Addressing seasonal vulnerability of orchard pollinators through restoration of floral communities

Samantha Ardin

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Bless air's gift of sweetness, honey from the bees, inspired by clover, marigold, eucalyptus, thyme, the hundred perfumes of the wind. Bless the beekeeper

who chooses for her hives a site near water, violet beds, no yew, no echo. Let the light lilt, leak, green or gold, pigment for queens, and joy be inexplicable be *there* in harmony of willowherb and stream, of summer heat and breeze, each bee's body at its brilliant flower, lover-stunned,

strumming on fragrance, smitten.

For this,

let gardens grow, where beelines end, sighing in roses, saffron blooms, buddleia; where bees pray on their knees, sing, praise in pear trees, plum trees; bees are the batteries of orchards, gardens, guard them.

– Carol Ann Duffy, Virgil's Bees

Abstract

Pollinators are critical for the production of many of the World's crops; however, both wild and managed pollinator populations have undergone serious declines driven by, among other factors, habitat loss. Restoring floral communities in a habitat can increase the availability of food for pollinators and can be an effective way to promote pollinator populations and the associated ecosystem service of crop pollination. For floral restoration to be effective, it must ensure that pollinators are supported throughout their lifecycle, especially in landscapes dominated by mass-flowering crops, where pollinators can experience disjointed pulses of floral resources. To study this issue, a suitable framework is required for considering temporal aspects of flower-pollinator interactions.

In this thesis, I collect flower-pollinator networks from habitats dominated by the mass-flowering crop, apple, and develop a novel *in silico* approach for studying the structure of flower-pollinator networks through the season. I use this to demonstrate the exposure of pollinators to food shortage in mass-flowering crops by comparing pollinator persistence and network structure through the season in two crops with a short (apple) and long (strawberry) flowering phenology. I then evaluate differences in temporal network structure between floristically improved and unimproved apple orchards, and use a field-experiment to demonstrate that floral improvement can increase pollination service later in the season by increasing the persistence of pollinators through the season. Finally, I develop a novel modelling approach to identify the best floral compositions for supporting pollinators throughout the season in apple orchards, and use these compositions to demonstrate that existing floral management options could be markedly improved to provide greater abundance and stability of nectar through the season.

By combining field surveys, field experiments and multiple modelling approaches, this thesis extends our current understanding of how flower-pollinator networks are structured through the season, and provides a novel toolkit with which to explore this topic in other habitats and restoration scenarios.

Author's Declaration

I declare that the work in this dissertation was carried out in accordance with the requirements of the University's Regulations and Code of Practice for Research Degree Programmes and that it has not been submitted for any other academic award. Except where indicated by specific reference in the text, the work is the candidate's own work. Work done in collaboration with, or with the assistance of, others, is indicated as such. Any views expressed in the dissertation are those of the author.

S.E. Ardin 20th September 2017

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Chapter 1

Introduction

1.1 Background

1.1.1 The value of pollinators

Animals contribute to the pollination of over 87% of the World's flowering plant species (Ollerton et al., 2011), including over three-quarters of globally important food crops (Klein et al., 2007). Loss of all pollinators could reduce the total supply of fruit, nuts and seeds by an estimated 22 percent and vegetables by 16 percent (Smith et al., 2015), reducing global crop production by an estimated 58% (Aizen et al., 2009). The potential annual economic value of animal-mediated pollination is therefore significant, with current estimates ranging from US\$127-152 billion (Bauer and Sue Wing, 2016) to US\$235-577 billion (Lautenbach et al., 2012). Furthermore, a loss of pollinators could significantly deplete supplies of a range of important vitamins and minerals, including vitamin A, vitamin C and folic acid (Eilers et al., 2011), with significant implications for human health. If pollination services were halved, the resulting loss of available nutrients could lead to 132 million human years lost annually due to ill-health, disability or early death (Smith et al., 2015).

1.1.2 The value of managed versus wild pollinators

Managed honey bees (*Apis mellifera*) are important pollinators of a wide range of crops (Rader et al., 2009; Breeze et al., 2011; Brittain et al., 2013). However, current evidence suggests there are insufficient honey bee colonies to pollinate crops in 90% of European countries (Breeze et al., 2014). Furthermore, over-reliance on a single pollinating species can make pollination services vulnerable, as exemplified by recent, widespread losses of

honey bee colonies in the United States (Ellis et al., 2010; VanEngelsdorp et al., 2009) and Europe (Potts et al., 2010b).

There is increasing evidence that wild insects are valuable pollinators, working synergistically with managed pollinators to deliver pollination services that are more robust and effective (Winfree et al., 2007; Garibaldi et al., 2013; Mallinger and Gratton, 2015). For example, Mallinger and Gratton (2015) demonstrated that fruit set in commercial apple orchards significantly increased with the species richness of native, wild bees during bloom, whereas the abundance of honey bees had no significant impact. Garibaldi et al. (2013) found that this association held across 41 important crops, with an increase in wild pollinator visitation increasing fruit set twice as much as a similar increase in honey bee visitation.

1.1.3 Pollinator decline

Despite their importance for food security, wild pollinator populations have decreased significantly (Biesmeijer, 2006; Cameron et al., 2011; Carvalheiro et al., 2013) such that, within Europe, at least 9.2% of bees (European Red List) and 9% of butterflies (IUCN, 2011) are threatened, with almost 30% of these threatened bee species endemic to Europe (European Red List). This has the potential to influence ecosystem service provision as shifts in the abundance and phenology of plant and pollinator species can result in changes to the structure of pollinator communities (Bommarco et al., 2012b; Bartomeus et al., 2013a; Burkle et al., 2013), reducing the level and stability of pollination services. For example, by comparing observations from across 120 years in US temperate forest understorey, Burkle et al. (2013) found that the majority of bee species had either become locally extinct or experienced changes in their phenology. These changes to the pollinator communities, the yields of crops with a higher pollinator dependence are increasing more slowly than less pollinator dependent crops (Garibaldi et al., 2011).

Habitat degradation is a principal driver of pollinator decline (Potts et al., 2010a; Vanbergen and Garratt, 2013; González-Varo et al., 2013; Montero-Castaño and Vilà, 2012), as it reduces the availability of nesting sites and floral resources for pollinators (Baude et al., 2016; Carvell et al., 2006; Goulson and Hughes, 2015; Roulston and Goodell, 2011; Scheper et al., 2014; Wallisdevries et al., 2012). In particular, agricultural intensification is thought to have contributed significantly to the decline of pollinators (Ollerton et al., 2014); the total area of agricultural land increased by 466% worldwide from 1700 to 1980 (Meyer and Turner, 1992) and this habitat can have among the

lowest quantity and diversity of nectar resources for pollinators (Baude et al., 2016). This highlights a potential opportunity to support pollinators in agricultural habitats by increasing the provision of floral resources and/or nesting sites.

1.1.4 Ecological restoration

Restoring habitats by providing additional floral resources can change the structure of the associated pollinator community, boosting pollinator abundance, species richness (Potts et al., 2003) and pollinator health (Alaux et al., 2010; Goulson and Hughes, 2015). These benefits can be realised when floral resources are available at either the local or landscape scale. For example, areas of semi-natural habitat, which can be rich in floral resources, enhance pollination services in nearby agricultural areas (Kremen et al., 2004; Ricketts et al., 2008; Carvalheiro et al., 2010; Holzschuh et al., 2012; Grass et al., 2016). In a recent meta-analysis, Garibaldi et al. (2011) found that pollinator richness, visitation rate and fruit set were more stable in areas near to semi-natural habitat, across a range of crop types. However, areas of semi-natural habitat may be scarce in agricultural landscapes. Furthermore, relying on floral resources in semi-natural habitats may leave crops vulnerable to future landscape changes. In addition, less mobile species may be unable to access areas of semi-natural habitat within the wider landscape.

Integrating floral resources into arable land could be an effective way to increase pollinator populations by ensuring a consistent, local supply of food for pollinators regardless of pollinator mobility. There are many examples of pollinator populations increasing in abundance and/or diversity following the local addition of non-crop floral resources (Carvell et al., 2004, 2007, 2015, 2017; Haaland and Gyllin, 2010; Kennedy et al., 2013; Morandin and Kremen, 2013; Cole et al., 2015; Feltham et al., 2015; Kremen and M'Gonigle, 2015; M'Gonigle et al., 2015). Most notably, recent research has shown that the between-year survival of bumblebee (*Bombus* spp.) family lineages (from summer worker to spring queen stage) is significantly increased by the presence of high-quality floral resources within 1km of the colony (Carvell et al., 2017). This is the first study to establish a direct link between the provision of floral resources and the inter-annual survival of bumblebee colonies, demonstrating that increasing floral resources has the potential to increase populations of this key pollinator genus.

Increases in pollinator abundance following the addition of non-crop floral resources can augment pollination services (Carvalheiro et al., 2012; Blaauw and Isaacs, 2014; Barbir et al., 2015; Feltham et al., 2015; Campbell et al., 2017; Dainese et al., 2017; Häussler et al., 2017). For example, Blaauw and Isaacs (2014) found that floral plantings adjacent to blueberry fields increased pollinator visitation to crop flowers and increased wildflower seed set. The authors estimated that the cost of such an intervention would be offset by increases in pollination services within 3-5 years.

In light of these potential benefits, many countries now offer financial incentives for farmers and land managers to increase the availability of floral resources for pollinators. In the UK, for example, the Countryside Stewardship scheme is designed to encourage farmers to adopt a range of environmentally-minded management approaches. Within this scheme, the Wild Pollinator and Farmland Wildlife Package was designed specifically to provide floral resources for pollinators (Dicks et al., 2015). Under this package, farmers must grow at least 500m of flowering hedgerow per 100ha and commit 2% of their land to flower-rich habitat. Dicks et al. (2015) tentatively estimate that this package can provide six common pollinating bee species with sufficient pollen to feed their larvae, based on the lowest estimates of pollinator requirements. However, they highlight the need for more research to determine the ability of existing agri-environmental schemes to provide resources for pollinators.

1.1.5 Challenges in ecological restoration

Restoring habitat for pollinators in agricultural landscapes is not always effective (Williams et al., 2015; Wood et al., 2015; Campbell et al., 2017). For example, Wood et al. (2015) found no differences in the total number of aculeate or flowering plant species recorded on farms with or without added flower-rich habitats. In this study, bumblebees and hon-eybees frequently visited the added flower-rich habitats, but the majority of bee species foraged from wild flowers not included in the intervention. For ecologically-motivated bursaries for farmers to be effective, there needs to be a better understanding of the factors that contribute to this inconsistency.

A factor that might influence the effectiveness of floral enhancement is the extent of phenological matching between the available flowers and target pollinator species. Periods of low floral availability may have significant negative impacts on pollinators (Di Pasquale et al., 2016; Benedek, 1997), especially those with a narrow flight season (De Palma et al., 2015), but this can only be understood by assessing changes in the floral and pollinator communities throughout the season (Carvell et al., 2007; Robson, 2014; Rundlöf et al., 2014; Williams et al., 2015; Orford et al., 2016).

