, 2006; Hogg *et al.*, 2011) to attract some but limited natural pest enemies in this study. Other studies, however, including work in Australia (Gámez-Virués *et al.*, 2009), have found high abundance of parasitoid wasps associated with *L. maritima*. Different sampling methods than visual observations used in this study are likely needed to gain more indepth insight on particiular floral usage of parasitoid wasps to varied flowers in diverse agroecosystems.

The high diversity of visitors to plants in the Apiaceae family, including natural pest enemies highlights the importance of leaving some of those crops to go to further or integrating c ornamental varieties, including ornamental carrot - *Daucus carota*, or Queens Anne Lace - *Ammi majus* (Wilson *et al.*, 2018; Nobes *et al.*, 2022). Other ornamental plants often found in flower, *Echinaceae purpurea*, *Zinnia elegans* were found to be less suitable to promote both pollinators and natural pest enemies, and were further visited by brassica pest butterflies (*Pieries rapae*). Similar plants in the Boraginaceae family attracted visits by mainly *P. rapae* along with *A. mellifera*. In other parts of the world Boraginaceae, including *Borago officinalis*, are often used in wildflower strips to promote native bumblebee (Campbell *et al.*, 2017a), however these plants do not appear to be useful for native bees found in this study (south-east NSW), nor in Tasmania (Chapter 3).

Research recommendations

Further work is needed to test if certain plant species or combination of plant species may be most useful to integrate in insect friendly cover-crops and flower-strips. Both in terms of supplying floral resources to beneficial insects (Barbir *et al.*, 2015), along examining potentially disservice in terms of increasing pest populations (Silva and Moore, 2017; Howlett *et al.*, 2021). Here studies could focus on examining if sporadic occurrence of plants, for example leaving some crops and ornamental plants to go flower, leaving some weeds to establish etc., has a different effect on supporting beneficial insects compared to targeted floral enhancements (e.g., floral strips, plantings).

To examine if there is variation of crop pollination services delivery between production systems, future work could test if crops grown in highly diverse systems such as market-gardens, compared to monocultural crops, receive lesser or more visits by bees, particularly examining if native bees preferentially visit other potentially more attractive co-flowering plants (Ye *et al.*, 2014; McDougall *et al.*, 2022)

Further, when identifying suitable plants to enhance abundance and diversity of beneficial insects it remains critical to examine their potentially disservice in terms of supporting and increasing pest populations (Silva and Moore, 2017; Howlett *et al.*, 2021). Brassicaceae may be more susceptible to pests (Sivapragasam *et al.*, 1997) compared to Asteraceae, Lamiaceae and Apiaceae however this warrants further investigation.

Our study offered limited insight into the role of native vegetation in sustaining beneficial insects in market-gardens, due to the lack of present flowering species around production areas. However, the integration of native vegetation around production areas is likely an important component of sustaining the diversity of pollinators along with natural pest-enemies (Howlett *et al.* 2021). We see that more work is needed comparing different plant species, including examining if certain native or introduced plants are more suitable for promoting particular ecosystem services by beneficial insects (crop pollination/pest control). An experimental study conducted in Australia for example found native mint (*Mentha satuireioides*) to be more effective compared to introduced plants at increasing parasitism rate of diamondback moth (Pandey and Gurr, 2019). Based on our findings we recommend testing the impact of different introduced plants, including plants in the Apiaceae family which were found to show the highest network metrics in our study and comparing these to native plants.

To increase native plant species around production areas growers could plant out shelterbelts along fencelines and borders, which could aid both beneficial insects, along with protecting crops from prevailing winds (Smith *et al.*, 2015). Planting out floral strips between crop rows – floral strips (Pandey and Gurr, 2019). Another way could be to plant out native shrubs at the front/end of crop rows, prickly box- *Bursaria spinosa* and other shrubs have been proven to attract natural pest enemies into vineyards using this method (Retallack *et al.*, 2019). However further work is needed to examine how selection of plant species, planting design impacts ecosystem service delivery, both in terms of pest control along with crop pollination services.

4.4 CONCLUSION

Findings from our study highlight that management measures that support the abundance of certain plant species may be more important to promote the diversity and abundance of beneficial insects in market-gardens compared to merely encouraging high richness in plant species. Management measures can include letting some crops and culinary herbs to go to flower, cover-cropping with buckwheat and integrating ornamental flowers in particular in the plant families Asteraceae - e.g. calendula (*Calendula officinalis*) and Apiaceae – e.g. Lovage (*Levisticum officinale*). Whilst crop and other plants in the family Brassicaceae, along some ornamental plants (zinnia – *Zinnia elegans*, borage – *Borago officinalis*) also attracted a high diversity these plants are likely more prone to sustain pest species. Further work is needed to test the effect of adding particular and combination of plant species into fruit and vegetable production systems, in attracting pollinators and measuring impact on crop-pollination, along with measuring effect on natural pest enemies their pest controlling services.

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Chapter 5: Pollinating insects varied in their responses to short-term exposure of non-crop insectary plant species

5.1 ABSTRACT

Floral enhancements in agricultural settings will sometimes have a beneficial, non-competitive effect on crop pollination, by increasing the abundance and diversity of insect pollinators visiting the crop when in flower. In other cases, however, non-crop floral resources may have no impact or a competitive impact (i.e., decreasing visitor abundance) on crop visitation. This variation may arise from differences in the foraging behaviour of different pollinator species, but how common insect pollinators respond during foraging to the presence of co-flowering plants remains a poorly understood aspect of crop pollination ecology. In this study we used a highly attractive insectary plant species (*Phacelia tanacetifolia*), grown in pots, to examine whether short-term exposure to a non-crop plant changed foraging behaviours of pollinating insects visiting nearby crops in small-scale market-gardens in Tasmania, Australia. We found that of the two highly abundant pollinators in these gardens, only *Bombus terrestris* and not *Apis mellifera* quickly integrated *P. tanacetifolia* into their foraging. The high visitation of *B. terrestris* to *P. tanacetifolia* led to increased visitation to crops in the market-gardens both during when *P. tanacetifolia* was present and after its removal. Our study highlights that differences in the foraging behaviours of pollinating taxa may help to account for the variable impacts of non-crop floral resources to crop pollination.

Covid border restrictions prevented second year of study

During the summer 2020 (prior to covid-19 border restrictions) I conducted an experiment in Tasmanian market gardens that tested the effect on pollinator-crop visitation of adding a flowering insectary plant species (*Phacelia tanacetifolia*) to market-gardens. The original aim of this experiment was to test the effect of such non-crop flowers on visitation to different flowering crops and other plant species grown at the market-gardens and was planned to run over two years. However, due to Covid-19 border restrictions beginning in 2020, I was no longer able to travel from Sydney, NSW where I was living and studying to my study sites in Tasmania. The scope and sample size of this experiment is hence smaller than originally planned.

5.2 INTRODUCTION

Co-flowering plants that share pollinators can interact with each other in a competitive, facilitative or neutral way (Rathcke, 1983; Moeller, 2004; Mitchell *et al.*, 2009; Ye *et al.*, 2014). Competition for pollinators between plants can occur when co-flowering plants compete for limited pollinator resources, whereby each extra plant at a location reduces the availability of pollination services being delivered to all plants (Waser, 1978; Chittka and Schürkens, 2001; Mitchell *et al.*, 2009; Morales and Traveset, 2009; Ye *et al.*, 2014). Alternatively, competition can occur through reproductive interference via the deposition of pollen from another plant (i.e. heterospecific pollen transfer), which can interfere with the fertilisation and pollination success of plants (Waser, 1978; Morales and Traveset, 2008; Morales and Traveset, 2009).

Facilitation may occur between co-flowering plants when an attractive plants attracts visitors into an area resulting in increased visitation on neighbouring plants; this is sometimes known as a ‘magnet effect’ (Thomson, 1978). Facilitation can also occur due co-flowering plants forming complementary floral displays that are collectively more attractive than a single species alone (Morales and Traveset, 2009). Co-flowering plants can also have a neutral effect on their neighbours, where, although they share pollinators, the presence of the neighbour does not substantially change visitation rates and/or reproduction success of either plant (Totland *et al.*, 2006).

Pollinator-mediated plant-plant interactions play an important role in influencing management decisions aimed to increase pollination services to agricultural crops. The presence of non-crop co-flowering plants around crops during bloom is often discouraged due to concerns about competition (Somerville, 1994). Such thinking can lead to concerns by growers that adding wildflower strips of co-flowering crops or wild plants around their focal flowering crops could result in lower crop pollination (Lundin *et al.*, 2019; Nicholson *et al.*, 2019; Lowe *et al.*, 2021). Resource-rich plant species (high pollen/nectar) or patches of plants may distract pollinators away and lead to reduced visitation of focal crops (*circe principle* (Bartomeus and Winfree, 2011; Lander *et al.*, 2011). Yet such competitive effects have mainly been found with mass-flowering crops (e.g., oilseed rape) drawing away highly social pollinators (e.g. the honeybee *Apis mellifera*) from sparser flowering plants, including crops (Diekötter *et al.*, 2010; Grab *et al.*, 2017; Bänsch *et al.*, 2021).

In contrast, studies which examined other types of non-crop co-flowering plants, including wild or weedy plants in fields and margins (Carvalho *et al.*, 2011; Knapp *et al.*, 2019) and floral enhancements (e.g., wildflower strips, hedgerows) (Albrecht *et al.*, 2020; Lowe *et al.*, 2021) have found that co-flowering plants typically have a neutral or positive effect on the pollination of adjacent crops.

Similar effects have also been found in studies examining companion planting, a method embedded within different traditional and alternative farming systems, with the aim of increasing the abundance of pollinators and other beneficial insects (Franck, 1983; Griffiths-Lee *et al.*, 2020). Studies which have tested the effect of companion plantings found facilitative effects to crop production, including increased yield (however not fruit quality measures) of jalapenos and cucumber (Montoya *et al.*, 2020), and increased fruit production in strawberry (Griffiths-Lee *et al.*, 2020).

The composition, density and size of plant communities can shape whether plants have a competitive, facilitative or neutral effect on other co-flowering plants (Rathcke, 1983; Ghazoul, 2006; S. Feldman, 2006). Companion plants and wildflower strips are often smaller in size than the flowering crops (Griffiths-Lee *et al.*, 2020, (Campbell *et al.*, 2017b); this size difference may partially explain why there is generally no competitive effect of co-flowering wildflower strips and companion plants on crop visitation (Nicholson *et al.*, 2019). There is also increasing evidence that the presence of non-crop flowering resources around crops can increase the diversity and abundance of pollinators visiting crops (Blaauw and Isaacs, 2014; Norfolk *et al.*, 2016; Alomar *et al.*, 2018; Gilpin *et al.*, 2022), and through this facilitate more successful crop pollination (Mallinger and Gratton, 2015). In this sense the presence of non-crop co-flowering plants around crops can have a potential ‘magnet-effect’ (Molina-Montenegro *et al.*, 2008), by increasing visitors into an area where those visitors then also forage on flowering crops.

Different crop pollinating insects may vary in their responses to the presence of non-crop flowering plants. (Knapp *et al.*, 2019) for example, recorded significantly higher bumblebee abundance and richness visiting flowering cucurbits in fields with greater diversity of non-crop flowering plants, whilst honeybee visitation to cucurbits remained the same. It is likely that the presence of co-flowering plants has a stronger effect on increasing visitation to crop flowers for pollinators that move more readily between different flowering species, including non-crop and crop flowers, during their foraging (Knapp *et al.*, 2019), compared to pollinators that are more constant foragers on only one or a few plant species (Free, 1963; Gilpin *et al.*, 2019b). High floral constancy has been observed in foraging honeybees (Free, 1963; Waser, 1986; Grüter *et al.*, 2011), whilst bumblebees have been shown to move more readily between plant species during foraging trips (Raine and Chittka, 2007). However, evidence for strong floral consistency in honeybees may arise in part because most experiments use highly-rewarding artificial flowers, which may give a misleading view of the foraging behaviour of honeybees in general (Grüter *et al.*, 2011; Latty and Trueblood, 2020). Further, floral constancy may also not be expressed all the time by every member of a species but rather may vary between different individuals of the same species (Latty and Trueblood, 2020). For solitary bees, that need to collect all resources themselves, visiting multiple flower species during foraging trips may increase their nutritional uptake (Hayes and Grüter, 2022), and is seen as a reason why solitary bees are predicted to be associated with lower flower

constancy (Waser, 1986; Hayes and Grüter, 2022). Lower floral constancy in solitary bees may further influence their higher crop visitation abundance in the presence of non-crop flowers.