This is particularly pertinent in agricultural areas dominated by mass flowering crops, which can produce large pulses of resources separated by periods of resource deficit (Tscharntke et al., 2005; Blitzer et al., 2012; Kennedy et al., 2013; Scheper et al., 2013).

Pollinators in landscapes dominated by mass flowering crops may therefore depend on wild flowers and weeds to add diversity to their diet and provide resources between the crop flowering periods (Kovács-Hostyánszki et al., 2013; Requier et al., 2015). If pollinator species are not supported throughout their entire lifecycle by the available floral resources they can be negatively affected by the presence of mass flowering crops (Holzschuh et al., 2016). However, studies rarely consider changes in floral and pollinator composition throughout the season.

The aim of this thesis is, therefore, to study pollinator communities throughout the season with a view to identifying and addressing periods of vulnerability for pollinators. By adopting a temporal perspective and considering resource provision throughout the season, we could be better placed to support pollinators regardless of their phenology, and maximise the opportunity for pollinator populations to establish and grow.

1.2 A temporal perspective

To understand the importance of a temporal perspective, we must first consider the nutritional needs of pollinators and how well these needs are currently met in agricultural habitats throughout the season. In the following section, I will therefore introduce the focal mass flowering crop, apple, with a particular focus on its pollinator requirements and associated pollinator communities. I will then briefly outline the lifecycle of key pollinating insects and our current understanding of their food requirements. In doing so, I highlight the mismatch between the resources required by pollinators and those typically provided by mass flowering crops.

1.2.1 Study system: the mass flowering crop, apple

Apple (*Malus domestica*) is the third most valuable fruit crop in the world (behind only tomatoes and grapes), with an estimated annual value of USD\$51.7 billion (FAO, 2014). Apple yield is highly dependent on pollination (Garratt et al., 2014a) and could be reduced by an estimated 40-90% in the absence of pollinators (Klein et al., 2007). Evidence suggests that, within the UK, apple crops can currently experience a pollination deficit (Garratt et al., 2014b).

Wild bees are the most important pollinators of apple because they are frequent visitors to apple flowers and their visits result in higher seed set (Bosch and Vicens, 2000; Garratt et al., 2016). However, the short, early-season flowering phenology of apple is insufficient to cover the entire flight period of key bee pollinators of apple

(see Section 1.2.3 below). Consequently, commercial apple orchards may be unable to sustain robust populations of wild bees, which could make pollination services to apple vulnerable. Conversely, extensively managed apple orchards often contain highly diverse plant communities which exist as part of the orchard grassland understorey and hedgerows (Smart and Winnall, 2006; Natural England, 2009). The extra flowers available in these habitats can ensure a year-round supply of nectar and pollen, reducing pollinator exposure to food shortages (García and Miñarro, 2014).

1.2.2 The value and vulnerability of wild bees

A wide range of insect families act as crop pollinators (Rader et al., 2009) and there is strong evidence that diverse pollinator communities provide the most effective (Hoehn et al., 2008; Albrecht et al., 2012; Brittain et al., 2013) and reliable (Bartomeus et al., 2013b) pollination services, perhaps by increasing functional diversity and redundancy of the underlying pollinator community. To encapsulate this diversity, this thesis primarily adopts a community-level approach; however, there is a focus on wild bee species throughout, for which there are several reasons:

- Bees are consistently and repeatedly identified as important pollinators, across a wide range of crops (Klein et al., 2007; Roulston and Goodell, 2011) and there is strong evidence that they are the most effective pollinators of apple (Garratt et al., 2016).
- 2. There is strong evidence that bee populations have declined (Bartomeus et al., 2013a; Burkle et al., 2013; Goulson and Hughes, 2015; Senapathi et al., 2015) and this has been linked to agricultural intensification and expansion (Carvalheiro et al., 2013; Ollerton et al., 2014). A reduction in bee populations is particularly concerning in these habitats, as this is where they can confer the greatest benefits.
- 3. Bees are particularly vulnerable because they are centrally-placed foragers (Falk and Lewington, 2015), meaning the resources available to them are limited to those within a specific radius of their home. More mobile pollinators such as bumblebees, which can readily forage up to several hundred metres from their nest (Darvill et al., 2004; Osborne et al., 1999; Knight et al., 2005; Cresswell et al., 2000), may have access to floral resources throughout a landscape. However, smaller and less mobile pollinators such as some solitary bees, may only be able to use floral resources at a more local scale (Albrecht et al., 2007; Greenleaf et al., 2007; Jönsson et al., 2015; Marini et al., 2012; Cresswell et al., 2000; Williams et al., 2010; Öckinger

et al., 2010; Winfree et al., 2011). This makes it important that floral resources are available locally within agricultural habitat.

1.2.3 The lifecycle and nutritional requirements of bees

Bees require flowers as a source of protein-rich pollen and sugar-rich nectar. Nectar is required throughout the entire flight period of a bee as the primary source of energy to fuel mobility (Harder and Barclay, 1994). Pollen is required as a protein source for developing larvae (Falk and Lewington, 2015), and shortages can reduce the rate of larval development (Di Pasquale et al., 2016). There are four main life cycles that bee species can follow, each of which demands nutrients at different times of year.

Social bumblebees follow an annual colony cycle in which new queens hibernate in autumn and emerge in spring, in search of a nesting site (Falk and Lewington, 2015). The survival and re-establishment of overwintering queens is crucial for population persistence, and requires a good supply of early-season floral resources (Harder and Barclay, 1994). Queen bees will produce up to several hundred workers, which will forage for pollen and nectar throughout spring, summer and early autumn to provide for new male and queen offspring (Falk and Lewington, 2015). The energy demands of a bumblebee colony is typically at its greatest in late summer, when the rate of brood rearing is at its highest (Harder and Barclay, 1994). Social bumblebee species therefore require a continuous supply of energy from approximately March until September, and may benefit from resources beyond this (Figure 1.1).



Figure 1.1: The flight season of bumblebee species (dark grey), relative to the apple flowering phenology (red). All of the species shown were among the twenty most common visitors to apple flowers in a recent study by Garratt et al. (2016). Bee phenology data is taken from Falk and Lewington (2015) whereas apple flowering phenology was directly surveyed (see Chapter 2).

These resource needs are somewhat similar for primitively eusocial solitary bee species, such as many furrow bees (*Halictus* spp., *Lasioglossum* spp.), where a single nesting cycle is split into two distinct phases: female workers are produced earlier in the season and males and queens produced later (Figure 1.2). These species are particularly vulnerable to inconsistencies in food supply throughout the season as they cannot complete a full reproductive cycle without completing both reproductive phases (Falk and Lewington, 2015).



Figure 1.2: The flight season of *Lasioglossum* species (dark grey), relative to the apple flowering phenology (red). Both species shown were among the twenty most common visitors to apple flowers in a recent study by Garratt et al. (2016). Bee phenology data is taken from Falk and Lewington (2015) whereas apple flowering phenology was directly surveyed (see Chapter 2).

Conversely, univoltine solitary bee species produce a single generation per year, within a specific window (Figure 1.3). This window varies between species, but can begin as early as late-February (e.g. Andrena clarkella) and as late as late-August (e.g. the ivy bee, *Colletes hederae*). Univoltine species have often evolved greater specialism on historically-abundant flowers available in their flight period (Falk and Lewington, 2015), which can make them vulnerable to food shortages if floral resources are inappropriate.



Figure 1.3: The flight season of univoltine mining bee species (dark grey), relative to the apple flowering phenology (red). All of the species shown were among the twenty most common visitors to apple flowers in a recent study Garratt et al. (2016). Bee phenology data is taken from Falk and Lewington (2015) whereas apple flowering phenology was directly surveyed (see Chapter 2).

Bivoltine species, including some mining bee (Andrena spp.) and nomad bee (No-

mada spp.) species, complete two independent nesting cycles at different times in the year (Figure 1.4). A deficit in floral resources during a single nesting cycle would only directly impact that cycle, although populations of some species (in particular, mining bees) are rarely maintained with only a single successful cycle (Falk and Lewington, 2015).



Figure 1.4: The flight season of bivoltine mining bee species (dark grey), relative to the apple flowering phenology (red). Both of the species shown were among the twenty most common visitors to apple flowers in a recent study by Garratt et al. (2016). Bee phenology data is taken from Falk and Lewington (2015) whereas apple flowering phenology was directly surveyed (see Chapter 2).

Of the most common bee species that visit apple flowers (Garratt et al., 2016), only three are supported for at least 80% of their potential phenophase by apple flowers. Adding floral resources to apple orchards could support key apple pollinators by extending their food supply beyond the crop flowering period, but floral management regimes currently vary in their ability to provide continuous forage for pollinators (Carvell et al., 2006; Havens and Vitt, 2016; Wood et al., 2017). This may jeopardise the establishment and persistence of many bee species. Providing a reliable source of diverse flowers throughout the season should be the target for all pollinator-focused agri-environment schemes as only this can ensure that pollinators are supported regardless of their specialisation, seasonality or flight period.

1.3 Ecological networks as a restoration tool

So far, I have outlined that pollinators need floral resources throughout the season and that different pollinators have different phenophases. Consequently, resource gaps could jeopardise the growth of long-season pollinators and prevent short-season pollinators from establishing. I have discussed the relevance of this problem in landscapes dominated by mass-flowering crop, where floral resources may fluctuate throughout the season. However, to study the continuity of floral resources through time, and the effect this has on the pollinator community, we need a suitable framework for studying restoration efforts from a temporal perspective. In this section, I introduce ecological networks and their potential to address questions in restoration ecology. I then outline the challenges of using ecological network approaches to track plant-pollinator communities through the season.

Ecological networks are mathematical representations of plant-pollinator communities, in which nodes (species) are connected by links (observed interactions). Ecological networks have been used to address a wide range of ecological questions regarding community dynamics and stability (Bastolla et al., 2009; Thebault and Fontaine, 2010), habitat restoration (Albrecht et al., 2007; Forup and Memmott, 2005; Forup et al., 2008; Devoto et al., 2012; Pocock et al., 2012; Kaiser-Bunbury et al., 2017) and ecosystem service provision (MacFadyen et al., 2009, 2011; Carvalheiro et al., 2010, 2011; Gagic et al., 2011; Peralta et al., 2014).

Ecological networks provide a convenient framework for studying ecological restoration as they incorporate species composition and the behaviour of the constituent pollinator species (Tylianakis et al., 2010; Memmott, 2009; Gray et al., 2014). In this regard, they capture characteristics of the plant-pollinator community that are relevant for biodiversity conservation and ecosystem service provision.

Studying ecological networks throughout the season is challenging because, even with high sampling effort, a significant proportion of interactions can go unobserved (Chacoff et al., 2012). This can prevent researchers from acquiring detailed, representative network data for individual days or weeks; instead, most ecological networks are assembled by aggregating observed interactions across one or more seasons. Unfortunately, this process often aggregates interactions that could never feasibly occur together and, in doing so, may provide a false impression of the network structure (Rasmussen et al., 2013), dynamics (Olesen et al., 2008; Tanaka et al., 2012) and robustness (Kaiser-Bunbury et al., 2010). In habitats dominated by short-flowering crops, the network topology and identity of interacting species are likely to undergo sharp changes. In these habitats, networks constructed for different points throughout the season could give greater insight into how consistently pollinators are supported.

1.4 Thesis Structure

The aim of this thesis is to develop and employ a broad analytical toolkit to evaluate: how well pollinators are supported throughout the season in apple orchards; how this affects pollinator activity after the flowering period of the crop; and how we can best support pollinators in apple orchards by restoring floral communities.

In Chapter 2, I outline a new approach for studying the structure of ecological networks through a season and use this to highlight fundamental differences in the temporal network structure of flower-pollinator networks in a crop with a long and short flowering phenophase. More specifically, I use highly-temporally resolved flower-pollinator networks for 6 floristically improved and 6 unaltered apple orchards and 3 strawberry farms to develop a new approach to reconstruct networks throughout the season. Using these network reconstructions, I demonstrate that pollinator persistence is lower in apple orchards but that adding floral resources increases pollinator persistence to match that of strawberry, which is reflected in a distinctive temporal network structure. This chapter highlights the importance of filling gaps in floral resources in apple orchards and identifies potential target network structures as restoration goals.

In Chapter 3, I evaluate whether differences in the temporal network structure of improved apple orchards influences the activity of pollinator communities beyond the crop-flowering period. In particular, I address whether increased pollinator persistence in improved orchards is due to aggregation of pollinators from the surrounding habitat, or local-scale increases in pollinator persistence. To consider this, I combine measures of orchard-level nectar and phytometer pollination and find that improved orchards are providing more resources beyond the flowering period of apple, and that this is allowing pollinators to persist for longer at a local scale. This suggests that floral improvements in orchards could increase the abundance and diversity of pollinator populations by providing a longer reproductive window for pollinators, regardless of their mobility.

In Chapter 4, I identify ways to fill gaps in floral resource provision for pollinators in apple orchards. Specifically, I use an in silico approach, inspired by an existing economics framework, to identify floral compositions that offer the highest quantity, stability and diversity of nectar for pollinators throughout the season. I then demonstrate that optimised floral mixes have the potential to significantly outperform surveyed floral areas managed under existing agri-environmental schemes, both in terms of the total amount and stability of nectar provided throughout the season. In doing so, I highlight a significant opportunity for improving the quality of resource provision for pollinators in apple orchards.

In Chapter 5, I collate my key findings and, in doing so, highlight the exposure of pollinators to food instability in the mass-flowering crop, apple, before evaluating existing restoration efforts in this crop. I conclude by outlining key limitations of my research and worthwhile future avenues in the field of restoration ecology.

By combining intensive field observations, a field experiment and novel computational approaches, this thesis considers how restoration efforts could be better targeted to support pollinators in agricultural habitats and highlights the importance of adopting a temporal perspective when studying habitat restoration for pollinators.

Chapter 2

Floral enhancement and the temporal structure of flower-pollinator networks in apple orchards

2.1 Introduction

Over the past 50 years, the proportion of global agriculture dependent on animal pollination has increased by over 300% (Aizen et al., 2009). However, the growth of honey bee populations is insufficient to match growth in agricultural demand for pollination (Aizen et al., 2009) whilst populations of wild pollinators have declined (Biesmeijer, 2006; Bommarco et al., 2012a; Cameron et al., 2011; Carvalheiro et al., 2013; Potts et al., 2016), driven by factors including disease pressure, pesticide use and habitat degradation (Ellis et al., 2010; Potts et al., 2010a). Consequently, the yields of the more highly pollinator dependent crops, including many of our most nutrient-rich crops (Eilers et al., 2011), are increasing more slowly than less pollinator dependent crops (Garibaldi et al., 2011) such that a continued loss of pollinators could undermine food production and human nutrition (Allen-Wardell et al., 1998; Kevan and Phillips, 2001; Steffan-Dewenter et al., 2005; Klein et al., 2007; Gallai et al., 2009).

Habitat degradation decreases the availability of nesting sites and food for pollinators (Baude et al., 2016; Goulson and Hughes, 2015; Roulston and Goodell, 2011; Scheper et al., 2014; Wallisdevries et al., 2012) and is recognised as a primary driver of pollinator

decline (Aguilar et al., 2006; Ferreira et al., 2015; Potts et al., 2010a; Vanbergen and Garratt, 2013). In particular, floral resources have undergone severe declines in both abundance and diversity, especially in agricultural habitats (Goulson and Hughes, 2015; Baude et al., 2016). Reduced diversity and abundance of nectar sources in a habitat can decrease pollinator abundance and species richness (Potts et al., 2003), most likely by failing to meet the nutritional requirements of pollinators (Alaux et al., 2010; Goulson and Hughes, 2015).

Restoring floral communities can increase pollinator abundance (Carvell et al., 2007; Pywell et al., 2005), diversity (Hannon and Sisk, 2009; Carvell et al., 2011; Sardiñas and Kremen, 2015) and contribution to crop pollination (Barbir et al., 2015; Blaauw and Isaacs, 2014; Campbell et al., 2017; Carvalheiro et al., 2012; Feltham et al., 2015; Häussler et al., 2017). For restoration efforts to be mutually beneficial for wildlife and agriculture, they must support individual populations whilst also promoting beneficial interactions between plants and pollinators. However, choosing appropriate restoration targets and monitoring progress towards those targets is challenging. This is especially difficult in agricultural habitats, where restoration efforts must support biodiversity whilst allowing commercial yield targets to be achieved. The ideal is for restoration efforts to be mutually beneficial for pollinators and the crops they pollinate, satisfying both conservation and commercial needs.

Ecological networks, in which nodes (species) are connected by links (observed interactions between species), provide a useful framework for studying ecological restoration and ecosystem service provision as they capture both species composition and the foraging behaviour of pollinator species (Tylianakis et al., 2010). Consequently, networks capture all the necessary information to analyse the impacts of restoration efforts on pollinator communities and pollination services.

Within the field of ecological networks, community detection could be an important tool for understanding the link between network structure and network function. Community detection involves the identification of *modules*, which are network regions with particularly high interaction density relative to the overall network. Importantly, modules can represent clusters of species that fulfil a particular ecological function (Pimm and Lawton, 1980; Montoya et al., 2015) and so studying the modular structure of a network may reveal information about network functioning.

Within ecological modules, different species fulfil different topological network roles (Guimerà and Amaral, 2005; Olesen et al., 2007), depending on their pattern of interaction with other species in the network. For example, species that form many interactions within their own module are classified as provincial hubs, and may have a role in the



Figure 2.1: Basic examples of string-periphery and multi-star network structures, as described by Guimera et al. (2007).

stability of individual modules (Crucitti et al., 2004). Species that interact with a wide range of modules are classified as connectors. Connectors may contribute to both overall network cohesiveness and the flow of perturbations between modules (Guimerà and Amaral, 2005). Due to their potential influence on network stability and functioning, some authors have suggested that hub and connector species should be considered conservation priorities (Tylianakis et al., 2010).

Finally, the number of links formed between species of different roles can reveal otherwise hidden structural network features. In a general study of network properties, Guimera et al. (2007) used these counts, which they termed *role-role connectivity profiles*, to analyse the structure of four different non-ecological network types (e.g. protein interaction networks). They found that metabolic and air transportation networks were examples of *stringy-periphery networks*, containing long chains of nodes that were otherwise poorly connected (Figure 2.1). For example, in metabolic pathways, these chains might represent the degradation of metabolites into a series of simpler molecules. Conversely, Internet and protein interaction networks formed *multi-star networks*, containing a higher frequency of links between poorly-connected nodes and module hubs, creating star-like structures (Figure 2.1). The authors hypothesise that these fundamental structural differences reflect differences in the growth and functioning of different network types. Whilst this approach is rarely, if ever, applied to ecological networks, it could be a useful way to summarise how functionally important species are interacting with other species in the network.

Modules, species' roles and role-role connectivity profiles all provide simple measures with which to compare ecological networks, whilst capturing structural features of the network that are relevant to network functioning. However, the usefulness of ecological networks are currently limited by their lack of temporal information (Olesen et al., 2011), which limits their application in restoration ecology. Ecological networks are typically constructed by aggregating observed interactions over an entire season, or over multiple years. However, within ecological networks, the constituent species have a fixed phenophase, which will determine when that species is able to form interactions (Visser, 2016). Species can also show plasticity in their interaction partners throughout time (Olesen et al., 2011). Static, aggregate networks mask this temporal variability, which may have important implications for the dynamics and stability of the overall network (Tanaka et al., 2012). For example, Han et al. (2004) demonstrated that hubs in yeast protein interaction networks can be split into two types, each with a different temporal profile: *party hubs*, interacted with most of their partners simultaneously whereas date hubs interacted with their partners at different times. The network was much more vulnerable to collapse following the simulated removal of date hubs than party hubs, demonstrating the importance of including information on the temporal nature of interactions.

This date/party distinction could be useful when considering floral resource provision for pollinators. For example, a generalist pollinator with a long flight period may have many interaction partners through the season, fulfilling a hub role in the aggregate, season-long flower-pollinator network. However, if the majority of these interactions are formed during a short time window (i.e. partying) then it could suggest the pollinator cannot find sufficient food at other points in the season. Conversely, if these interactions are formed sequentially through the season (i.e. dating), it suggests that the pollinator is accessing a continuous food supply, which is more likely to allow that pollinator species to complete its lifecycle. The most favourable scenario would be for this species to form many interactions at each point in time (i.e. partying and dating) as this would suggests the species is able to find ample and/or diverse floral resources throughout the entire season.

This classification is also useful for plant species within the network. For example, a plant species that forms the majority of its interactions in a narrow time window (i.e. partying) could promote biodiversity by offering a hub with which pollinators entering the network can interact. This is in line with the preferential attachment model of network growth, which states that species entering a network tend to do so by forming interactions with already well-connected species (Barabasi and Albert, 1999; Olesen et al., 2008). Conversely, plants that form interactions more uniformly through time (i.e. dating) are providing a consistent resource for both long-season pollinators and chronosequences of functionally similar pollinators. Of course, this reasoning depends on the specific resource needs of pollinators during a season, but understanding how both pollinator and plant species form interactions through time could be very informative when planning restoration efforts.