One way of testing changes in foraging patterns and examining the effect of plant-plant interactions is to experimentally manipulate the availability of flowering plant species (Ghazoul, 2006; Ogilvie and Thomson, 2016). Plants that are known to be highly attractive to flower-feeding insects (insectary plants) (Laubertie *et al.*, 2012), can be used to examine potential competitive versus facilitative effects on crop visitation (Griffiths-Lee *et al.*, 2020).

In this study we examined the behavioural responses of different flower-visiting insects to short-term exposure to a highly attractive insectary plant (*Phacelia tanacetifolia*) in small-scale market-gardens. Market-gardens are diversified production systems, where crops are grown in shorter rows (Montoya *et al.*, 2020), this gave us the unique opportunity to examine the effect of co-flowering plants on multiple crops grown in the same localised environment. As market-gardens grow crops in short rows, rather than large fields, these study systems further allowed us to examine potential changes on foraging behaviour through the addition of potted plants (Lazaro and Totland, 2010). Crops grown in larger fields on the other hand would potentially require the addition of larger amounts of non-crop flowering resources (e.g. wildflower strips), as effects from a small amount of flowers may otherwise be too diluted.

Specifically, we used potted plants of *P. tanacetifolia*, and placed them next to rows of flowering crops at market-gardens over four days to examine:

- i) which insects integrated *P. tanacetifolia* into their foraging
- ii) if exposure to *P. tanacetifolia* changes visitation rates to adjacent flowering crops during and post-exposure
- iii) if insects switched from feeding on *P. tanacetifolia* to feeding on adjacent plant species

5.3 METHODS

Study systems

Experiments were conducted during summer January 2020 at six small-scale diversified fruit/vegetable growers (market-gardens) on the traditional land of the Melurkerdee and Lyluequonny people in southern Lutruwita/Tasmania (Huon Valley and Kingorough council), Australia.

The climate of Tasmania is temperate oceanic climate (Cfb Koeppen climate classification). The average temperate during our experiment (January 2020) was 24C° and the total rainfall in the region for the month was 46.8mm (Australian Bureau of Meterology, 2022). Experiments were only conducted on days without rainfall.

Tasmania has two introduced bee species found as feral (wild) populations: honeybees (*A. mellifera*) and bumblebees (*Bombus terrestris*). Honeybees have become widespread across Australia (Hinson *et al.*, 2015) since their introduction in the 1830s (Hopkins, 1886) onwards for honey production and to aid in crop pollination. Bumblebees were accidentally introduced from New Zealand in the early 1990s (Buttermore, 1997; Schmid-Hempel *et al.*, 2007) and are now widespread around Tasmania (Kingston *et al.*, 2002). Native flower feeding insects in Tasmania span various guilds, including around 120 native bee species (Hingston, 1998), all of which are solitary or non-eusocial (Armstrong, 1979; Houston, 2018).

Phacelia tanacetifolia is a purple annual flowering plant in the Boraginaceae family, native to southwestern US and north-western Mexico. We chose *P. tanacetifolia* as our insectary plant as it is used around the world as a fast-growing pollinator-attractive plant, with high pollen protein content (Sprague *et al.*, 2016). *Phacelia tanacetifolia* has been further shown to attracts diverse insect pollinators, in particular bees and hoverflies in varied geographical locations around the world (Carreck and Williams, 2002; Laubertie *et al.*, 2012; Nicholls and Altieri, 2013).

We raised *P. tanacetifolia* seed in seed-raising mix then transplanted one small seedling each into 13cm diameter pots with potting mix. Seedlings were continuously watered and kept outdoors in butterfly cages to exclude any insects visiting flowers. Once plants were flowering, we placed eight pots into larger plastic tubs filled with a shallow amount of water to stop plants from drying out during the experiment.

Experimental set-up and flower-visitor observation

To test the influence of *P. tanacetifolia* on visitation to neighbouring plants, we placed tubs with flowering plants next to crop rows at market-gardens (Figure 5.1). Tubes with flowering plants were placed in boxes with shallow water to avoid drying out in the field. As market gardens varied in the type of crops they grew, there was no single crop species that we could compare between all sites. Instead, we choose two rows of crops per site, this included two different crops at most sites (exception one site Zucchini measured two different locations at same farm) (Table 5.1). We placed boxes next to representatives of one of seven focal crops: two Fabaceae (French bean, Scarlett Runner), two Solanaceae (Tomato, Tomatillo) and three Cucurbitaceae (Pumpkin, Zucchini, Squash) (Table 5.1). At each site, a box with *P. tanacetifolia* was placed next to two different crop rows (one box per row, Fig. 5.1) of flowering crops at a site (N=12). Crops were selected which had rows >10 meters in length and were > 25 meters apart from each other. We choose crops that were in peak flower at each of the sites. At two farms where multiple crops fit our criteria, we ran initial experiments with two crop rows, and a subsequent experiment a week later with the other two crop rows.

Table 5.1. Crop flowers monitored at Tasmanian market-gardens before, during and after the introduction *P. tanacetifolia*.

Plant family	Crop	Scientific name	Total replication	Sites	Insect pollinator reliance
Fabaceae	French bean	<i>Phaseolus vulgaris</i>	4	4	N
	Scarlett Runner	<i>Phaseolus coccineus</i>	1	1	Y
Solanaceae	Tomatillo	<i>Physalis philadelphica</i>	2	2	Y
Cucurbitaceae	Pumpkin	<i>Cucurbita maxima/moschata</i>	1	1	Y
	Zucchini	<i>Cucurbita pepo</i>	2	1	Y
	Summer Squash	<i>Cucurbita pepo</i>	1	1	Y

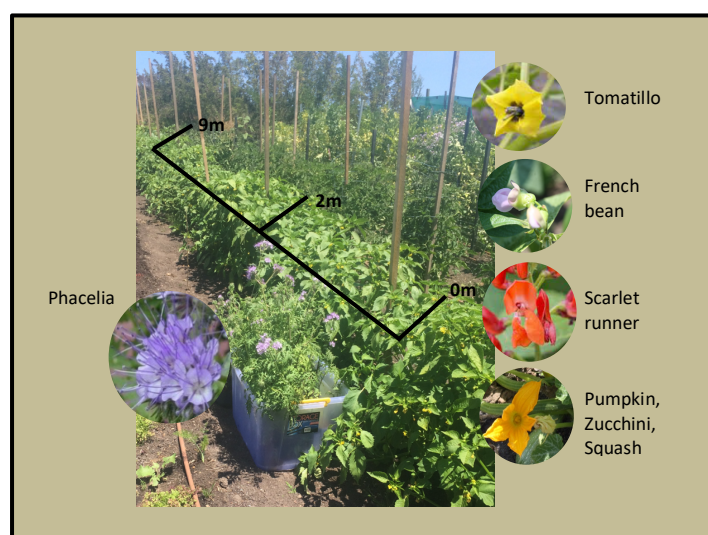


Figure 5.1 visual schematic of methods.

Visitation to six different crops was measured pre, post and during short-term (4 day) exposure with an insectary plant – *Phacelia tanacetifolia*. Crop visitation rates were considered at 0, 2 and 9 meters from the *P. tanacetifolia*.

Flower-insect observations

To identify which insects were visiting the different plant species and examine if the exposure (adding) of *P. tanacetifolia* changed visitation to the crop flowers, we monitored insect visitation during three time intervals (pre-exposure, during-exposure, post-exposure).

During each time interval we monitored visitation to crops along the chosen crop rows. Here we monitored visitation to crop flowers immediately next to the subsequent placement of *P. tanacetifolia* boxes at 0 meters, plus at further distances along the crop rows at 2 meters, and 9 meters away (Fig. 4.1). We choose these spatial intervals to test if there was a potential dilution of effect over space. The chosen distances were shaped by the overall short-distances of crop rows (around 12 meters) in market-gardens, with 9 meters being maximum distance comparable across sites and each distance being at least 1 meter from the end of the row. The chosen distances are not representative of foraging distances or spill-over of bees between plant species, which has been found fairly frequently within distance of 10-30 meters, yet also up to 100 meters (Ogilvie, 2014)

To gain better insight into overall community assemblages of flower visiting insects, we further monitored visitation to other non-crop flowering plants found within a 4-meter radius around *P. tanacetifolia*. Within the 4-meter radius we monitored one of each flowering plant species occurring.

During the pre-exposure phase we monitored visitation to both crops and non-crop flowering plants for all distances (crop 0, 2, 9 meters). Once measurements were completed to both crop rows at a site, we placed the boxes with *P. tanacetifolia* immediately next to row of flowering crops at 0 meters. No further measurements were taken on the same day.

During the exposure phase we monitored visitation to crops and non-crop flowering plants along with visitation to *P. tanacetifolia*. The during-exposure phase measurements were taken twice, with the first measurement on days 1 or 2 post adding of *P. tanacetifolia* (early exposure), during this time plants were also watered, and second measurement taken between days 4 or 6 (late exposure). Plants were left in-situ for the whole length of the experiment. The variation in sampling times was due to rainfall during days that the experiment was running. Once the monitoring to all plants was completed, we removed boxes with *P. tanacetifolia*.

We took our first post-exposure measurement 30-60 minutes after the removal of *P. tanacetifolia*, again recording visitation to crop and non-crop flowers. We then took our second post-exposure measurement 1-2 days following the removal of *P. tanacetifolia*.

Each flower-visitation measurement consisted of a 10-minute timed recording of all insects observed feeding on the flowering plants (touching reproductive parts of plants with mouthparts). When monitoring visitation to crop or non-crop flowering plants we focused on counting visitation of flower feeding insects to all flowers of given plant species within an area of $\sim 0.6\text{m}^2$. One exception were cucurbits, here we monitored only one open female flower (if no female flowers available then male flowers), instead of monitoring all flowers within $\sim 0.6\text{m}^2$. This was because cucurbits measured in this study, including Pumpkin, Zucchini and Squash, had relatively large flowers and showed inconsistency in the number of open flowers. For *P. tanacetifolia* insect visitation was counted to all open flowers within boxes.

Insect movements between plant species

During the 10 min observation of visitation to *P. tanacetifolia* we also recorded if any of the visiting insects switched from feeding on *P. tanacetifolia* to feeding on adjacent flowering plant species. We recorded a switch if an insect observed feeding on *P. tanacetifolia* moved over and continued feeding on adjacent crop or non-crop flowers. Insects were not followed beyond the adjacent crop or non-crop plants.

Statistical analysis

All analysis was performed in R-studio Version 1.4.1106.

i) which insects will visit P. tanacetifolia during short-term exposure

To identify which insects integrated *P. tanacetifolia* into their foraging we calculated basic metrics (total visits, percent of visitation) from the flower-insect observations to crop and non-crop flowers, along with visitation to *P. tanacetifolia*.

ii) if exposure to P. tanacetifolia changes visitation rates to adjacent flowering crops during and post-exposure

To test if short-term exposure to *P. tanacetifolia* changed visitation to adjacent flowering crops we constructed generalized linear mixed-effects model using the 'glmer' function in the 'lme4' package (Bates *et al.*, 2009). We constructed models for *B. terrestris* visitation to crops only, as these were the only insect frequently visiting both *P. tanacetifolia* and crop flowers. In the model we tested if there were significant differences of *B. terrestris* visitation to crops between the time intervals of measurements including, pre-exposure, during-exposure, and post-exposure.

We set each ‘Crop row ID’ (N=12) as our random effect. We tested model assumptions using the ‘DHARMA’ package (Hartig, 2020), and we set distribution as ‘poisson’ as this showed best fit of model when inspecting model residuals.

We ran separate models for 0m, 2m and 9m. This was because models in which we instead fit distance as a co-variable had some dimensions of the variance-covariance matrix estimated as exactly zero, likely due to the random effects structure being too complex. For models with significant effects we performed Tukey-post hoc analysis using the ‘glht’ function in the ‘multcomp package (Hothorn *et al.*, 2016) to examine variation between each of our response variables (time intervals of measurements).

During initial examination of all trials, we identified two trials that were potential outliers. At one site we measured the same crop type (zucchini) at two different crop rows (>25 meters apart). Pre-exposure measurements to both crop rows was exceptionally high being 5-7 visits by *B. terrestris* per flower, compared to an average of 1-2 visits per zucchini flower. High visits pre-exposure at one site were likely shaped by very high temperature prior to a storm on the day of observations. To test if these trials substantially influenced results, we ran models both including and excluding these two trials.

iii) Do insects switch from feeding on P. tanacetifolia to feeding on adjacent plant species

To examine the proportion of times insects switched from feeding on *P. tanacetifolia* to feeding on neighbouring plants, we divided the number of insects switching to crop plant species from total number of visits recorded to insectary plant. We also calculated the proportion of switches per 10-min observation to *P. tanacetifolia*.

5.4 RESULTS

i) which insects will visit P. tanacetifolia during short-term exposure

The main insects visiting *P. tanacetifolia* were *B. terrestris* (n=125 visits to *P. tanacetifolia*, all sites) making up 85% of overall recorded visits. *B. terrestris* (n=505) were also the most abundant visitor to crops (83 % of all visitors) and non-crop flowers (48 %), (425 visits to crops, 80 to non-crops, all sites).

Other visitors to *P. tanacetifolia* included native bees in the genus *Lasioglossum* (*chilalictus*) (8 visits to *P. tanacetifolia* from non-identified species, 1 visit *L.littovillum*, 5/6 sites). *Lasioglossum* (*chilalictus*) spp. overall were found visiting non-crop and crops in low abundance (4 visits to crops, 6 to non-crops, 5/6 sites).

A. mellifera were found in very low abundance visiting *P. tanacetifolia* (2 visits to *P. tanacetifolia*, 2/6 sites), however they were otherwise found in much higher abundance making up 16 % of all visits to crops, and 41 % to non-crops (n=148, 81 visits to crops, 67 visits to other non-crops, 5/6 sites).

Other insects recorded during observations included Muscidae sp. (n=10, unidentified) at one site only visiting *P. tanacetifolia*, and single visits by *Megachilidae heriadiformis* and cabbage white pests (*Pieris rapae*). Along with drone hoverflies (n=5, *Eristalinae tenax*, 1 out of 6 sites,) and slim hoverflies (n=5, *Melangyna* spp., 1 out of 6 sites,) and *Megachile* sp.2 (n= 2) to non-crop flowers only.

ii) if the short-term exposure with insectary plant changes visitation to adjacent flowering crops during and post-exposure (competition/facilitation)

When all trials were included (N=12), there were no significant differences in *B. terrestris* visitation to crop flowers between pre/during/post exposure of *P. tanacetifolia* at any of the observed distances from the introduced plant (0, 2, 9 meters, Table 4.2).

However, when two replicates that potential acted as outliers were excluded (see detail methods), we found that *B. terrestris* visitation to crops immediately next to the placement of *P. tanacetifolia* (0 meters) significantly increased post exposure (Table 3, Fig.4.2).

Posthoc tests (tukey contrasts) in this case found significant differences between the post exposure and pre exposure measurement (estimate=0.88, std. error=0.31, z value=2.8, $\Pr(>|z|)=0.036$) (Fig.5.2), with higher visits during post exposure (Fig. 5.2).

Bombus terrestris visitation further significantly increased during 4-day exposure at the two spatial intervals further away from placement of *P. tanacetifolia* (2m, 9m) (Table 5.3, Fig. 5.2). Posthoc tests for each model (2 meters and 9 meters) however showed not significant differences in visitation.

Table 5.2 Results of generalized mixed-effect models testing if there were significant differences in *Bombus terrestris* crop visitation pre/during/post exposure with *Phacelia tanacetifolia*. All crop rows included. Separate glmer model for each rep 0 meters immediately next to exposure with *Phacelia tanacetifolia* and 2 meter, 9 meters away.

glmer - all crop flowers				
66 observations, 12 different crop rows measured				
0 meters				
	estimate	SE	z value	Pr(> z)
Pre	0.32	0.36	0.88	0.38
During - 1 day	- 0.21	0.29	- 0.7	0.46
During - 4 day	0.05	0.27	0.19	0.85
Post - same day	0.24	0.26	0.92	0.36
Post - day after	0.27	0.26	1.05	0.29
2 meters				
pre	0.38	0.33	1.16	0.25
during - 1 day	-0.22	0.2	-1.08	0.28
during - 4 day	0.11	0.19	0.56	0.58
post - same day	-0.07	0.19	-0.39	0.7
post - day after	-0.05	0.19	-0.27	0.8
9 meters				
pre	0.38	0.33	1.16	0.25
during - 1 day	-0.22	0.20	-1.08	0.28
during - 4 day	0.11	0.19	0.56	0.58
post - same day	-0.08	0.19	-0.39	0.7
post - day after	-0.05	0.19	-0.27	0.8

Table 5.3 Results of generalized mixed-effect models testing if there were significant differences in *Bombus terrestris* crop visitation pre/during/post exposure with *Phacelia tanacetifolia*. Two crop rows acting as potential outliers were excluded (see method for detail). Separate glmer model for each rep 0 meters immediately next to exposure with *Phacelia tanacetifolia* and 2 meter, 9 meters away.

glmer - two crop rows excluded				
56 observations, 10 different crop rows measured				
0 meters				
	estimate	SE	z value	Pr(> z)
pre	-0.26	0.47	-0.54	0.59
during - 1 day	0.25	0.35	0.71	0.47
during - 4 day	0.43	0.33	1.27	0.2
post - same day	0.66	0.32	2.03	0.042*
post - day after	0.88	0.31	2.84	0.0045 **
2 meters				
pre	-0.37	0.46	-0.81	0.42
during - 1 day	0.58	0.37	1.6	0.02
during - 4 day	0.84	0.35	2.38	0.017 *
post - same day	0.59	0.37	1.62	0.15
post - day after	0.67	0.36	1.88	0.06
9 meters				
pre	-0.25	0.42	-0.6	0.55
during - 1 day	0.38	0.38	1.02	0.31
during - 4 day	0.82	0.35	2.35	0.018 *
post - same day	0.31	0.39	0.79	0.42
post - day after	0.38	0.37	1.02	0.31

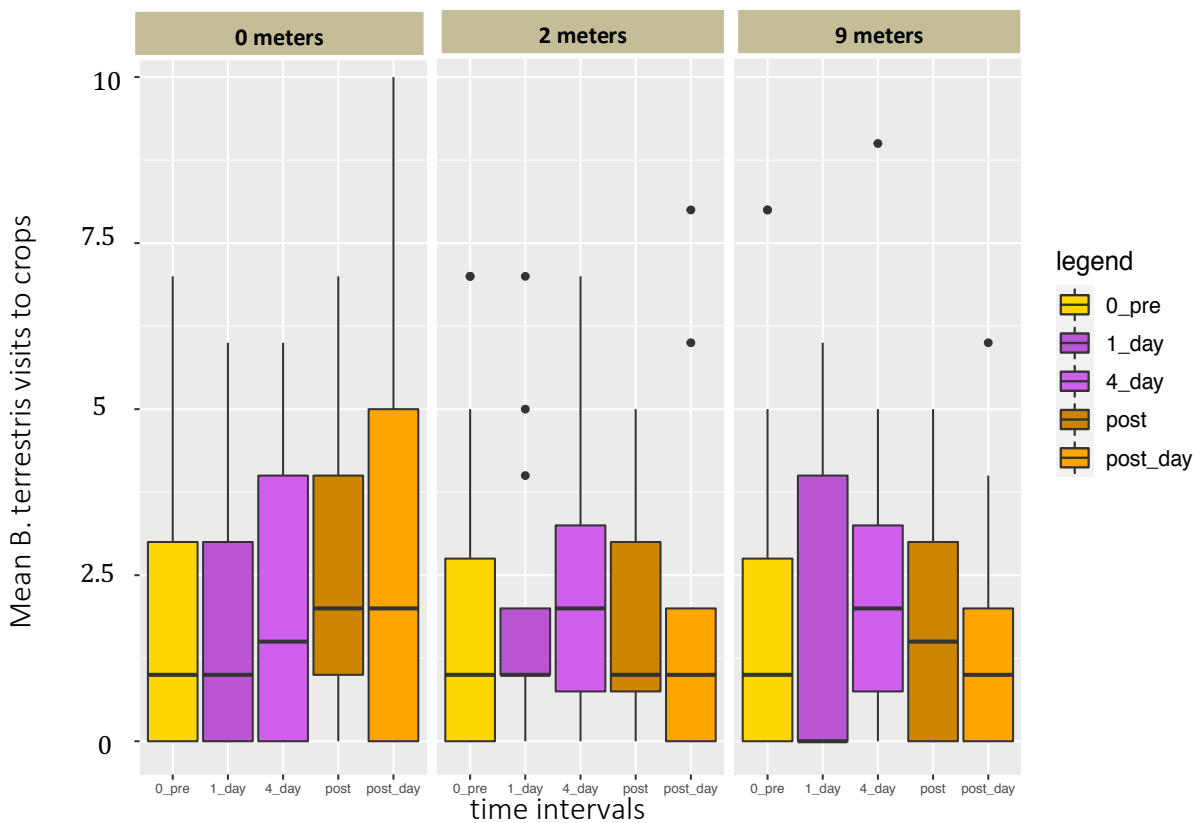


Figure 5.2 *Bombus terrestris* visitation to crop pre, during and post exposure with *Phacelia tanacetifolia* – all crop rows at 0 meters immediately next to exposure and 2 meters and 9 meters away. Total crop rows included N= 10, two crop rows as potential outlier excluded. Legend: 0_pre – prior to adding of *P. tanacetifolia*, 1_day – one day after adding, 4_day – four day after adding, post- 30-60 minutes following removal of *P. tanacetifolia*, post_day – one-two days following removal.

iii) if insects switched from feeding on insectary plant to feed on adjacent plant species

In total, 11.7% of the *B. terrestris* observed feeding on *Phacelia tanacetifolia* switched to foraging on an adjacent crop species. *B. terrestris* were encountered moving from *Phacelia* to nearly all of the different crops measured (except Squash), including switching to Scarlett runner (2), French Bean (4), Zucchini (3), Pumpkin (2), Tomatillo (2), and also to non-crop flowers (weedy, post-harvest crops) *Lotus corniculatus* (1), Brassica sp. (2), Spinach (1). *A. mellifera* were encountered in very low numbers visiting the insectary plants and no movement to other species was noted.

5.5 DISCUSSION

Our study highlights that abundant bumblebee workers (*B. terrestris*) found at market-gardens in Tasmania quickly integrated *P. tanacetifolia* into their foraging. The second most abundant flower-feeding insects recorded, honeybees (*A. mellifera*) on the other hand, were very infrequently found visiting *P. tanacetifolia*. We recorded some native bees visiting *P. tanacetifolia* (mainly *Lasioglossum (chilalictus)* spp.), however solitary native bee abundance was generally low.

Our results suggest that *A. mellifera* continued foraging on plants they were already visiting (flower constancy) (Free, 1963; Waser, 1986; Grüter *et al.*, 2011), whilst *B. terrestris* more readily changed, or integrated *P. tanacetifolia* into their foraging (Raine and Chittka, 2007). Evidence elsewhere highlights both bumblebees and honeybees appear to be highly attracted, and preferentially found foraging on *P. tanacetifolia* (Carreck and Williams, 2002; Pontin *et al.*, 2006; Mallinger *et al.*, 2019). It is hence unlikely that *A. mellifera* was not be attracted to this plant species. However, *A. mellifera* may have been less attracted to *P. tanacetifolia* in this experiment due to small-patch sizes and due to exposure with *P. tanacetifolia* only for a relative short period of time (4 days).

We found evidence that some *B. terrestris* switched between plant species (Raine and Chittka, 2007). Approximately 12% of the *B. terrestris* we observed switched from feeding on *P. tanacetifolia* to adjacent plants (mainly to crops). These individuals may have already been foraging on adjacent plants prior to our experimental exposure, then integrated *P. tanacetifolia* into their foraging, or were attracted into the area by *P. tanacetifolia* (magnet-effect) (Molina-Montenegro *et al.*, 2008), and then moved onto foraging on crops.