In this chapter, I develop a new network reconstruction method to improve the temporal resolution of plant-pollinator networks. I use this method to analyse the impact of floral improvement on pollinator persistence and the temporal structure of plantpollinator networks. My objectives are four-fold: (1) To develop a novel approach to predict plant-pollinator networks through the season in apple orchards and strawberry farms. I expect predicted network slices to be less sparse and more continuous through the season than those directly observed, as interactions that were missed due to inevitable under-sampling will be included in predicted networks. (2) To compare the persistence of pollinators in apple orchard and strawberry farm networks. I predict that pollinators will persist for a larger proportion of their potential phenophase in strawberry farm networks, as crop floral resources will be available more continuously through the season. (3) To compare the persistence of pollinators in floristically improved and unimproved apple orchard networks. I predict that pollinators will persist for a larger proportion of their potential phenophase in improved apple orchard networks, as non-crop flowering species will increase the continuity of floral resources outside the flowering period of the apple crop. (4) To compare the temporal network structure of improved apple orchard, unimproved apple orchard and strawberry farm networks. I predict that each of these network types will have a distinct temporal network structure that reflects differences in the roles that plant and pollinator species are fulfilling through the season.

2.2 Methods

2.2.1 Study system

Due to their contrasting flowering phenologies, apple (*Malus domestica*) and strawberry (*Fragaria anassa*) crops are excellent systems in which to compare the structure of plantpollinator networks through the season. Apple is an early-season mass-flowering crop, which produces a peak of flowers in spring, whereas commercial strawberry farms provide crop flowers continuously from c. mid-spring to c. early-autumn. Both crops are highly pollinator dependent (Klein et al., 2007). Wild and managed bees are key pollinators of apple (Garratt et al., 2016), but apple flowers have too short a phenophase to support the entire lifecycle of many bee species. Conversely, strawberry farms will provide a continuous supply of floral resources. Where non-crop floral resources are present, apple orchards may have greater overall plant diversity, which could increase pollinator diversity. However, if these non-crop flowers provide insufficient or discontinuous resources, apple orchards could be more vulnerable to network collapse.

2.2.2 Field Sites

Twelve apple orchards were studied and ranged in size from 1.5 - 3ha; they were grouped into three geographically distinct blocks of four orchards (grid references of the sites are provided in Appendix A), all within the South West of England. The first block of orchards (improved: B.St, B.Ra; unimproved: B.Ba, B.Mo), located in Dymock, Gloucestershire, consisted of young (<10 years since planting) bush, dessert apple orchards grown intensively. These sites are representative of commercially grown apple orchards in terms of their apple cultivars, chemical and physical management and planting density. The surrounding landscape of these sites consisted primarily of improved grassland that was periodically grazed by cattle. The second block of orchards (improved: D.A, D.M; unimproved: D.K, D.T), located in Brookthorpe, Gloucestershire, England consisted of diverse mixtures of standard apple trees grown organically and extensively and lightly grazed by sheep. These sites are representative of organic, traditional orchards in terms of their apple cultivars, chemical and physical management and planting density. The associated landscape was a mosaic of gardens, deciduous woodland and semi-natural grassland habitat. Site D.A sustained damage from overgrazing in July of the study year. The final block of orchards (improved: T.N, T.S; unimproved: T.E., T.W), located in Sandford, Somerset, consisted of young (<10 years since planting) intensively grown bush cider orchards. These sites are representative of intensive, commercial cider apple orchards in terms of their apple cultivars, chemical and physical management and planting density. These orchards were primarily surrounded by arable farms, including apple orchards. Each geographical block consisted of two floristically improved and two unimproved orchards. In floristically improved sites, 0.8 - 1.2% of the total orchard ground area had been left as unmown, unimproved grassland strips, and each improved site had at least 50m of flowering hedgerow. This is in line with the requirements of the Wild Pollinator and Farm Wildlife Package, which forms part of the UK's Countryside Stewardship Scheme. Typically, improvements included the addition of willow (Salix sp.) and blackthorn (Prunus spinosa) to hedgerows, and unmown strips

included high quantities of summer-flowering perennials such as thistles (*Cirsium* sp.). These improvements had been in place for at least 2 years in all sites. Within each block, all other management options, such as the timing and composition of chemical/fertiliser application, floral thinning, mowing regime and crop tree density were similar.

All orchards within a block were between 700 and 1,500m apart, which is beyond the typical foraging range of most pollinating bee species (Osborne et al., 1999; Greenleaf et al., 2007). Nevertheless, bumblebees can have foraging ranges exceeding 700m and hence could be moving between orchards. However, the close-proximity of orchards within one block made it logistically possible to sample all sites within a block on the same day. This minimised the effect of weather and the timing of weather-dependent chemical applications on network structure. It also made it possible to study orchards managed by the same owner (within a block), minimising the effects of management decisions on the pollinator community. Finally, their closeness ensures that all orchards within a block were within a similar landscape, such that differences in pollinator composition within sites could be largely attributed to site-specific differences, rather than the species pool within the wider landscape. Network differences have been identified in adjacent habitat patches before (Forup et al., 2008), indicating that local-scale differences in a network can be revealed even when exposed to an very similar pool of species in the landscape.

Three commercial strawberry farms (hereafter referred to as sites StrawbA, StrawbB and StrawbC) were sampled by Rachel Gibson, in 2009. Strawberry sites ranged in size from 8 - 19ha, and grew strawberries in fields and open-sided polytunnels. Natural and semi-natural habitats in strawberry sites consisted of grassy and naturally occurring wildflower margins plus hedgerows and associated hedge-base flora. Site StrawbB used a small number (approx. 10) of commercial bumblebee (*Bombus terrestris*) colonies between late-April and mid-June to supplement pollination.

2.2.3 Field sampling

In apple orchards, surveys were conducted between the 1st April and the 9th September 2016. For each sampling date, floral abundance counts were conducted for 25 randomly positioned 1 m x 1 m quadrats in both the cropped and boundary habitats. Random quadrat locations were determined by using a random number generator to select a random latitude and longitude within the appropriate bounds. Quadrats were placed centrally on this coordinate, with a flat surface directed northwards. The cropped habitat included apple trees and the permanent grassland understorey, which were surveyed as a

single habitat because they were so closely interlinked. The boundary habitat included areas of hedgerow and unmown margins. In each quadrat, the number of open floral units (Saville, 1993) of each flowering species was counted.

Flower-pollinator networks were constructed for each site using standard transectbased sampling (Memmott, 1999). Sampling was conducted along three randomly placed 2 x 25m transects in the morning and two randomly placed 2 x 25m transects in the afternoon, in both the cropping and boundary habitats (resulting in a total of 10 x $50m^2$ of sampling per site per sampling round). Random transect start-locations were determined by using a random number generator to select a random latitude and longitude within the appropriate bounds. A random number generator was used to provide a direction of travel between 0 and 359 degrees, where 0 represents directly North and 180 represents directly South. Any insect seen contacting the reproductive part of a flower was caught. With the exception of bumblebee (*Bombus* sp.) queens and honeybees (*Apis mellifera*), insects were killed and collected for identification by taxonomists (see Acknowledgements). Bumblebee queens and honeybees were caught and identified in the field before being released once the transect sampling was complete.

Strawberry farms were sampled at the whole-farm scale between the 16th of March and the 28th of September 2009 (collected by Rachel Gibson). Each site was sampled approximately once per week, resulting in a total of 24 sampling events per site. For each sampling date at site StrawbA, ten randomly positioned 25 m x 2 m transects were sampled in both the cropped and non-cropped areas (boundary habitats such as grass margins and hedgerows). At sites StrawB and StrawbC, five transects were sampled in each habitat such that sites StrawB and StrawbC were sampled at half the intensity of site StrawbA. The number of open floral units (Saville, 1993) of each flowering species were counted along each transect, and any insects seen contacting a flower's reproductive parts were caught. With the exception of bumblebee queens, insects were killed and collected for identification by professional taxonomists. Bumblebee queens were caught and identified in the field before being released. To standardise the networks from the three sites, StrawbA networks from each sampling date were rarefied by randomly removing 50% of the observed transects for each sampling date.

In both crop types, sampling was limited to dry, warm $(>10^{\circ}\text{C})$ days where wind speed was less than 5 ms⁻¹, so timing between samples varied (mean for apple = 16 days; mean for strawberry = 7 days). To remove the difference in sampling frequency between apple and strawberry networks, every other strawberry sampling round was removed during analysis. This created two sets of strawberry samples for each site, depending on which half of the sampling dates were removed. Each set was analysed separately, and the results averaged for each strawberry site.

2.2.4 Objective 1: Develop a novel approach to predict plant-pollinator networks through the season in apple orchards and strawberry farms

Predicting networks for specific dates through the season involved four steps, which are summarised in Table 2.1 and Figure 2.2. For an explicit definition of the method, see Appendix B. This approach was repeated for each of the 12 apple orchards and 3 strawberry farms.

Network metrics were calculated for each predicted network slice. All calculations were conducted in the R programming environment (Yan et al., 2011). Interaction diversity (Shannon Index) was calculated using the *vegan* package (Oksanen et al., 2015). Interaction evenness was calculated by dividing the interaction diversity for each predicted network slice by the log of the number of interactions in that slice, which gives Pielou's evenness (McCune and Grace, 2002). Interaction turnover was calculated using the Bray-Curtis index of similarity between adjacent predicted network slices, using the *vegan* package (Oksanen et al., 2015). Both evenness and interaction turnover had a negative skew and so were subtracted from 1 and square root transformed to normalise before analysing.

To evaluate the effect of date on each metric, I used linear mixed effect modelling with date as a fixed effect and site as a random effect. I modelled apple orchards and strawberry farms separately. For each metric, the full model was compared to a reduced model in which date was removed. The likelihood ratio test was used to compare the relative likelihood of each model. All linear mixed models were carried out using the lme4 package (Bates et al., 2014) in the R programming environment (Yan et al., 2011)

2.2.5 Objective 2: Compare the persistence of pollinators in apple orchard and strawberry farm networks.

To assess whether seasonal pollinator persistence varied between apple orchards and strawberry farms, a linear mixed effect model was constructed with crop type as the independent variable and pollinator persistence as the dependent variable. Pollinator persistence is defined as the proportion of prediction network slices a pollinator is present in relative to the total number of prediction dates in which it could feasibly be present.

the process, see Appen	dix B.	
Step	Approach Outline (for details see Appendix B)	Justification
1. Determine predic- tion dates	Identify a series of dates, henceforth <i>prediction dates</i> , which are spaced at fortnightly intervals through the field sampling season. These are the dates for which networks will be predicted.	This is necessary as sampling dates are not spaced completely evenly (largely because of the weather) and a larger distance between two networks could increase the probability of network change.
2. Predict floral abun- dance	Predict the floral composition of each site on each prediction date, using observed floral abundance data.	As sampling dates and prediction dates are not the same, floral abundance surveys were not necessarily carried out on prediction dates, but this information is required for the network prediction method.
3. Smooth networks through time	This method uses network data collected at regular intervals through a season (observed network slices) to create a series of predicted network slices. Each predicted network slices, where the weighting is deter- mined by the level of ecological correlation between the field site on the sampling and prediction dates. This is such that an observed network slice will be given greater weighting during the prediction when it is more similar in date and floral composition (see Figure 2.2 for an example).	Observed network slices are unlikely to be an accurate reflection of the true network on that date. This is because sampling a site thoroughly enough in a small number of sampling rounds is not feasible. Accordingly, many interactions will go undetected, including common interactions. However, by combining network information with independent floral abundance surveys, it is possible to draw information from a wider range of sampling dates when determining network structure for a specific date.
 Remove forbidden links (Olesen et al., 2011) 	Remove any predicted interactions outside the ob- served phenophase of each species.	The network smoothing function (step 3) may pre- dict low occurrences of certain interactions outside the phenophase of one or both of the interacting species. These interactions could never feasibly oc- cur, so are removed.