Findings from our study show that the integration of *P. tanacetifolia* into the foraging of a large number of *B. terrestris* workers did not lead to a reduction of visitation to adjacent crop flowers. Instead, our results highlight that exposure to *P. tanacetifolia* had a neutral effect on *B. terrestris* visitation to crop flowers. Our study gives further evidence that the presence of non-crop flowers can have a non-competitive effect on visitation to crops, as found in other studies examining the effect of companion plants (Griffiths-Lee *et al.*, 2020; Montoya *et al.*, 2020), wildflower strips (Blaauw and Isaacs, 2014; Campbell *et al.*, 2017b).

Whilst our study found no competitive effect, we also found no strong evidence of magnet-effect, in terms of increased visitation (potential facilitation) to crop flowers with the addition of *P. tanacetifolia*. Our data do show significantly more visits from *B. terrestris* to crop flowers during 4-day exposure for the further away distances (2m, 9m). However, there were no significant differences between pre and during exposure when running post-hoc Tukey tests. Our results highlight that the placement of *P. tanacetifolia* potentially influenced visitation along the crop row. Work by (Ogilvie, 2014) shows that

there can be a frequent spillover of bumblebees from one plant to another at a distance of up to 30 meters. Designing an experiment which allows us to measure the same crops between sites (by sowing those out simultaneously across farms), along with marking of individual workers, would be a way to examine this further.

The strongest effect detected in our study was for increased visitation of *B. terrestris* to crop flowers once *P. tanacetifolia* was removed, compared to visitation to the same crops prior to exposure. This effect was significantly higher for crop flowers immediately (0 meters) next to the *P. tanacetifolia*. Visitation to crop flowers at 2 meters and 9 meters away from prior placement of *P. tanacetifolia* meanwhile did not appear to increase following post-removal. High visitation to crops post-removal could be explained by *B. terrestris* showing site constancy, with some *B. terrestris* staying within area and continuing to forage on crop flowers once their preferred *P. tanacetifolia* was removed.

Site consistency in several bumblebee species has been reported elsewhere (Ogilvie and Thomson, 2016). Olgivie and Thompson 2016, observing marked individual bumblebee workers, found that once a frequently visited plant (*Delphinium barbeyi*) was removed, a large proportion of workers (78 %) continued foraging on subsequent flowering plants at the same site. In our study, we found increased visits post-removal of *P. tanacetifolia* to crop flowers only at 0 meters, whilst spillover effect of bumblebees from one plant species to another has elsewhere been reported to up to 30 meters (Ogilvie, 2014). There may be a stronger impact over distances if the patch size of plants removed is larger. Furthermore, the effect we measured was potentially transient. We cannot make predictions about whether or not the effect of increased visits immediately next to placement of *P. tanacetifolia* diluted or changed over time, as we only took measurements one-two days post removal.

Overall, our study highlights that when measuring the effect of non-crop flowers on visitation to crop flowers it is advisable to further test if effect varies between different insect species. Short-term experimental manipulation highlighted that some *B. terrestris* workers appeared to quickly alter their foraging behaviours and visiting a newly added plant species *P. tanacetifolia*. This subsequently increased visitation by *B. terrestris* to crop flowers once *P. tanacetifolia* plants were removed.

Another pollinator, *A. mellifera*, which was also found in high abundance throughout our experiment visiting crop and other flowers, was rarely found visiting *P. tanacetifolia*. Low spillover of *A. mellifera* has also been reported in a study conducted in NSW, Australia, where excluding (bagging) of native plants did not impact visitation to adjacent flowering plants (Gilpin et al., 2019a). Our data is consistent with suggestions elsewhere that insects that more readily switch between resources, as found in bumblebees, are also more likely to show changes to visitation to crop flowers with the presence of

neighbouring co-flowering non-crop flowers (Knapp et al., 2019). Whilst pollinator systems dominated by *A. mellifera*, or other species that less readily switch between floral resources in their foraging bouts, show lesser impact (Gilpin et al., 2019b).

Furthermore, the site constancy found in some foraging bumblebees could potentially be strategically used by growers to increase visitor abundance to crops, by having plants flowering prior to crop bloom (Eckerter *et al.*, 2022). Yet taxa that are more prone to resource-switching may also come at some cost to a crop's reproduction success (Ghazoul, 2006). This is because they increase the chance of heterospecific pollen transfer, which can interfere with the fertilisation and seed/fruit set of plants (Waser, 1978; Morales and Traveset, 2008; Morales and Traveset, 2009; Ye *et al.*, 2014).

We propose that further work is needed to examine if the increase in visitation to crop flowers observed in this study is short-term only, or if there are longer-term effects of site constancy for individual bumblebee workers. Marking individually workers (Ogilvie and Thomson, 2016) will further allow to examine changes in foraging behaviour in greater detail, including examining their movement over space. More generally, future tests of extended exposure periods would allow to examine if other common pollinators, such as *A. mellifera* or native bees, respond differently to introduced plants depending on the duration of their availability. Future work should also trial the addition of varying patch sizes of non-crop plants, to see if the neutral-to-facilitative response observed in our study stays or changes when there is a larger ratio of non-crop to crop plants (Nicholson *et al.*, 2019).

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Chapter 6: General Discussion

6.1 THESIS SYNTHESIS

Beneficial flower-feeding insects play an integral role in supporting our agricultural production via crop pollination, and by aiding in the natural control of agricultural pests (Kremen and Chaplin-Kramer, 2007) along with being an essential part of sustaining broader healthy ecosystems (Ollerton *et al.*, 2011). The way land is managed for agricultural purposes, whether it is large or small scale, urban or rural, can impact insect abundance and diversity (Gurr *et al.*, 2003; Lin *et al.*, 2015; Garibaldi *et al.*, 2017b). However not all actions that are aimed at enhancing ecosystems or biodiversity values will necessarily have the same response (Landis, 2017; Tschamntke *et al.*, 2021). To guide management actions that are more likely to have a positive effect on directly supporting beneficial insects and the ecosystem services they provide requires localised knowledge on insect-plant interactions (Saunders *et al.*, 2013; García and Minarro, 2014; Sutter *et al.*, 2017; Scheper *et al.*, 2021).

The overarching aim of this thesis was to gather baseline data on, and new insights into, the flowering resources available in Australian horticultural systems and the types of insects they sustain. This aim encompasses both identifying the insects that are likely contributing to the pollination of crops and examining which non-crop flowers and management approaches may be most useful for enhancing flower-feeding insect biodiversity and key ecosystem services such as pollination and pest control.

I focused my data collection on horticultural systems that grew insect-pollination-dependent crops, including:

- **perennial orchards (apple, blueberry) in Tasmania (Chapter 2):** here I specifically compared visitation profiles of flower-feeding insects between crops, non-crop introduced plants and native plants.
- **small-scale diverse fruit and vegetable farms (market-gardens) in Tasmania (Chapter 3):** here I examined insect-plant interactions between different flowering plants at market-gardens to identify which beneficial insects (pollinator and natural pest enemies) and pest insects were feeding on plants and if there were key plant species.

- **market-gardens in south-east NSW (Chapter 4):** I tested the impact of local plant composition on diversity and abundance of flower-feeding insects, examined insect-plant interactions as in Chapter 3, and compared these findings with those in Tasmania.
- I further conducted an **experimental study at market-gardens in Tasmania (Chapter 5)**. I used short-term exposure to a highly attractive insectary plant to examine changes in foraging of flower-feeding insects (Chapter 5).

For this final synthesis and discussion of my thesis I will now revisit three overarching questions embedded within my thesis, discuss some of the overall findings, highlight some of the limitations of my research in addressing these questions, and outline some of the research recommendations I identified from the findings of my thesis.

6.2 DISCUSSION OF OVERARCHING RESEARCH QUESTIONS

6.2.1 Are crop pollination services in Australia potentially at risk because crops are mainly visited by a single pollinator species (*A. mellifera*)?

Brief background

Relying on a single species for pollination services of our varied pollinator-dependent crops is extremely risky (Cunningham *et al.*, 2002; Klein *et al.*, 2009; Rader *et al.*, 2016; Cook *et al.*, 2020). Dependence on a single pollinator is particularly concerning as trends around the world have been highlighting substantial negative effects on the health of the western honeybee – *Apis mellifera* (Klein *et al.*, 2009). In many parts of the world there have been observed population instabilities of wild and managed *A. mellifera* hives, which has likely been exacerbated by *Varroa* mite (*V. destructor*) (Flores *et al.*, 2021). Decline in available *A. mellifera* has contributed to substantial pollination shortages and rapid increase in the cost of pollination services around the world (Sumner and Boris, Klein *et al.* 2009). The 2022 *Varroa* mite incursion in New South Wales (DPI, 2022) has the potential to severely impact honey bee populations in Australia, and the free pollination services delivered from feral (wild) honeybees. To safeguard pollination services in Australia and minimize economic risks requires an increased understanding on which other insects are contributing to the pollination of our crops (Cunningham *et al.*, 2002).

This allows us to identify which management initiatives are most useful to aid specific alternative pollinators (Brown *et al.*, 2020; Cook *et al.*, 2020) along with identifying which crops are most at risk because they are not attractive to our native insect communities (Brown and Cunningham, 2022b).

Discussion and Future Directions

Horticultural crops were mainly visited by A. mellifera and B. terrestris

In this thesis I surveyed multiple flowering crops, many of which require or benefit from insect pollination for successful fruit and seed development. Two crops were surveyed in Tasmanian orchards (apple, blueberry, Chapter 2) and others in market-gardens (Tasmania Chapter 3, NSW Chapter 4). My results highlight that a large proportion of the crops both in orchards and market-gardens, were overall received most abundant visits by honeybees – *A. mellifera* (summary see Table A.6.1.). In Tasmania, a secondary introduced bee species *Bombus terrestris* was further visiting numerous crops, including blueberries, and was the most abundant visitor to legumes and nightshades in market-gardens, but were very infrequent visitors of apple (Table A.6.1). Larger flowering cucurbit (pumpkin, squash, zucchini) appeared to be crops most unattractive to native insects in my study, with nearly all visits recorded being the two introduced bees (in NSW only *A. mellifera*).

While some crops were nearly exclusively visited by introduced bees, other crops were frequently visited by native insects. Reed bees – *Exoneura* for example were found visiting both apple and blueberry (Chapter 2), along with caneberries (raspberry, boysenberry, blackberry) (Chapter 3). Hoverflies - Syrphinae were found visiting apple (Chapter 2) and were most frequent visitors to strawberries in spring (Chapter 3). Other native bees showed low contributions to melon, cucumbers and nightshades (Solanaceae) in NSW (Chapter 3).

Specific management initiatives to enhance alternative pollinators to orchard crops are discussed in more detail in (Chapter 3), including the role native vegetation plays for *Exoneura* (see summary Table of recommended native plants based on findings Chapter 3, Table 6.1), and introduced forbs for certain hoverflies and Lasioglossum (*Chilalictus*). Another measure not discussed in Chapter 3. is the potential of integrating later flowering caneberry crops (raspberry, boysenberry, blackberry) with earlier flowering orchard crops - apple, blueberry. Complementary flowering crops (apple, blueberry followed by raspberry) in the landscape were beneficial in prolonging available flowering resources and enhancing diversity of crop pollinating taxa in Canadian study (Martins *et al.*, 2018). Integrating caneberries crops within orchard systems in south-east Australia may further be beneficial to enhance nesting resources, due to caneberry stems, unlike apple or blueberry, being a suitable nesting material for *Exoneura* (Coates *et al.*, 2022).

Table 6.1. Flowering native plant species and common visitors observed surveyed at apple and blueberry orchards in southern Tasmania.