Table 2.1: A summary of the four stages of network slice prediction with justification for each. For an explicit definition of





Pollinator presence was deemed feasible on a prediction date if that pollinator species had been observed within one week of that date in any one of the sites. Given that the composition of local pollinator populations might influence the occurrence of pollinators, the site was included as a random effect in the model.

We considered only species seen pollinating the crop in both apple and strawberry farms and observed in at least 50% of sites. The reason for limiting the focal species were twofold. Firstly, considering only pollinating species that visit both crop types ensured that focal pollinators were directly exposed to the contrasting temporal flowering pattern of apple and strawberry crops. Secondly, it ensured that taxonomic differences between pollinator communities was not influencing the average value of pollinator persistence. For example, a site with a higher proportion of early-season pollinators could have a higher average overall pollinator persistence.

2.2.6 Objective 3: Compare the persistence of pollinators in floristically improved and unimproved apple orchard networks.

To assess whether seasonal pollinator persistence varied between improved and unimproved apple orchard networks, a linear mixed effect model was constructed with treatment (i.e. improved/unimproved) as the independent variable and pollinator persistence as the dependent variable. Given that the management of a site (e.g. pesticide usage, human traffic) might influence the occurrence of pollinators, block was included as a random effect in the model. I considered only pollinator species seen pollinating apple in at least 75% of apple orchards. This was to exclude rarer pollinator species, which could be absent due to poor resource provision (i.e. zero pollinator persistence) or because that species does not occur in the area.

2.2.7 Objective 4: Compare the temporal network structure of improved apple orchard, unimproved apple orchard and strawberry farm networks.

Simulated annealing, a standard module detection algorithm (Guimerà et al., 2004), was used to identify modules within networks. Species roles (*hub, connector, peripheral*) were determined using a standard protocol (outlined by Guimerà and Amaral (2005) and first applied to ecological networks by Olesen et al. (2007). This procedure was repeated for each predicted network slice, to determine the network role of each species through the season. To determine the overall role of each species, this was repeated for season-long aggregate networks, which were constructed by summing all predicted network slices for each site.

Each species' role in both the aggregate network and predicted network slices was used to create a distinction between *date* and *party* network roles. Date roles were allocated where a species develops its role through the season (i.e. it occupies a role in the season-long aggregate network as a result of interactions formed at different times). Party roles were allocated where a species fulfills a role only at a specific point in the season. *Global* roles were allocated where a species fulfills a role at several points across the season and in the aggregate network, and represents species with dating and partying characteristics (see Table 2.2 for explicit role definitions). Both date and global roles represent species that are present for a minimum of three time slices, which represents a minimum phenophase of between 4 and 8 weeks (depending on whether a species occurs between these dates exactly, or extends to nearly occur in the adjacent network slices). Crucially, this period is sufficient for many key pollinators to complete their lifecycle (Falk and Lewington, 2015).

As outlined in the introduction of this chapter, *role-role connectivity profiles* provide a mathematical summary of how functionally important species are interacting with other species in the network. Role-role connectivity profiles were constructed, using an approach defined below, for all strawberry farms, unimproved apple orchards and improved apple orchards. Networks that form similar structural patterns through time are likely to have similar *temporal role-role connectivity profiles*.

To create role-role connectivity profiles for each site, the proportion of links between plants of role i and pollinators of role j was calculated (for all values of i and j). To evaluate the impact of including temporal role definitions in role-role connectivity profiles, this approach was repeated for standard role-role connectivity profiles (i.e. including hub, connector, and peripheral role definitions) and temporal role-role connectivity profiles (i.e. also including global, date and party distinctions). This created two connectivity profiles for each site (standard and temporal profiles), represented as vectors (Figure 2.3).

The networks of unimproved apple orchards, improved apple orchards and strawberry farms likely have distinct temporal role-role connectivity profiles due to their particular pattern of floral resource provision through time. To evaluate the similarity of role-role connectivity profiles between different sites, the cosine similarity was calculated between corresponding vectors. This was repeated separately for the standard and temporal analysis. Cosine similarity is a widely used metric that measures the cosine of the angle between two vectors and varies between 1 (similar) to -1 (dissimilar). In this case, a value of one indicated that two sites have similar connectivity profiles. This approach is
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2.2: Net	on a spe	not alloci
Table	based	were I

		Hub			Connector	
	Date	Party	Global	Date	Party	Global
Description	These form hubs	These form hubs	These form hubs	These form	These form	These form con-
	in the aggregate	in 1-2 network	in at least 3	connectors in	connectors in	nectors for at
	network but do	slices during	network slices	the aggregate	1-2 network	least $c.6$ weeks
	so by establish-	the season,	during the sea-	network but do	slices during	during the sea-
	ing interactions	but might not	son, and are	so by establish-	the season, but	son, and are
	across multiple	form hubs in	hubs in the ag-	ing interactions	might not form	connectors in
	dates.	the aggregate	gregate network.	across multiple	connectors in	the aggregate
		network.		dates.	the aggregate network.	network.
Role in season-	Hub species	Any role	Hub species	Connector	Any role	Connector
long aggregate network				species		species
Role in predicted	Never a hub	A hub species in	A hub species in	Never a connec-	A connector	A connector
network slices	species	1-2 slices	>=3 slices	tor species	species in 1-2	species in $>=3$
					slices	slices
Occurrence	Present in >2	Present in at	Present in >2	Present in >2	Present in at	Present in >2
	slices	least 1 slice	slices	slices	least 1 slice	slices
Example	A pollinator	A flower species	A pollinator	A generalist	A generalist	A generalist
	species that	that attracts	species that	pollinator that	pollinator that	pollinator that
	interacts with a	many pollina-	interacts with	interacts with	interacts with	interacts with
	different flower	tors for a short	many flower	flowers from	flowers from	flower species
	species at differ-	period of the	species across	different network	different func-	from different
	ent points in the	season.	multiple points	modules at dif-	tional groups at	network modules
	season.		in the season.	ferent points in	a specific point	at any one time,
				the season.	in the season.	and through the
						season.



Figure 2.3: Vector representations of hypothetical standard and temporal role-role connectivity profiles. based on the fact that a vector provides a co-ordinate in space. Each co-ordinate can be reached from the origin of this space by following a particular angle. If two co-ordinates are close together in space, there will only be a small difference in this angle and the cosine of this difference will be close to 1. Conversely, if these points are in near-opposite directions, the difference in angle will be close to 180°, the cosine of which equals -1. To identify relationships between site network structures, complete-linkage clustering was implemented via the *heatmap* function in R (Yan et al., 2011).

2.3 Results

2.3.1 Objective 1: Develop a novel approach to predict plant-pollinator networks through the season

The new network prediction approach was used to predict networks through the season for each apple orchard and strawberry farm. Predicted network slices had a significantly higher interaction diversity (apple: $\chi^2(1) = 10.6$, p = 0.00112; strawberry: $\chi^2(1) = 14.0$, p < 0.001) and lower interaction turnover (apple: $\chi^2(1) = 23.0$, p < 0.001; strawberry: $\chi^2(1) = 21.3$, p < 0.001) than observed network slices (Figure 2.4). This suggests that, in line with expectations, predicted network slices are less sparse and more continuous through the season than those directly observed.

In apple networks, there was a significant effect of date on interaction diversity $(\chi^2(1) = 12.7, p < 0.001)$, evenness $(\chi^2(1) = 28.8, p < 0.001)$, and interaction turnover $(\chi^2(1) = 9.12, p < 0.00253)$. For strawberry networks, there was a significant effect of date on interaction diversity $(\chi^2(1) = 14.4, p < 0.001)$ but not on evenness $(\chi^2(1) = 0.766, p = 0.381)$ or interaction turnover $(\chi^2(1) = 2.17, p = 0.141)$. In line with expectation, this suggests strawberry farm networks are more consistent through time than apple orchard networks, both in terms of species identity and overall structure.

2.3.2 Objective 2: Compare the persistence of pollinators in apple orchard and strawberry farm networks.

There was a significant difference in the persistence of the focal pollinators through the season between apple orchards and strawberry farms ($F_{1,13} = 15.8$, p = 0.0016; Figure 2.5). Whilst pollinator species were present for an average of 79.6% of their feasible phenological breadth in strawberry farms, they only occurred in 44.1% of their feasible phenological breadth in the apple orchards.



Figure 2.4: An example of observed (top) and predicted (bottom) networks for a single apple orchard (B.Mo) through the season. Each species is represented as a node and each interaction as a link, with link width log-log proportional to the frequency of the interaction. Note the different time scales, representing the dates of observations (top) and evenly spaced dates used for network prediction (bottom).



Figure 2.5: Pollinator persistence for floristically improved and unimproved apple orchards for (top) individual species, where dark blue denotes a value of 1 (i.e. maximally persistent) and (bottom) with data from all species combined as boxplots showing median with 95% confidence intervals).

2.3.3 Objective 3: Compare the persistence of pollinators in floristically improved and unimproved apple orchard networks.

When comparing a different set of pollinator species (i.e. those believed to be the most important pollinator of apple), there was a significant difference in pollinator persistence through the season between floristically improved and unimproved orchards ($F_{1,92} = 6.2$, p = 0.0145; Figure 2.6, 2.7). Improved orchards had an average pollinator persistence of 0.724 compared to 0.397 in unimproved orchards, indicating that these pollinator species were interacting for 72.4% and 39.7% percent of their potential phenophase in improved and unimproved orchards, respectively.



Figure 2.6: Pollinator persistence for 12 apple orchard sites (top), when considering the most important pollinators of apple. Dark blue denotes a value of 1 (i.e. maximally persistent). Persistence of these pollinators in floristically improved and unimproved apple orchard sites (bottom).

Whilst the honey bee (*Apis mellifera*) was persistent throughout its entire feasible phenology in 9 out of 12 sites, bumblebees (*Bombus* sp.) and solitary mining bees (*Andrena* sp.) were supported for their entire phenology in only 3 and 2 sites, respectively, when averaging across the relevant species. This demonstrates that pollinators were not occurring for as long as they could in the majority of apple orchards surveyed, and highlights an opportunity for supporting crop pollinator populations through increasing floral provision.

When considering bumblebees, each species had on average 7 sites in which they were





present for only part of their possible phenophase. Of these incidences, 36% were caused by bumblebee species occurring only for the duration of the crop; 25% were caused by bumblebee species occurring continuously during crop flowering and one prediction date either side; 39% were caused by bumblebee species occurring during crop flowering before returning to the site in July or August after a period of absence. This suggests that, in some apple orchards, pollinators may periodically enter into the network from the surrounding landscape.

When considering solitary mining bees, each species had, on average, 6.33 sites in which they occurred for only part of their possible phenophase. In every such case, these species were lacking resources either directly before or after apple flowering, such that their phenophase was curtailed. There was therefore no evidence of species entering and leaving the network at different times in the season, even when those species are known to be bivoltine.

2.3.4 Objective 4: Compare the temporal network structure of improved apple orchard, unimproved apple orchard and strawberry farm networks.

It was predicted that improved apple, unimproved apple and strawberry farm networks would have distinct temporal structures; temporal role-role connectivity profiles should reveal these patterns, which were previously hidden in standard role-role connectivity profiles. In the following section, I describe the identified standard role-role connectivity profiles before comparing them to role-role connectivity profiles created using temporal role definitions. I then describe specific differences in network structure that are revealed by adding a temporal perspective.

Role-role connectivity profiles using standard role definitions

When comparing all 15 networks using standard role definitions (i.e. hub, connector, peripheral), the networks for each site fall into one of four main role-role connectivity profiles (Figure 2.8; Table 2.3; see Appendix C for a depiction of role-role connectivity profiles for each site).



Similarity of standard role-role connectivity profiles

Figure 2.8: The cosine similarity of role-role connectivity profiles for each pairwise combination of sites constructed using standard role definitions where paler colours indicate greater similarity.

Table 2.3: The four main role-role connectivity profile types when using standard role definitions, and the likely ecological implications of these categories.

		Zo	ne	
	Α	В	C	D
Most common role-role	Peripheral plants in-	Hub and peripheral	Hub plant species	s interacting with
interaction types	teracting with both	plants interacting with	hub and peripheral pol-	<i>peripheral</i> pollinators
	hub and peripheral pol-	<i>peripheral</i> pollinators	linators	4
	linators			
Likely Implications	Pollinators are using a	Isolated interac-	As for Zone D, but	Abundant, generalist
	wider range of flower	tions are occurring	with some pollinators	plants are attracting
	species but crop flow-	alongside the main	foraging from a wider	specialist pollinators,
	ers are not forming	crop-pollinator inter-	range of plants. For	or that generalist pol-
	network hubs. Crop	actions. For example,	example, a scenario	linators are interacting
	pollination, in this sce-	a scenario in which a	in which some crop-	with a limited range of
	nario, may be depen-	subset of pollinators	visiting generalist pol-	plants. For example, a
	dent on a small number	were exclusively inter-	linators were also visit-	scenario in which mo-
	of generalist pollina-	acting with the crop	ing non-crop flowers.	bile, generalist pollina-
	tors that are also for-	whilst a second subset		tor species were exclu-
	aging extensively from	of specialist pollinators		sively visiting the crop
	a wide range of other	were each interacting		plant would result in
	floral species.	with different non-crop		this connectivity pro-
		plants.		file.

Network similarity using standard versus temporal role-role connectivity profiles

When using temporal role definitions to create connectivity profiles (Figure ??), there are two notable changes in the clustering of sites based on their profile similarity (i.e. networks that appeared similar using standard network role definitions but appear dissimilar when using temporal network role definitions) (Figure 2.10, Zone 1 and 2). This demonstrates that a temporal perspective can highlight otherwise hidden differences in the structure of networks.



Similarity of temporal role-role connectivity profiles

Figure 2.9: The cosine similarity of temporal role-role connectivity profiles for each pairwise combination of sites constructed using temporal role definitions where paler colours indicate greater similarity.



Figure 2.10: The absolute difference in site similarity between the standard and temporal profiling methods, where a dark red indicates a greater change in similarity (i.e. a pair of sites that have changed most in their similarity when moving from the standard to temporal connectivity profiles).

By considering the reasons for these changes in clustering, it is evident that temporal role-role connectivity profiles are revealing ecologically relevant features of the network. For example, the first shift in clustering (Figure 2.10, Zone 1) can be attributed to changes in pollinator role. Using standard role definitions, the connectivity profiles of these networks were dominated by interactions with hub pollinators. However, when using temporal role definitions networks, these pollinator hubs are discerned as either party hubs (apple orchards T.W, B.Ra), forming most interactions in a small number of time slices, or date/global hubs (apple orchards B.St, D.M), interacting with flowers more consistently through the season.

The second shift in clustering (Figure 2.10, Zone 2) is explained by the network role of plants. When using standard network role definitions, most interactions in these sites occurred with hub plants. However, in all strawberry networks and one apple orchard (B.Mo), interactions most frequently involve global hub plants, whereas in the remaining four apple orchards in Zone 2 (D.T, T.N, B.Ra, B.St, D.M), interactions were more frequently with party hubs.

Temporal role-role connectivity profiles of improved and unimproved apple orchard networks

The temporal role-role connectivity profiles of improved apple networks form a separate cluster (Figure 2.10, Zone E) to the strawberry farms and unimproved apple networks (Figure 2.10, Zone F), with the exception of a single unimproved apple orchard (D.T). This two-way clustering was statistically significant (p = 0.00458). This suggests that there are fundamental differences in the topology of improved and unimproved orchard networks, which are only revealed when adopting a temporal perspective.

Networks in Zone E (including all improved apple networks) are characterised by a significantly smaller proportion of interactions involving global hub plants ($t_{10.2} =$ -3.03, p = 0.0125) and interactions involving peripheral pollinators ($t_{10.3} =$ -3.30, p = 0.00779) relative to networks in Zone F (most unimproved apple orchards and strawberry farms). Instead, these networks had a significantly larger proportion of interactions involving party hub plants ($t_{7.9} = 2.55$, p = 0.0344) and date/global-role pollinators ($t_6 =$ 0.0367, p = 0.0367). This suggests that highly attractive generalist plants are forming chronological sequences throughout the season, supporting the persistence of generalist pollinators.

2.4 Discussion

By developing an approach to predict flower-pollinator networks through the season, this chapter has demonstrated the importance of considering temporal network structure when restoring habitats for pollinators. In line with prediction, pollinator species were supported by flowers for almost twice as long in strawberry farms relative to apple orchards. However, modest enhancement of floral resources (covering 1% of the total orchard area) in apple orchards increased the phenophase of key pollinators at a local scale. Floristically improved apple orchards had a fundamentally different temporal network topology such that pollinators were interacting with more plant species over a longer period (dating), whereas plants were forming hubs at specific points in the season (partying). This specific temporal fingerprint, which was seen only in improved orchards, has implications for both the functioning and stability of flower-pollinator networks. In this section, I first discuss the limitations of my approach. I then focus on the value of adopting a temporal perspective and the potential implications of temporal network structure on network functioning. I finish by outlining future directions in the study and application of ecological networks in restoration ecology.

2.4.1 Limitations

There are two main limitations to my approach. Firstly, constructing networks with a high temporal resolution is time intensive, which made it necessary to sample a relatively small number of sites. As such, this study includes no replication of crops with shortand long-season flowering phenologies. More studies are needed to test whether the differences in temporal structure between these crop flowering regimes are generalisable.

Secondly, simplifying assumptions have to be made when using a modelling approach. The network prediction method developed in this chapter assumes that the changes in a network through a season are determined by the passage of time and changes in floral composition. Whilst these are likely to be key drivers of network change, there are several others factors that may have an effect, including regular habitat disturbances, the species composition of pollinator populations and landscape-level differences in species composition. However, these factors are mostly addressed by having a block-design, such that orchards within one block are managed consistently and exposed to a similar landscape structure.

2.4.2 A temporal perspective when studying mass-flowering crops

Mass-flowering crops can provide beneficial resources for pollinators (Herrmann et al., 2007; Jauker et al., 2012; Kallioniemi et al., 2017; Westphal et al., 2003) but can also undermine pollinator populations (Benedek, 1997; Kallioniemi et al., 2017) by reducing the continuity of floral resources in a landscape (Di Pasquale et al., 2016). Pollinators require a continuous supply of floral resources throughout their lifecycle (Menz et al., 2011; Vaughan et al., 2007) and so will utilise non-crop flowers (Bernardino and Gaglianone, 2008; Requier et al., 2015) or even the honeydew secretions of other invertebrates (Meiners et al., 2017) when crop flowers are unavailable. Ecological networks could provide a valuable tool for planning the restoration of pollinator communities in agricultural habitats dominated by mass-flowering crops. However, they are rarely analysed through the season as gathering accurate networks for a specific time windows is impractical.

By combining observed network data in an ecologically justifiable way, I predicted networks for specific dates throughout the season. This reduced the number of interactions missing in a network due to under-sampling, allowing networks to be compared through the season. I was able to identify clear differences in how the networks of a short-flowering crop, apple, and long-flowering crop, strawberry, changed through time. Apple orchard networks showed rapid turnover of interactions at the start and end of apple bloom. Conversely, in strawberry farms, new interactions gradually added to an otherwise stable network. These interpretations were supported when considering the persistence of a subset of pollinators shared by apple and strawberry, which was almost 50% lower in the networks of apple orchards.

These findings highlight that pollinator species are indeed more vulnerable to food shortages in the short-flowering crop, apple. For many spring-flying species, including several species of bumblebee and solitary mining bee, apple flowers do not appear early enough in the season to feed reproductive females. This could prevent these species from successfully establishing a nest (Harder and Barclay, 1994; Falk and Lewington, 2015). In addition, many bee species will have phenophases that extend beyond the flowering period of the crop. This is true of all 20 of the most common bee visitors to apple that were identified by (Garratt et al., 2016) (see Chapter 1). The fitness of these bee species could be compromised if non-crop floral resources are unavailable to extend the flowering season; for example, honeybee fitness drops significantly after exposure to a moderate 5-10% drop in pollen supply (Di Pasquale et al., 2016). This could explain why the negative impacts of mass-flowering crops on pollinator populations can be alleviated by the addition of late-season flowering resources (Kallioniemi et al., 2017; Rundlöf et al., 2014).