Species	Family	Flowering time	Common flower-visitors observed
<i>Goodenia ovata</i>	Goodeniaceae	Spring/early summer	<i>A. mellifera</i> , Exoneura, Lasioglossum
<i>Pultenaea juniperina</i>	Fabaceae	Spring	Lasioglossum, Exoneura, <i>A. mellifera</i>
<i>Oxylobium ellipticum</i>	Fabaceae	Spring	<i>A. mellifera</i> , Exoneura, Syrphinae
<i>Melaleuca squarrosa</i>	Myrtaceae	Spring/early summer	Exoneura, <i>A. mellifera</i> , Lasioglossum
<i>Ziera arborescens</i>	Rutaceae	Spring	Exoneura, <i>A. mellifera</i> , Syrphinae
<i>Senecio linearifolius</i> i)	Asteraceae	Summer	Syrphinae, Exoneura, <i>A. mellifera</i> , <i>B. terrestris</i>
<i>Cassinia aculeata</i>	Asteraceae	Summer	Lasioglossum, Syphinae

i) caution to similar looking introduced fireweed *S. madagascariensis*, Tasmanian declared weed species

Native insects and vegetable seed production

Within market-gardens, several vegetable crops that were left to go to flower (e.g., carrot, leek, brassicas) were attractive to a high diversity of insects (Chapter 3, 4). The production systems I studied in no way resemble the large fields used for seed production. The results from my study do however give a list of candidate insect species that are potential alternative pollinators of seed crops (Table 3.1) and overlaps with species identified also identified by (Hogendoorn and Keller, 2011; Gaffney *et al.*, 2018). As in the horticultural industry the Australian seed industry appears to heavily rely on *A. mellifera* for pollination of many insect depended seed crops (Cook *et al.*, 2020). To further aid in securing the pollination of our seed crops, I recommend further work to examine to which degree native insects are attracted to larger fields of vegetable seed crops, which of the insects are most effective, and what management initiatives could be used to promote their abundance.

Further work needed to test efficiency/effectiveness of pollinators

For this thesis I focused on identifying which crops were being visited by different flower-feeding insects. This provides insights into which insects were attracted to different crops. However, my work does not give insight into their relative contribution to crop pollination, and not all visitation leads to pollination. Quantifying efficiency and effectiveness is very time consuming and would not have been achievable for the varied crops examined. Instead, the candidate pollinators identified in this thesis could be screened further for efficacy/effectiveness. In particular Exoneura – blueberry pollination, Syrphinae – apple, Syrphinae, *Eristalis tenax*, and Lasioglossum(Chilalictus) - varied vegetable seed crops.

Impact co-flowering plants on crop visitation

The visitation profiles to crops grown in the small-scale production systems (market-gardens, Chapter 3, 4) examined in my thesis may vary compared to observations made in larger monocultural production. The presence of co-flowering plants on the one hand can enhance pollinator diversity to flowering crops (Pereira *et al.*, 2015; Norfolk *et al.*, 2016; Alomar *et al.*, 2018). However, plant diversity can however also lead to competition or dilution of pollinators visiting crops (Nicholson *et al.*, 2019; Delphia *et al.*, 2022; McDougall *et al.*, 2022). Future work could compare visitation and pollination effectiveness between crops grown in monocultural versus diverse polyculture systems, in particular for crops found to be more attractive to native bees in this thesis, example *Rubus* spp., apple/blueberry, smaller cucurbits in NSW.

Further the impact of adding a highly attractive plant species to insects visiting flowering crops was tested in Chapter (5) of this thesis. The results from this study highlighted non-competitive impact of adding a plant to the visitation of *B. terrestris* to crops (Chapter 5). Yet, the overall low abundance of insects other than *B. terrestris* visiting experimental plant did not allow to test effect on other insects (i.e. native bees, *A. mellifera*). To examine impact of co-flowering plants on native bees visiting crops in south-east Australia, I recommend experiments next to crop flowers more attractive to native bees, including *Exoneura* – *Rubus* spp. or *Lasioglossum* – Brassicas.

B. terrestris as crop pollinator in Tasmanian systems

Whilst *B. terrestris* was found to be a frequent visitor of several of the crops I surveyed in Tasmania, I do not recommend this taxa being moved into mainland Australia. Accidental or purposeful introduction of insects poses high ecological risks, including competition for floral resources and spread of diseases (McQuillan and Hingston, 1999; Dafni *et al.*, 2010; Fung *et al.*, 2018); along with potential of increasing spread of dormant weed species (Hingston, 2006b; Goulson and Rotheray, 2012). Within Tasmania *B. terrestris* eradication of this species is not longer an achievable option, as they have naturalised throughout the island (Hingston, 2006a). Whilst *B. terrestris* appeared to so far be relative healthy (Fung *et al.*, 2018), the severely inbred populations in Tasmania (3-4 founding female queens from New Zealand) (Schmid-Hempel *et al.*, 2007) could make them at high risk to rapid decline in the future. Whilst *B. terrestris* visited several crops and likely aided in their pollination services (Knapp and Osborne, 2019; Kendall *et al.*, 2020), I do not recommend management interventions to encourage their abundance, due to potential damage they cause to some crop flowers, and already high abundance of this introduced species. I recorded damage of *B. terrestris* to tubular crop flowers, with both blueberry and broad-beans being frequently ‘nectar robbed’. Nectar robbing is used by bumblebees to access nectar more easily, by puncturing holes into the side of flowers. Such holes are then often subsequently

used by honeybees to also access nectar. Nectar-robbing can then led to plants not being pollinated, or reproduction parts of plants being severely damaged, thus negatively impacting yield (Macfarlane, 1992; Smith-Ramirez *et al.*, 2021). Growers specifically highlighted that they have been seeing unsuccessful yields in their broad-bean crops, which appeared to come from damage to flowers. This has been observed elsewhere (Smith-Ramirez *et al.*, 2021), and warrants further investigation in Tasmania. It has been observed that nectar robbing is lesser associated with larger *B. terrestris* queens, that emerge first in early spring and more associated with smaller workers, due to their inability of accessing nectar/pollen of blueberry flowers (personal communication, L. Evans). This could make earlier flowering blueberry crops less susceptible to flower damage.

Managed honeybee hives to aid pollination services

My results highlight that several crops likely heavily depend on *A. mellifera* as a major crop pollinator, with native insects being lesser abundant or not found to be attracted to some crops. Within Tasmania some crops were visited further by *B. terrestris*, however others were not, including apple which is a major horticultural crop grown in Tasmania. These findings highlight that potential loss of feral *A. mellifera* will likely also warrant increased need of the deployment of managed honeybees, with large proportion of growers currently relying on free pollination services.

An Australian survey ‘*Understanding practices in key pollination areas*’ (Leech and Australia, 2014) outlines that most fruit-growers in Australia had a high awareness around the importance of pollination for their production and that many growers relied on feral honeybees visiting their crops. This also resembled in the conversations I had with fruit-growers (apple, blueberry) with only one blueberry and one apple farm renting hives during bloom to help with their crop pollination. All other orchards relied on free pollination services. Some market-garden growers had honeybee hives on their farms, conversations highlighted that these were mainly added for honey production with most market-gardens appearing to also rely on ‘free’ pollination services.

A decline of feral honeybees in the Australian landscape would likely lead to increasing pollination shortages which further will necessitate growers increasing the use of managed honeybees for pollinator depended crops (Tasmania, 2019). This was further highlighted in Leech’s survey with most fruit growers stating that decline in feral and managed honeybees would have substantial implications on their fruit production. To aid our crop pollination services I suggest gaining more insight into the relationship between the growers and beekeepers, and what measures may be useful to enhance these two important industries working together. And may further be aided by governmental incentives that makes agricultural land more attractive to beekeepers (Leech, 2012).

6.2.2 Are flowers found in agroecosystem valuable in sustaining native insect community, or do they mainly support a few highly generalist species?

Brief background

Landscape disturbance, simplification and fragmentation, in particular the loss of semi-natural habitat in agroecosystems and urban landscapes leads to decreases in the diversity of bees and other insects (Landis *et al.*, 2000; Winfree *et al.*, 2009; Winfree *et al.*, 2011; Kennedy *et al.*, 2013; Harvey *et al.*, 2020). However, some insects can benefit from moderate levels of disturbance, if they are able to utilize resources found within disturbed areas (Cane, 2001; Westphal *et al.*, 2003; Kremen *et al.*, 2007; Winfree *et al.*, 2007).

Discussion and Future Directions

Most common flower-feeding insects observed

The agroecosystems I surveyed were overall dominated by two introduced bees, *A. mellifera* and (in Tasmania only), *B. terrestris*. Both bees are known to be ‘super’ generalists and were found visiting a variety of plants in my studies (Table 3.1). As both bees are social (eu-social *A. mellifera*, primitive eusocial (*B. terrestris*)) this makes them establish in much large number of workers per hive, as compared to non-social insects that only have individual foragers.

More abundant species are also more likely to be observed feeding on different flowers, as their abundance increases chance of encounters, which in turn can result in higher chance to show greater diet-breath compared to insects observed less frequently. In NSW the native eusocial stingless bee (*Tetragonula carbonaria*) was also found to be the most abundant species following *A. mellifera* (Table 4.3). *T. carbonaria* also showed higher diet breath compared to other insects, and was most frequently found visiting plants from only three plant families (Results Chapter 4, Fig. 4.2). High abundance of *A. mellifera* and other social bees has further been reported elsewhere in Australia, including other studies conducted in agroecosystems but further also for studies that examined natural systems. (Johanson *et al.*, 2018; Elliott *et al.*, 2021).

Other native insects more commonly observed (>15 total observations) were also generalist, in terms of feeding on varied flower in the agroecosystems I studied (Fig. 3.2, 4.2). Whilst their narrow diet breath was likely shaped by low encounters, my data further highlights that certain introduced plants

appeared to be more suitable to promote native insects over others. For example, some introduced plant families (Cucurbitaceae, Fabaceae, Boraginaceae) were predominately visited by introduced bees, particularly in Tasmania. Other plant families and species sustained a much greater variety of native insects (Fig 3.2 , Fig 4.2). Most native insects were also more commonly found on certain groups, or families of plant species. Highlighting that more generalist species may still show preferences towards particular plants and plant families (Fründ *et al.*, 2010; Jeavons *et al.*, 2020). For example, Asteraceae and Brassicaceae were frequently visited by hoverflies and *Lasioglossum (Chilalictus)* spp. in all study systems (Fig. 2.3, Fig. 3.2, 4.2). *Exoneura* spp. on the other hand were frequently found visiting Rosaceae crops in Tasmanian orchards (Chapter 2), however overall showed a fairly varied diet and no direct patterns of being more associated with certain plant families in market-gardens, apart from higher visits to *Rubus* spp. (Chapter 3,4). Within market-gardens in Tasmania (Chapter 3) I further found distinct floral association between *Megachile* spp. and an introduced Fabaceae (*Lotus corniculatus*). High association was also found for beetles with most encounters on introduced plants being to plants in the Apiaceae family. Wasps were further mainly found on introduced plants in the Lamiaceae, Apiaceae and few Asteraceae plant families (Fig 3.2, 4.2, family associations, Fig. 3.3, Fig. 3.4 plant species associations).

However, methods used in this thesis do not allow to make direct predictions on specific preferences of native insects to certain introduced plants. My study systems showed high variation in terms of specific flowers being found within each market-garden shaped by each farmer's land management. These systems varied compared to for example more natural herbaceous meadows which show a greater overlap in their plant composition for others that show a greater overlap in plant composition found for example in (Fründ *et al.*, 2010; Sutter *et al.*, 2017). To further test preferences of native insects to specific introduced plants and how this varies between taxa further experimental studies are needed. Recommended introduced plant species to use in experiments are included in (Table 6.2).

Composition of native insect community

Overall, my data suggests that there were some groups of introduced plants more suitable than others to support native insects. However, the overall composition of insects further highlights that only certain insects were commonly found feeding on the mainly introduced flowers I studied in the agroecosystems. In the following I will now more specifically examine the groups of native insects I encountered.

The most common native bees found in this study showed high overlap with observations found elsewhere in south-east Australia. Including high presence of halictidae bees, in particular *Lasioglossum (Chilalictus)* spp. and Apidae - *Exoneura* spp. for my datasets in Tasmania (Fig. 2.3, Table 3.2), similar to that found by (Goulson *et al.*, 2002; Lentini *et al.*, 2012; Brown *et al.*, 2020). Higher abundance was

also found for Halictidae bees in south east NSW (Table 4.3) including *Lasioglossum (chilalictus) spp.*, *Lipotriches spp.*, *Homalictus spp.*, along with bees in the Apidae family *Tetragonula carbonaria* and *Exoneura spp.* Here my findings overlap with other rural and urban agroecosystems in south-east NSW (Makinson *et al.*, 2017; Gilpin *et al.*, 2022a).