By predicting networks through time, I was also able to develop a new framework to summarise key features of temporal network structure. Analysing the patterns of connections between species of different roles highlighted fundamental differences in the structure of different networks. The temporal network structure of strawberry farms suggests that pollinators were fulfilling mostly peripheral network roles or, occasionally, short-lived hub roles. Network studies have repeatedly shown that abundant species have a tendency to be generalists (Vázquez et al., 2007), so we would expect these species to be forming hubs that interact with multiple plant species. The lack of longlived hub pollinators in strawberry farms could indicate that pollinators are receiving a low-diversity diet. This is in line with previous findings of low floral diversity in agricultural habitat (Baude et al., 2016). Low floral resource diversity can reduce the health of pollinators, which need a varied diet of nectar and pollen to maintain good immune-functioning (Alaux et al., 2010; Goulson et al., 2010). Pollinators might be better supported in strawberry farms if more diverse floral resources were available.

Analysing temporal network structure also highlighted differences in apple orchard sites that had been improved through the addition of non-crop floral resources, relative to those left unimproved. In improved apple orchards, there was a greater prevalence of plant species acting as short-lived hubs (party hubs). These plant species, which included members of the Apiaceae family (*Anthriscus sylvestris, Daucus carota, Her*- acleum sphondylium) and Apiaceae family (*Taraxacum* agg., *Cirsium arvense*), were providing a popular resource at specific points through the season. Given that species entering a network tend to interact with already well-connected species (Olesen et al., 2008), party hub plants could facilitate network growth and diversity by allowing new pollinator species to join the network.

Pollinator species in improved apple orchards more frequently fulfilled a long-lived (date or global) hub or connector role, suggesting these species were interacting with a greater diversity of plant species for a larger portion of the season. In combination, the increased proportion of partying plant species and dating pollinator species suggests that plant species are forming chains of resources through the season, offering sequences of high-quality resources for pollinators. This specific temporal fingerprint, with many interactions involving partying plants and dating pollinators, suggests that improved orchards can support greater pollinator abundance and diversity than either unimproved apple orchards or strawberry farms.

2.4.3 Future directions

If temporal network analysis is to be used as a restoration tool, it is crucial that the ecological properties of networks with different temporal structures are evaluated, either through field observation or *in silico* simulation. In particular, it would be beneficial to determine how robust and resilient different temporal network topologies are to perturbation and how different network topologies affect the transfer of pollen within the plant community. In addition, we need a better practical and mechanistic understanding of how to manipulate an ecosystem to achieve desirable temporal network structures.

Secondly, there is a need to consider a wider range of species when evaluating restoration efforts. Manipulating floral communities will influence a wide range of insect species (Balzan et al., 2016; Blaauw and Isaacs, 2012; Tschumi et al., 2015; Wäckers, 2004) which will affect the provision of both ecosystem services and disservices. The flowering and cropping window for apple are separate, which creates a temporal distinction between the ecosystem service of pollination and the ecosystem disservice of crop herbivory. This temporal decoupling gives opportunity for ecologically-minded management that promotes pollinators whilst minimising pests. However, this approach would require a greater understanding of the temporal structure of plant-herbivore networks in apple orchards.

2.5 Conclusion

The complex lifecycle of pollinators demands a continuous supply of floral resources. For many pollinators, these needs are not met in landscapes dominated by crops, especially where these crops flower for a short period. Ecological networks are a useful tool when planning and evaluating land management options for pollinators. However, studying networks through a season is made difficult by the high sampling intensity required to accurately depict network slices. To overcome this limitation, I developed a new tool to predict networks through the season. I used this to show that pollinators can be vulnerable to food shortages in the short-season crop, apple, but that this can be addressed by adding non-crop floral resources. Floristically improved apple orchards all shared a specific temporal network structure, with pollinators taking less of a peripheral network role, supported by sequences of plants through the season. This suggests that improved apple orchards have the propensity to support pollinators at least as well as the long-season crop, strawberry. This specific temporal fingerprint could represent a desirable restoration target when supporting pollinator communities in crops with a short flowering season.

Chapter 3

Reducing gaps in floral resource provision increases pollination services later in the season

3.1 Introduction

Animal pollinators are of great importance for food security, fertilising over 87 of the world's leading food crops (Klein et al., 2007). However, pollinator populations have undergone serious declines (Biesmeijer, 2006; Cameron et al., 2011; Carvalheiro et al., 2013) and the conservation and restoration of pollinator populations is now of utmost concern, both from the perspective of biodiversity conservation (Goulson and Hughes, 2015) and food security (Garibaldi et al., 2011).

The intensification of agricultural habitat decreases the quantity and diversity of floral resources for insect pollinators (Baude et al., 2016) and has been linked to pollinator decline (Ollerton et al., 2014). The low floral diversity of agricultural habitats may support fewer functional groups of pollinator species (Kennedy et al., 2013) and reduce the immunocompetence of pollinators (Alaux et al., 2010). Enhancing the abundance and diversity of floral resources in agricultural habitat by adding extra areas of non-crop flowers could address these issues, resulting in larger (Carvell et al., 2007; Williams et al., 2015; Kallioniemi et al., 2017), healthier and more diverse (Carvell et al., 2007; Williams et al., 2015; Kallioniemi et al., 2017) pollinator populations.

Floral enhancement might be particularly beneficial where it increases the overall phenological coverage of flowers, especially in landscapes dominated by areas of a single, short-flowering crop (Benedek, 1997; Bernardino and Gaglianone, 2008; Menz et al., 2011; Kallioniemi et al., 2017). In these habitats, the addition of non-crop flowers could ensure that pollinators are fed throughout their flight season, regardless of their phenology. In the previous chapter, I explored this idea by analysing the temporal structure of flower-pollinator networks in apple orchards, an early-flowering crop. Apple orchards that had been floristically improved showed a distinct temporal network topology that suggested popular flowering species were forming chronosequences, supporting pollinators at different points through the season.

The results of Chapter 2 suggest that improved apple orchards have an increased phenological coverage of flowers, allowing pollinators to persist for longer through the season. However, the specific mechanism by which orchard improvement increased the persistence of pollinators cannot be fully addressed using ecological networks. A limitation of ecological networks is that the occurrence of plant and pollinator species in a network is dependent on the availability of interaction partners. For example, the absence of a species from a network could either be due to the true absence of that species from a site (i.e. it is not present in the area) or an absence of plausible interaction partners (i.e. it is present in an area, but not interacting with surveyed flowers). In the latter case, a species may be present at a site but will not feature in the network. This limits the ability of networks to identify correlations between floral resource provision and pollinator community composition. Specifically, network data is not best placed to distinguish between the following two scenarios: (1) Improved orchards are providing more consistent floral resources such that pollinators are surviving continuously through the season. This would suggest that floral improvement has the propensity to support a wide range of pollinator species (see Section 1.2.3). (2) Improved orchards are providing pulses of high-quality floral resources, causing periodic aggregation of pollinators from the surrounding landscape (Kohler et al., 2008). This would suggest that floral improvement may only benefit more mobile species that can readily move through the landscape.

Disentangling these scenarios requires a better understanding of how floral improvement affects both the consistency of floral resources through the season and pollinator activity beyond the flowering period of the crop. Phytometer species are a useful tool in this scenario, as they provide a measure of pollinator activity that can be readily compared between study sites. A phytometer is a plant whose attributes reflect some characteristic of its surroundings. For example, the shape of a strawberry is determined by the quality of pollination it has received (Figure 3.1). This makes phytometer species useful for evaluating the impact of ecological restoration on pollinator communities. For example, phytometer species have been used to evaluate the effectiveness of different



Figure 3.1: Strawberries that have been open pollinated, self-pollinated and wind-pollinated. The open pollinated strawberry has received greater pollination and therefore has no deformities. Photo by Kristine Krewenka, Agroecology, Göttingen, Germany.

agricultural management option for supporting wild pollinators (Albrecht et al., 2007; Andersson et al., 2012; Hardman et al., 2016; Orford et al., 2016) and the effects of mass-flowering crops on the pollinator community (Diekötter et al., 2010; Hanley et al., 2011).

By combining data on floral provision through the season with measurements of phytometer pollination later in the season, this chapter aims to evaluate the relationship between orchard improvement and pollinator persistence. Specifically, I predict that the addition of non-crop floral resources to apple orchards increases pollinator persistence by providing more consistent floral resources through the season. This can be addressed through the following two objectives: (1) determine if pollination of a phytometer species, placed towards the end of the season, varies between floristically improved and unimproved apple orchards. The prediction is that pollination will be higher in improved than unimproved apple orchards because pollinators will be have a larger window in which to reproduce, resulting in higher pollinator abundance and diversity. (2) Determine if patterns of nectar provision through the season vary between floristically improved and unimproved apple orchards. The prediction is that improved apple orchards provide and unimproved apple orchards. The prediction is that improved apple orchards provide and unimproved apple orchards. The prediction is that improved apple orchards provide and unimproved apple orchards. The prediction is that improved apple orchards provide and unimproved apple orchards. The prediction is that improved apple orchards provide a higher quantity of nectar between apple crop flowering and phytometer placement, but not during phytometer placement because pollinators will be able to persist later into the season.

3.2 Methods

3.2.1 Field sites

Twelve apple orchards, grouped into three geographically distinct blocks of four orchards, were studied between 1st April and 9th September 2016 (see Section 2.2.2). Each geographical block of orchards consisted of two floristically improved and two floristically unaltered orchards (see Section 2.2.2). In each orchard, floral abundance surveys were conducted between the 1st April and the 9th September 2016 (see Section 2.2.3). In one site, D.A, sheep destroyed the experimental set-up so this site is excluded from phytometer analysis.

3.2.2 Estimating nectar resources through time

The quantity of nectar available in a habitat can be used as measure of floral resource availability. Nectar and pollen are both important floral resources for pollinators (Harder and Barclay, 1994; Falk and Lewington, 2015; Hicks et al., 2016). However, nectar is required throughout the flight season as the principal energy source for many pollinators (Harder and Barclay, 1994). As such, the sugar content of nectar is an ecologically relevant currency with which to capture the nutritional value of different plant species (Baude et al., 2016). Measured flower nectar productivity data can be combined with estimates of floral abundance to quantify the total availability of nectar sugars in a given area (Baude et al., 2016).

To estimate the total nectar production on each orchard site for each sampling round, floral abundance surveys were combined with existing data on the nectar production of different flowering species (Baude et al. (2016) - this data provides direct measurements of daily nectar production for the UK's most common flowering species). For each plant species observed flowering in an apple orchard, the floral abundance was multiplied by the per-flower daily nectar production to estimate the total nectar produced by this species on this site. This value was summed across all flowering species for each sampling round to estimate total daily nectar production per round, per orchard. For each orchard, the total nectar production per sampling round was calculated for (a) the middle of June to the beginning of August, which represents the period of potential shortfall between apple flowering and phytometer placement, and (b) the duration of phytometer placement. By focusing on the resources available in the six weeks following apple flowering, this study covers a period of peak pollinator reproductive activity that is not covered by apple flowering. Of the plant species observed in apple orchard floral abundance surveys, the nectar production of 71% had been directly measured by Baude et al. (2016). This included the majority of the most common plants, such that 93% of sampled quadrats included only plant species with measured nectar production. The nectar production of the remaining flower species was estimated from the nectar production of plants with similar traits, as follows. For each plant species lacking directly measured nectar production values, plant species were identified from the Baude et al. (2016) database that shared their taxonomic family, height category and life span (annual/perennial) with missing plants. The mean of the daily nectar production of these plant species was used as an estimate for each missing plant species.