Other bees were found in low abundance. This included bees in the Megachilidae family, which appear to be generally less abundant in Tasmania (Hingston, 1998). However have been recorded more abundant in other south-east NSW studies compared to my findings in urban community gardens (Makinson *et al.*, 2017; Vanderstock *et al.*, 2022). To my knowledge the floral preferences of Megachilidae appear to be less known in Australia. However some insight highlights that they are thought to be more specialised in their feeding compared to highly generalist Halictidae bees (Cardale, 1993; Hingston, 1999). This further explains their preference to introduced Fabaceae (*Lotus corniculatus*) observed in my study and elsewhere (Johanson *et al.*, 2018).

I also found lower numbers of *Amegilla spp.* compared to south-east NSW studies in urban community gardens (Makinson *et al.*, 2017; Vanderstock *et al.*, 2022). Differences in my observations to other studies in NSW may have been shaped by varied nesting, floral resources in my study systems, which included both urban and rural farms, along with potential lower abundance in general during the year of my sampling.

Further I only found a small number of Colletidae bees mainly visiting Myrtaceae plants in orchards and market-gardens (Appendix 2.3). Along with a few single encounters of Colletidae bees feeding on introduced plants in market-gardens (Table 3.2, Table 4.3). The lack or low amount of flowering native plants around the agroecosystems I surveyed, highlights the lack of suitable flowering resources for more specialised insects. A well represented bee family in Australia Colletidae family (Euryglossinae, Hylaleina, Neopasiphaeinae- Leioproctus) have been found to be strongly associated with old lineages yet still well represented native plant families Myrtaceae and Fabaceae- Mirbelioid, Protaceae (Armstrong, 1979; Hingston, 1999; Hingston and Mc Quillan, 2000; Brown and Cunningham, 2022b).

The comparison of flower-feeding insects other than native bee (e.g., hoverflies, wasps and beetles), was difficult to make, as to my knowledge there is limited published work specifically from south-east Australia. This made it difficult to gain more specific insight if taxa observed were generally rare, or not supported by flowering resources found in the agroecosystem I studied.

Hoverflies were fairly well represented in all of my study systems, and included predatory hoverflies (*Melangyna spp.*, *Sphaerophoaria spp.*) which were also abundant taxa in all agricultural systems (Appendix 2.3, Table 3.2, Table 4.3), along with drone hoverflies (*Eristalis tenax*) in Tasmanian

market-garden during summer (Table 3.2). There is inconclusive insight from my study to highlight the overall species diversity sustained but broader genera overlap with those observed elsewhere (Robertson *et al.*, 2020; Tasker *et al.*, 2020; McDougall *et al.*, 2022). A study that looked more explicitly at diversity of Hoverfly and bee fly (*Bombyliidae spp*), found that overall dominance of only a few species in orchards (Robertson *et al.*, 2020). My data shows that some introduced plants attracted a high number of hoverflies, in particular those in the Asteracea and Brassicaceae family (Fig 3.2, Fig 4.2). More work is needed to examine if certain introduced plants support a greater diversity of hoverflies and other flies compared to others.

The total beetle abundance was further dominated by mainly a few species in market-gardens and orchards in Tasmania (*Phylotucus rufipennis*, *Chauliognathus lugubris*), and introduced ladybeetles (*Hippodamia variegata*) at market-gardens in both Tasmania and NSW. Several other beetles were also recorded (Appendix 2.3, Table 3.2, Table 4.3), some of which overlapped between sites however further several that were only recorded ones. Apiaceae flowers were the main plants that were visited by beetles. The list of beetles found in this study allows to give some insight on flower-feeding beetles sustain in Australian agroecosystems. How the compositions of beetles I observed to that found on other plants, including natives was difficult to, as I found very little published work on flower feeding beetles in Australia.

Wasps were overall recorded very infrequently, most which were single observations (Appendix 2.3, Table 3.2, Table 4.3). Findings elsewhere do however highlight that flower wasps (Thynninae), as seen in Colletidae bees, are also strongly associated with feeding on plants in the Myrtaceae family (Brown and Phillips, 2014). Findings from my flower-observations at market-gardens further highlight that some introduced plants further appear to be suitable food-sources for some wasps and beetles in Australian agroecosystem (Maingay *et al.*, 1991; Rizvi *et al.*, 2022) (discussed further in Chapter 2, 3).

Further research is needed to test the effect of integrating native vegetation to increase the abundance and diversity of rarer native bees that were found not, or little, supported by introduced plants (Smith *et al.*, 2015). This could in particular integrate important native plants families, including Myrtaceae and Fabaceae (Hingston, 1999; McQuillan and Hingston, 1999; Brown and Cunningham, 2022b).

Taxonomic limitations in this study

Insects were recorded to the lowest possible taxonomic group identifiable by eye and placed into morphospecies. Where reference collections were possible, they were subsequently identified. Whilst this method gives some insight there are further likely species that were missed, and others were only analysed based on morphospecies, for which inadequate reference collections were made. Diversity of some insects is therefore not as comprehensively captured, particularly for flies.

No direct comparison of habitat types in this study

I was not able to make direct comparisons of the insect community in less disturbed natural habitats in the broader landscape due to time and logistical constraints (large proportion of land around field sites was privately owned). This made it difficult to predict which insects were generally rare or common, in particular for those flower-feeding insect groups for which little data otherwise exists (beetles, wasps). Further work could in greater detail focus on examining in particular understudied groups of flower-feeding insects in varied habitat types, natural, disturbed rural/urban agroecosystem.

6.2.3 Are there key plant species that could be used to promote varied or specific ecosystem services and/or overall biodiversity?

Brief background

Whilst local plant diversity in agroecosystems has been found to support higher diversity of insects, including in rural (Norfolk *et al.*, 2016; Alomar *et al.*, 2018) and urban landscapes (Bennett and Gratton, 2012; Egerer *et al.*, 2017), this has not always been found to be the case (Makinson *et al.*, 2017; St. Clair *et al.*, 2020). The local composition of insect communities are likely to respond differently to altered ecosystems (De Palma *et al.*, 2016). Further, within agroecosystems, only a few key plant species may be most important for specific flower-feeding insects, and influencing overall insect diversity (García and Minarro, 2014; Sutter *et al.*, 2017). Which may be even more pronounced if most plant species found within agroecosystem are introduced (St. Clair *et al.*, 2020). This makes the identifying of plants which are most suitable to enhance specific and overall ecosystems and biodiversity services an integral part to guide management recommendations (Landis *et al.*, 2000; Russo *et al.*, 2013; García and Minarro, 2014).

Discussion

In market-gardens I used network metrics to test for key plant species (detail see method chapter 3,4) that likely sustained the greatest diversity of flower-feeding insects. Here my findings highlighted that key plants that attracted the highest species richness and were also visited by more specialized insects (or insects only able to feed on specific flowers) showed great overlap between the two distinct climatic regions I sampled (Table 3.2, Table 4.3) The high attraction of diverse insects to some introduced flowers highlights that future research is warranted to test the effectiveness of introduced plant species for supporting diverse beneficial insects and their ecosystem services. Experimental sowing out strips of specific or combined plant species could provide more insight on insect preferences (Lundin *et al.*, 2019) (Barbir *et al.*, 2015; Campbell *et al.*, 2017a) in both small and larger-scale vegetable production systems (Rizvi *et al.*, 2022). Experiments should also test the efficacy of, suitable native species (Fiedler *et al.*, 2008; Pandey and Gurr, 2019). Based on my findings I have compiled a list of introduced plant species that I recommend to further investigate (Table 6.2).

Table 6.2 List of plant species to further investigate, both for more targeted management approaches and in flower strips, or cover-cropping. In bold plant species that I suggest to use for comparison experiment. AS- Asteraceae, AP- Apiaceae, BR- Brassicaceae, PO- Polygonaceae, FA- Fabaceae, LA- Lamiaceae

Common name	Scientific name	Management	Target taxa
Carrot	<i>Daucus carota</i> – AP	Post-harvest crops Flower strips	Hoverflies, beetles, wasps, native bees
Fennel	<i>Foeniculum vulgare</i> - AP	Post-harvest crops	Hoverflies, beetles, wasps, native bees
Coriander	<i>Coriandrum sativum</i> - AP	Post-harvest crops	Hoverflies, beetles, wasps, native bees
Parley	<i>Petroselinum crispum</i> - AP	Post-harvest crops	Hoverflies, beetles, wasps, native bees
Lovage	<i>Levisticum officinale</i>	Post-harvest crops	Hoverflies, beetles, wasps, native bees
Chamomile	<i>Matricaria chamomilla</i> - AS	Flower-strips	Hoverflies, beetles, wasps, native bees
Calendula	<i>Calendula officinalis</i> - AS	Flower-strips	Hoverflies, native bees
Alyssum	<i>Lobularia maritima</i> - BR	Flower-strips	
Brassicas	Brassica spp. - BR	Post-harvest crops Cover-cropping	Hoverflies, native bees
Radish	Raphanus spp. - BR	Post-harvest crops Cover-cropping	Hoverflies, native bees
Smooth Hawksbeard	<i>Crepis capillaris</i> – AS	Weed management	Hoverflies, native bees
Buckwheat	<i>Fagopyrum esculentum</i> - PO	Cover-cropping	Hoverflies, native bees, ladybeetles
Birds trefoil	<i>Lotus corniculatus</i> – FA	Weed management Cover-cropping	Native bees- <i>Megachile</i> spp. i)
Mint	<i>Mentha picata</i> - LA	Culinary herbs	Native bees, larger wasps
Thyme	<i>Thymus vulgaris</i> – LA	Culinary herbs	Native bees, larger wasps
Oregano	<i>Origanum vulgare</i> – LA	Culinary herbs	Native bees, larger wasps
Basil	<i>Ocimum basilicum</i> – LA	Post-harvest crops	Native bees, larger wasps

i) could further be compared to native *Lotus australis* (Pandey and Gurr, 2019)

6.3 SUMMARY OF RESEARCH RECOMMENDATIONS

- Further exploring ways to enhance reed bees- *Exoneura* as potentially important alternative fruit-crop pollinators. Including testing supplementary nesting materials, enhancing native vegetation and polycultures (apple/blueberry alongside caneberries raspberry/boysenberry/blackberry)
- Candidate pollinators identified in this thesis should be screened further for efficacy/effectiveness. In particular *Exoneura* – blueberry pollination, Syrphinae – apple, Syrphinae, *Eristalis tenax*, and *Lasioglossum*(*Chilalictus*) - varied vegetable seed crops, native bees in Solanaceae in open/closed systems.
- Understanding social and financial incentives to strengthen the relationship between horticultural industry and beekeepers
- Testing the effect of different fast-growing introduced plants in supporting flower-feeding natural pest enemies if this subsequently suppresses pests in vegetable production systems. Recommended plant list of introduced species to explore further
- Examining the impact of altered landscapes on different flower-feeding insect orders (bees, beetles, wasps, flies) and functional groups (pollinator, natural pest-enemies). e.g. comparing different habitat types
- Testing the effectiveness of native floral enhancements on the diversity of insects, and specifically if this supports rarer more specialized flower-feeding insects

6.4 CONCLUSION

The findings from my thesis should be useful to horticultural producers and consultants, and researchers specifically but not limited to the field of ecological land management. I hope this work inspires more research, experimenting and innovative management approaches into the important world of diverse flower-feeding insects, to help sustain those insects that help support our agricultural production and diverse ecosystems.



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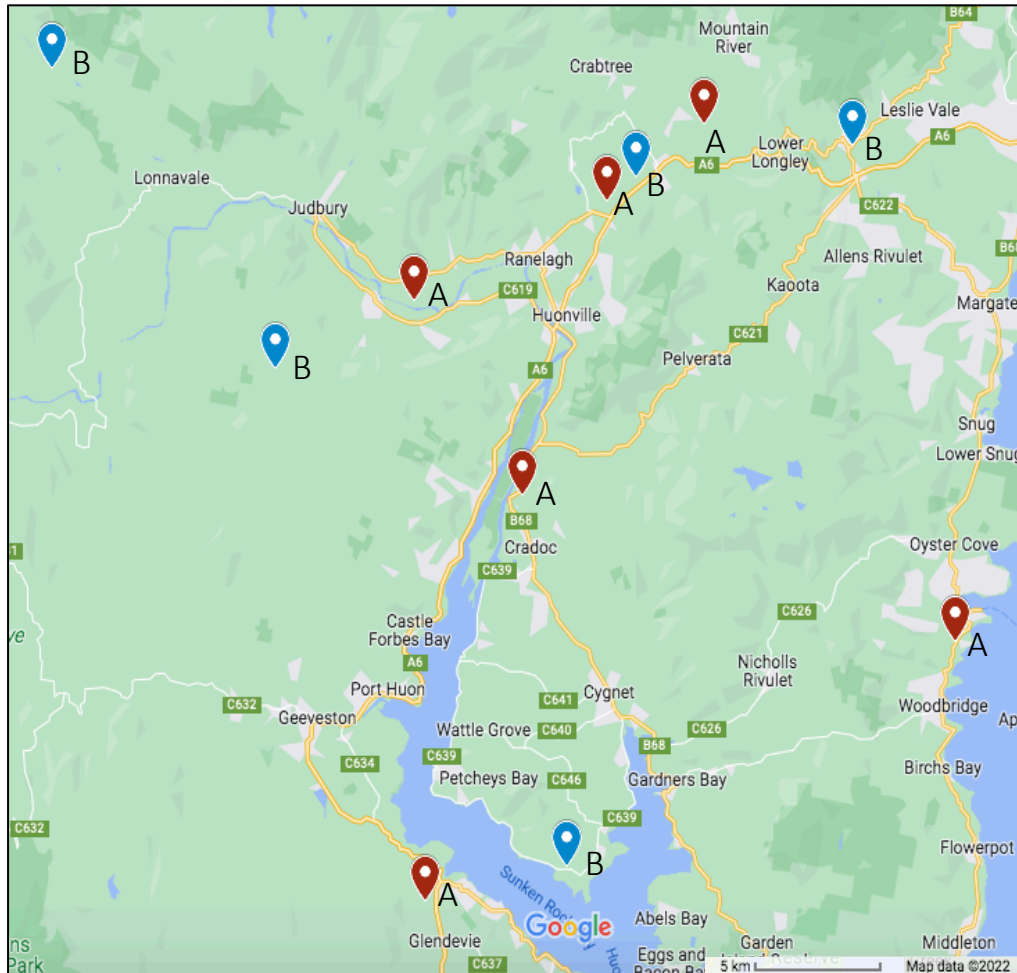
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Appendices

Appendix A– Chapter 2.



Appendix A- Figure A 2.1 Map field sites in the Huon and Channel areas – A – apple orchards, B – blueberry orchard

Table A 2.1 Details of field-sites Chapter 2

Ref. Code			Size	Vegetation types adjacent	Vegetation orchard rows	50m sampling-plot	HB hives
Blueberry							
B-LO	-42.97322	147.1935		sclerophyll flowering understory	Some grass, some small natives	1	0
B-TO	-42.98374	147.0866		sclerophyll only Eucalyptus, blueberries	Grass with exotic forbs	1	3 private kept on site
A-EA	-42.94777	146.79757		sclerophyll forest with flowering understory	marsupial lawn	1	1
B-TB	-43.21323	147.05235		sclerophyll forest with understory, damn with young natives, fenced nursery (exotic forbs on ground post-bloom)	marsupial lawn	1	3 outside more in netting (rented only during bloom)
B-AG	-43.04748	146.90812		Exotic hedge (Hebe spp.) along edge, removed in 2019	marsupial lawn	1	0
Apple							
A-GWS	-42.9919	147.07242		disturbed area with forbs including brassica spp. patch, apple rows		2 – 2018/2019 additional area with cover-crop in 2019	0
A-CR	-43.08984	147.03072		Sclerophyll forest with some understory			0
A-RWS	-43.02489	146.97714		Sclerophyll forest (control- burn 2019) riparian area with young natives, large orchard area and paddock	grass with exotic forbs	1-non-crop native sclerophyll/riperian zone 2- exotic forbs in newly planted (disturbed area)	3 rented during bloom
A-BB	-42.96647	147.12018		Some old eucalyptus riparian area no flowering understory, open paddock and orchard	grass some exotic forbs	1- Open paddock little exotic flowering	0
A-SB	-43.22469	146.98236					0
A-TB	43.13848	147.24428		Sclerophyll forest with understory, disturbed area with weedy patch	Grass with exotic forbs	1- Disturbed area with exotic forbs 2- Sclerophyll forest	0

Table A 2.2 Indicator species analysis (IndVAI) of floral group associations. Including potential outlier

	Apple		Blueberry		
	bloom	post-bloom	bloom	bloom excluding Hebe sp.	post-bloom
<i>A.mellifera</i>	crop 0.673, p 0.001***	-	exotic 0.262, 0.0134*	-	-
<i>B.terrestris</i>	-	-	crop 0.34, 7e-04***	crop 0.34, 0.0018**	-
<i>Exoneura</i>	crop 0.248, 0.0005***	natives 0.196, 0.0193*	natives 0.22, 0.0005***	natives (0.22, 0.0371*)	-
<i>Lasioglossum</i>	exotic and native 0.162, 0.0229*	natives 0.235, 0.0092**	-	-	-
<i>Syrphids</i>	exotic and crop 0.187, 0.016*	-	-	-	exotic 0.261, 0.0337*

(Hebe sp.)

Table A 2.3 Insect data collected Chapter 2, orchards Tasmania

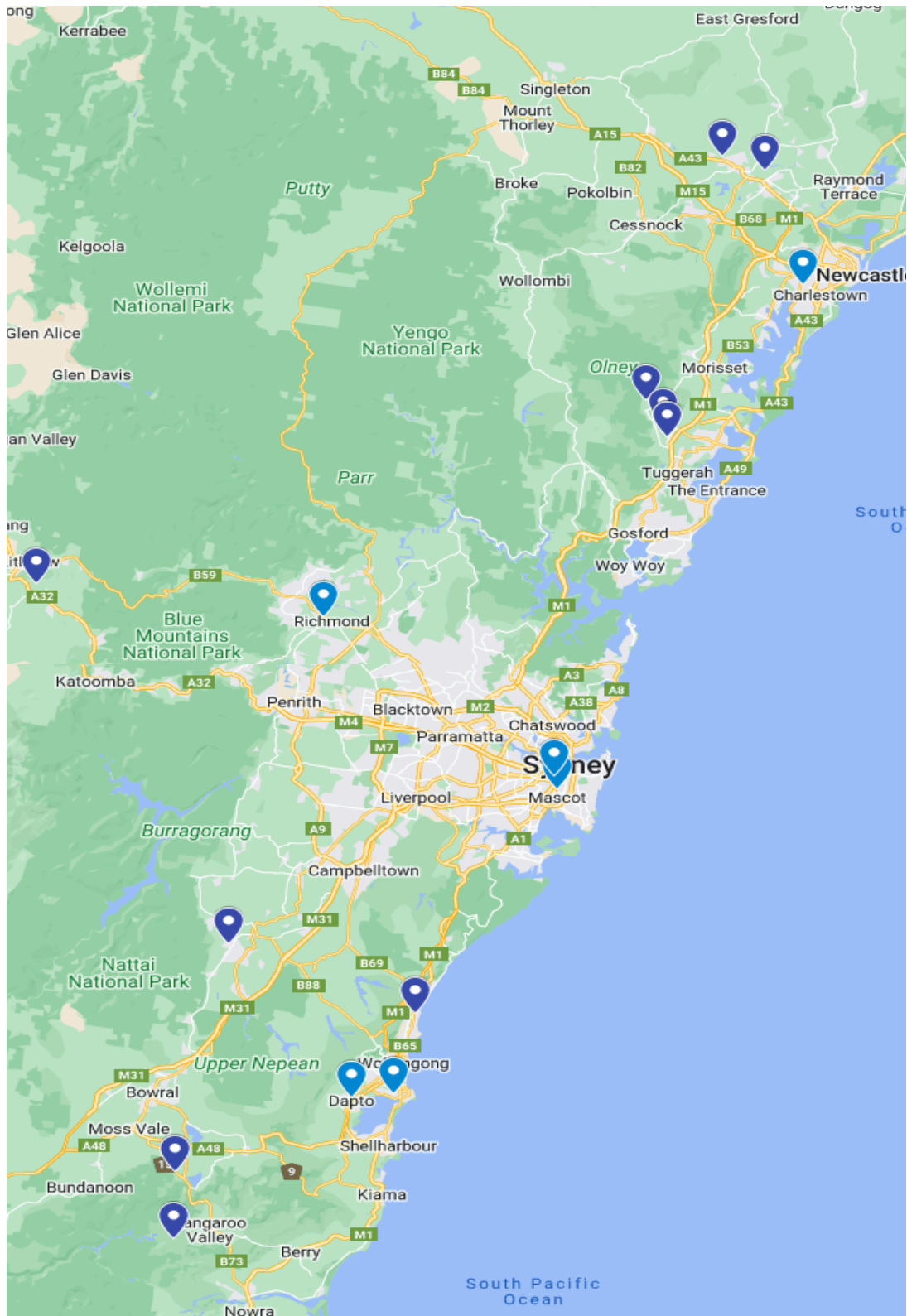
Native bees									
	Morpho-species	Genus	species	Apple bloom	Apple post bloom	Blueberry bloom	Blueberry post-bloom	collected on	
Halictidae	Lasio(para)	total recorded (right) species collected (below)		2	-	4	2		
		Lasioglossum	hilactum					<i>Hebe sp.</i>	
			sulthicum					<i>Maulus domestica</i>	
			sp.1					<i>Ziera arboresens</i>	
								<i>Ozylobium ellipticum</i>	
	Lasio(small)	Lasioglossum	mundulum		14	9	5	1	<i>Vaccinium corymbosum</i>
									See below I).
	Lasio(larger)	total recorded (right) species collected (below)			91	9	24	10	see below III)
		Lasioglossum	clelandi		31	5	8	2	<i>Brassica rapa, Vaccinium corymbosum, Cerastium glomeratum, Malus domestica, Trifolium repens, Goodenia ovata, Brassica, Pultaneae juniperina, Bellis perennis, Hypochaeris radicata,</i>
		Lasioglossum	sculperatum		2	1	1		<i>Pultaneae juniperina, Taraxacum officinale, Arctotheca calendula</i>
		Lasioglossum	repraesentans			2			<i>Hypochaeris radicata, Cassinia aculeata</i>
		Lasioglossum	tamburinei			1			<i>Melaleuca squarrosa</i>
		Lasioglossum	litteri			2			<i>Acaena novae-zelandiae, Taraxacum officinale</i>
	Homalictus	Homalictus	sphecoides			2	2	1	<i>Goodenia ovata Hypochaeris radicata, Crepis capillaris Ranunculus repens</i>
Homalictus		sp.2				1		<i>Vaccinium corymbosum</i>	
Apidae	Exoneura	Exoneura	spp.	48	33	45	31	see below III)	
		Exoneura	male	3					

Colletidae	Trichocolletes	Trichocolletes	sp.1				1	
	Leiproctus	Leiproctus	provictus	1				<i>Ziera arborescens</i>
		Leiproctus	sp.1 (male)				1	<i>Rubus fruticosus agg.</i>
	Colletidae small	Euryglossinae	sp.1	1				<i>Goodenia ovata</i>
			male	1				<i>Cassinia</i>
			male	1				<i>Pultaneae juniperina</i>
Megachilidae	Megachile	Megachile	male		1		1	<i>Rubus fruticosus agg.</i>
Other insects								
	Morpho-species	Genus	species	Apple bloom	Apple post bloom	Blueberry bloom	Blueberry post-bloom	observed on
Diptera	Syrphid slim							see below IV)
		Muscidae		9	13	2	1	<i>Brassica rapa, Malus domestica, conium maculatum, Hypochaeris radicata, Leucanthemum vulgare, myosotis arvensis</i>
		Eristalinae		2	-	1	1	<i>Brassica rapa, Hibbertia sp., Ziera arborescens</i>
		other diptera		5	8	1	2	<i>Malus domestica, bellis perennis, cassinia aculeata, cerastum glomeratum, conium maculatum, Hypochaeris radicata, Ranunculus repens, Veronica persica, Eucalyptus amygdalina, Hibbertia sp., Ranunculus repens</i>
Beetle		Mordellidae		-	15	-	7	<i>Cassinia aculeata, Leptospermum scoparium, Rubus fruticosus agg., Hypochaeris radicata, Oleria axillaris,</i>
	small beetle unid.			-	-	-	1	<i>Rubus fruticosus agg.,</i>
		Atoichus		2	-	2	-	<i>Brassica rapa, Myosotis arvensis, Acacia verticillate, Ziera arborescens</i>
		Solider beetle		1	8	-	-	<i>Malus domestica, Conium maculatum</i>
		Phyllotocus	rufipennis	-	20	-	-	<i>Conium maculatum, Senecio linearifolius</i>
		Dornia		-	-	-	2	<i>Melaleuca squarrosa, Oleria axillaris</i>
		Asclera		-	1	-	2	<i>Leptospermum scoparium, Oleria axillaris</i>
		Eleala		-	3			<i>Cassinia aculeata, Rubus fruticosus agg.</i>
		Stenoderus	saturalis	-	1	-	1	<i>Conium maculatum, Rubus fruticosus agg.</i>
		Pseudolycus	rufipennis	-	1	-	-	<i>Cassinia aculeata</i>
Hymenoptera		Bembix		-	2	-		<i>Rubus fruticosus agg.</i>
	native wasps (missed)			-	2	-	1	<i>Rubus fruticosus agg., melaleuca squarrosa</i>
Lepidoptera	moth (missed)			-	1	-	-	<i>Leucanthemum vulgare</i>

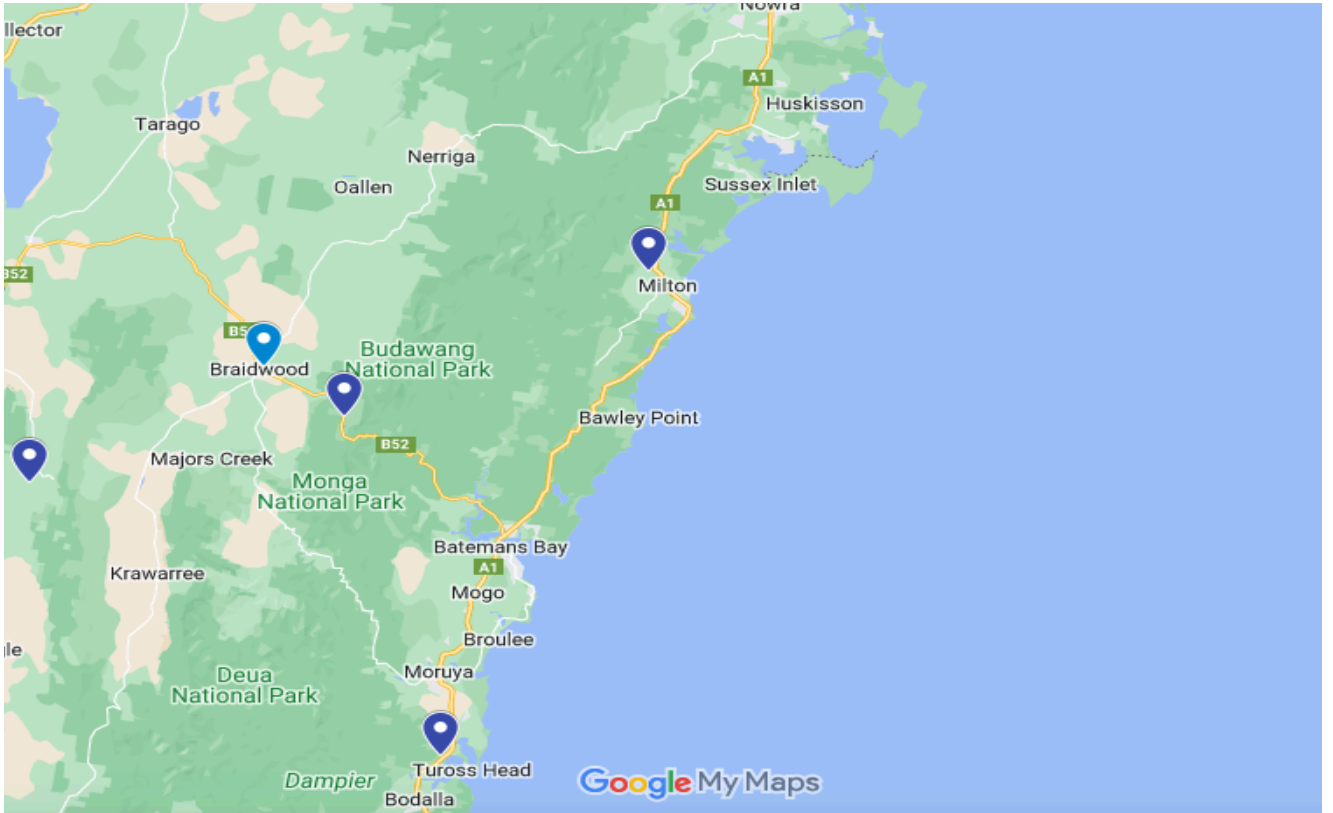
- I. **Lasioglossum smaller recorded visiting** = *Anagallis arvensis*, *Malus domestica*, *Arctotheca calendula*, *Vaccinium corybosum*, *Brassica rapa*, *Cassinia aculeata*, *Centaurium erythraeae*, *Cerastium glomeratum*, *Crepis capillaris*, *Taraxacum officinale*, *Hibbertia sp.*, *Hypochaeris radicata*, *Oxylobium ellipticum*, *Ranunculus repens*, *Rubus fruticosus agg.*, *Trifolium repens*
- II. **Lasioglossum larger recoded visiting** = *Acaena nova-zelandiae*, *Malus domestica*, *Arctotheca calendula*, *Barbarea verna*, *Vaccinium corybosum*, *Brassica rapa*, *Cassinia aculeata*, *Cerastium glomeratum*, *Comesperma volubile*, *Taraxacum officinale*, *Fumaria bastardii*, *Goodenia ovata*, *Hypochaeris radicata*, *Melaleuca squarrosa*, *Oleria axillaris*, *Oxylobium ellipticum*, *Philothea virgata*, *Pultenaea juniperina*, *Ranunculus repens*, *Raphanus raphanistrum*, *Trifolium repens*
- III. **Exoneura recorded visiting** = *Acacia verticillate*, *Malus domestica*, *Bauera rubioides*, *Vaccinium corybosum* , *Comesperma volubile*, *Goodenia ovata*, *Melaleuca squarrosa*, *Oleria axillaris*, *Oxylobium ellipticum*, *Philothea virgata*, *Pultenaea juniperina*, *Ranunculus repens*, *Richea procura*, *Rubus fruticosus agg.*, *Senecio linearifolius*, *Trifolium repens*, *Ziera arborescens*
- IV. **syrphid slim recoded visiting** = *Acaena nova-zelandiae*, *Anagallis arvensis*, *Arctotheca calendula*, *Malus domestica*, *Bellis perennis*, *Brassica rapa*, *Cardamine hirsute*, *Cassinia aculeata*, *Caesia parviflora*, *Crepis capillaris*, *Cerastium glomeratum*, *Conium maculatum*, *Taraxacum officinale*, *Hypochaeris radicata*, *Hibbertia sp.*, *Leucanthemum vulgare*, *Melaleuca squarrosa*, *Oxylobium ellipticum*, *Pomaderris elliptica*, *Hebe spp.*, *Myosotis arvensis*, *Ranunculus repens*, *Senecio linearifolius*, *Trifolium repens*, *Veronica persica*, *Ziera arborescens*

Appendix C. Chapter 4

Map field sites south-east NSW market-gardens



Map field sites south-east NSW market-gardens (continued)



Appendix D.

Table A.6.1 Flower-visitation to crops surveyed at orchards (southern Tasmania) and market-gardens (Tasmania and south-east NSW)

Crop	Scientific name	Plant family	Main visitors	Location	Chapter
Apple	<i>Malus domestica</i>	Rosaceae	91 % - <i>A. mellifera</i> 2.5% - <i>Exoneura</i> (i)	southern Tasmania Orchards	Chapter 2.
Blueberry	<i>Vaccinium corybosum</i>	Ericaceae	76 % - <i>A. mellifera</i> 19% - <i>B. terrestris</i> 4 % - <i>Exoneura</i>	southern Tasmania Orchards	Chapter 2.
Raspberry/ Boysenberry/ Blackberry	<i>Rubus spp.</i>	Rosaceae	Spring: 80 % - <i>A. mellifera</i> 8 % - <i>B. terrestris</i> 6 % - Syrphinae Summer: 47% - <i>B. terrestris</i> 40 % - <i>A. mellifera</i> 13% - <i>Exoneura</i>	Tasmania Market-gardens	Chapter 3.
Strawberry	<i>Fragaria x ananassa</i>	Rosaceae	Spring: 56% - Syrphinae 22% - <i>A. mellifera</i> 22% - <i>Lasioglossum</i> Summer: 75 % - Muscidae 16% - <i>B. terrestris</i> 8 % - <i>A. mellifera</i>	Tasmania Market-gardens	Chapter 3.
Cucumber	<i>Cucumis sativus</i>	Cucurbitaceae	84 % - <i>A. mellifera</i> 9 % - <i>B. terrestris</i>	Tasmania Market-gardens	Chapter 3.
			95 % - <i>A. mellifera</i> 3 % - <i>Tetragonula carbonaria</i>	South-east NSW Market-gardens	Chapter 4.
Rock melon	<i>Cucumis melo</i>	Cucurbitaceae	88% - <i>A. mellifera</i> 12 % - <i>Homalictus</i> (ii)	South-east NSW Market-gardens	Chapter 4.
Watermelon	<i>Citrullus lanatus</i>	Cucurbitaceae	83% - <i>A. mellifera</i> 16 % - <i>Homalictus</i> (ii)	South-east NSW Market-gardens	Chapter 4.
Zucchini	<i>Cucurbita pepo</i>	Cucurbitaceae	60 % - <i>A. mellifera</i> 36% - <i>B. terrestris</i>	Tasmania Market-gardens	Chapter 3.
			96 % - <i>A. mellifera</i> 4 % - <i>Lasioglossum</i> (ii)	South-east NSW Market-gardens	Chapter 4.
Pumpkin	<i>Cucurbita pepo/moschata /maxima</i>	Cucurbitaceae	100 % - <i>A. mellifera</i>	Tasmania Market-gardens	
			60 % <i>A. mellifera</i> 39% <i>B. terrestris</i>	South-east NSW Market-gardens	Chapter 4.
Broad-bean	<i>Vicia faba</i>	Fabaceae	50 % - <i>A. mellifera</i> 50% - <i>B. terrestris</i>	Tasmania Market-gardens	Chapter 3.
Scarlet-runner	<i>Phaseolus coccineus</i>	Fabaceae	51% - <i>B. terrestris</i> 43% - <i>A. mellifera</i> 2 % - <i>Lasioglossum mundulum</i>	Tasmania Market-gardens	Chapter 3.
Tomato	<i>Solanum lycopersicum</i>	Solanaceae	80 % - <i>B. terrestris</i> 20 % - <i>A. mellifera</i> (ii)	Tasmania Market-gardens	Chapter 3.
			37.5% - <i>Lipotriches phanerura</i> 12. 5% - <i>Amegilla pulchra</i> (ii) 12.5 % - <i>Amegilla bombiformis</i> (ii) 12.5 % - <i>Lasioglossum</i> (ii)	South-east NSW Market-gardens	Chapter 4.

Chilli	<i>Capsicum annum/frutescens</i>	Solanaceae	63 % - <i>B. terrestris</i> 36 % - <i>A. mellifera</i>	Tasmania Market-gardens	Chapter 3.
			80% - <i>A. mellifera</i> 6 % - <i>Tetragonula carbonaria</i> (ii) 6% <i>Lasioglossum</i> (ii) 6 % - <i>Lipotriches</i> (ii)	South-east NSW Market-gardens	Chapter 4.
Tomatillo	<i>Physalis philadelphica</i>	Solanaceae	67 % - <i>B. terrestris</i> 33 % - <i>A. mellifera</i>	Tasmania Market-gardens	Chapter 3.
			86 % - <i>A. mellifera</i> 7 % - <i>Amygilla pulchra</i> (ii) 7 % - <i>Megachilidae</i> (ii)	South-east NSW Market-gardens	Chapter 4.

i) high visits recorded single site during both years of surveying

ii) low visits all single visits