In all but 2 sites, this estimated (rather than directly measured) nectar formed <1% of the total nectar production across the entire season. It is therefore unlikely to impact results at most sites; however, in two sites, D.T and D.K, the predicted nectar provided 46% and 40% of the total nectar on the site, respectively. The vast majority (95%) of this predicted nectar was produced by vetch (*Vicia hirsuta*) and upright hedge-parsley (*Torilis japonica*). The flowers of vetch are significantly smaller than those of related flowers (e.g. other *Vicia* sp.), and hence likely to hold a smaller nectar volume. All analyses were therefore repeated with a 50% and 99% reduction in estimated nectar production for this species. For the purpose of sensitivity analysis, analyses were also repeated with a 50% reduction and 99% increase in estimated nectar production for upright hedge-parsley, as this covered the entire measured range of annual Apiaceae members. This created 9 possible nectar-value combinations.

3.2.3 Phytometer experiment

A strawberry consists of multiple achenes, each of which must be pollinated to develop. If few achenes are pollinated then a strawberry will be misshapen, indicating lower pollinator activity. Conversely, if the majority of achenes are pollinated, strawberries will have a typical, full symmetrical strawberry shape. Strawberry plants are an excellent phytometer species to use in apple orchards as strawberry and apple are members of the same plant family (Rosaceae) and their flowers are of a similar shape, colour and form (Figure 3.2).

Field work

Alpine strawberries (*Fragaria vesca*) were planted in John Innes Potting Compost No. 3 in 30 litre plastic buckets and grown in an unheated glasshouse until established. Five



Alpine strawberry (*Fragaria vesca*)

Apple (Malus domestica)

Figure 3.2: Typical flowers of apple (*Malus domestica*) and alpine strawberry (*Fragaria vesca*).

plants were grown per bucket which, once established, filled the majority of the bucket (>90% of the visible area was covered when viewed from above). Every three days, any open buds or flowers were removed and, a day before placement, all open flowers were removed, leaving only unopened buds.

Five buckets were placed in each orchard, resulting in a total of 25 plants per site. In each orchard, buckets were positioned in a sheltered spot in full sun, 10m away from the hedge. It was not possible to integrate strawberries within the apple crop as this area was regularly exposed to herbicide spray and general disturbance. Buckets were placed in a single cluster, with 30cm between each bucket, to maximise the visibility for pollinators. Each cluster of buckets was protected from herbivory by mammals using wide-spaced wire mesh to a height of 1.2m. Within each geographical block of orchards, buckets were placed on the same date (B block = 3rd August, D block = 4th August, T block = 5th August).

After two weeks, buckets were returned to an unheated glasshouse where they were arranged in a randomised block design. Pollinators were excluded from the glasshouse. All open flowers were counted and any unopened buds removed. Buckets were watered once every 3 days, directly to the soil to prevent water splashes transferring pollen. Plants were checked every two days for ripe strawberries, which were collected and frozen.

Immediately after picking, strawberries were assigned a class based on their shape, where Class 1 was allocated to symmetrical strawberries, with less than 10% deformed surface area. Class 2 was allocated to all other strawberries. Strawberry classification was carried out blind to orchard treatment.

Lab-based measurements

Frozen strawberries were placed in 50ml glass vials then thawed for 1 hour. 10ml of distilled water was added to each vial, which was lidded and shaken vigorously for either 30 seconds or until the strawberry flesh had fully disintegrated. After the addition of a further 10ml of distilled water, the strawberry mixture was transferred to a 200ml glass beaker. 80ml of distilled water was used to rinse any remaining seeds into the glass beaker. All the floating (non-fertilised) and sinking (fertilised) seeds were counted. The proportion of sinking seeds was used as a measure of phytometer pollination (Klatt et al., 2013).

Statistics

Mixed effect logistic regression was used to analyse whether strawberry class varied between improved and unimproved sites. A basic model was constructed including strawberry class as the dependent variable, sampling block as a fixed effect and a random effect of plant ID nested within bucket ID nested within site. Linear mixed-effects modelling was used to analyse whether phytometer pollination varied between improved and unimproved sites. A basic model was constructed including the proportion of sinking seeds as the dependent variable, sampling block as a fixed effect and a random effect of plant ID nested within bucket ID nested within site. In both cases, the basic model was compared to a second model - in which the independent variable, floral improvement treatment, was added as a fixed effect - using chi-square tests on the log-likelihood values. All analyses were carried out in the R programming language and environment (Yan et al., 2011) using the package lme4 (Bates et al., 2014).

3.3 Results

3.3.1 Field results

A total of 110 plant species were observed, with a mean of 37 observed species per site. In any one sampling round, a mean of 39 plant species were seen, with a minimum mean of 14 plant species in the final sampling round (mid-Sep), and a maximum mean of 53 in sampling round 6 (late-May). More than three thousand plant-pollinator interactions were recorded (3,329), consisting of 804 unique interactions. There was a mean of 277 observed interactions per site and a mean of 102 unique interactions per site.

3.3.2 Phytometer pollination

Of the 2,162 strawberries collected, 110 were damaged and excluded from the analysis, leaving a total of 2,052 strawberries (range = 155 - 212 per site). Strawberries placed in improved orchards had significantly higher class (65.6% categorised as class 1) than those in unimproved orchards (39.2% categorised as class 1) ($\chi^2(1) = 13.6$, p < 0.001; Figure 3.3). The proportion of fertilised seeds was significantly higher in improved ($\mu =$ 64.0%) than unimproved sites ($\mu = 39.9\%$) ($\chi^2(1) = 14.9$, p < 0.001; Figure 3.4).

3.3.3 Nectar provision throughout the year

Excluding the sheep-damaged site, D.A, there was significantly greater daily nectar production from mid-June until the beginning of August in improved relative to unimproved orchards (F₁ = 12.3, p = 0.00987, Figure 3.5). This significant difference was maintained (Table 3.1) when proxy measures were used as estimates of nectar production for site D.A (i.e. estimates of nectar production had sheep not caused damage to the site). There was no significant difference in the number of plant species (F₁ = 0.619, p = 0.457) or families (F₁ = 0.308, p = 0.596) present on improved and unimproved sites during this period.

Table 3.1: The measures used as an estimate of the daily nectar production of the damaged site, D.A.

Measure used as estimate for site D.A	Nectar (ug)	Statistics
Mean of all undamaged improved sites	19,036	$F_1 = 13.3, p = 0.00653$
Minimum of sampling block D	13,283	$F_1 = 9.40, p = 0.0155$
Mean of all undamaged sites	12,233	$F_1 = 8.65, p = 0.0187$

For the duration of the phytometer placement, there was no significant difference in the daily nectar production between improved and unimproved sites ($F_1 = 0.048$, p = 0.832, Figure 3.5). This result was maintained (Table 3.2) when proxy measures were used for nectar production for site D.A. A post-hoc Tukey test showed a significant difference in nectar production between blocks, with block D producing significantly more nectar in this period than either block B (p < 0.001) or T (p < 0.001).



Figure 3.3: Strawberry class in improved and unimproved apple orchards. Class 1 was allocated to symmetrical strawberries, with less than 10% deformed surface area. Class 2 was allocated to all other strawberries.

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Table 3.2: The measures used as an estimate of the daily nectar production of the damaged site, D.A.

Measure used as estimate for site D.A	Nectar (ug)	Statistics
Mean of all undamaged improved sites	5,058	$F_1 = 0.0177, p = 0.898$
Mean of all undamaged sites	4,969	$F_1 = 0.0143, p = 0.908$
Mean of sampling block D	$10,\!436$	$F_1 = 2.46, p = 0.156$

All results were consistent across all possible nectar-value combinations for the estimated species *Vicia hirsuta* and *Torilis japonica*.

3.4 Discussion

By combining measures of floral resource provision and phytometer pollination, this chapter demonstrates that floral enhancement of apple orchards can support pollinator populations by extending the availability of floral resources beyond the crop-flowering period.

Specifically, floristically improved orchards provided more nectar between apple flowering and phytometer placement than unimproved orchards, whereas there was no difference in nectar availability during phytometer placement. This suggests that floral improvement increased phytometer pollination by allowing pollinators to persist later into the season, rather than aggregating pollinators from the surroundings (e.g. Kohler et al. (2008)).

This has implications for the abundance of pollinator populations as it suggests that improved orchards provide pollinators with a greater window in which to reproduce. Furthermore, it suggests that by offering less mobile species access to continuous localscale resources, improved orchards could support a more diverse, and hence more effective (Garibaldi et al., 2016), pollinator population. Improving apple orchards through the addition of flowers could therefore provide a way to promote the establishment and growth of pollinator populations that are not fully supported by the flowering window of the crop, with potential benefits to crop pollination.

In the following section, I outline limitations of the approaches used in this chapter. I then discuss key findings within the context of previous research on ecological restoration of agricultural habitats, with a focus on the mechanism by which orchard improvement increases pollination services, and the potential economic implications. In doing so, I highlight the value of using a range of field approaches and analytical tools to study ecosystems through a season.



Figure 3.5: Daily nectar production across each orchard for mid-June to the beginning of August (top) and during phytometer placement (bottom). Different colours represent different plant species. The sheep image highlights the sheep-damaged site, D.A.

3.4.1 Limitations

Many factors are hard to measure directly in ecology and so proxies are frequently used. In this chapter, I have used nectar supply as a measure of food supply and phytometer pollination as a measure of pollinator activity; however, neither is a perfect measure.

Pollinators require pollen in addition to nectar, as this provides a protein source for developing larvae. Previous studies have found that nectar and pollen production of a plant species do not always correlate (Hicks et al., 2016). Furthermore, nectar and pollen requirements of different pollinator species will vary through time, but this is poorly studied in most pollinator species. There is therefore a need to determine the complete resource needs of different pollinator species through a season and match this to those provided by flowers in improved and unimproved orchards. However, nectar provides the most relevant available measure of resource provision as it represents an ecologically meaningful currency that can be used to compare orchards.

Phytometer pollination is a useful measure of pollinator activity; however, it offers no way to discern between differences in the structure of the pollinator community. Apple and strawberry flowers have a similar structure, but this does not guarantee that the pollinator community which promotes strawberry pollination will be the same as that which promotes apple pollination. However, bee species are known to be effective pollinators of both crops (Klatt et al., 2013; Garratt et al., 2016). Accordingly, phytometer pollination will still provide a useful measure of relevant features of the pollinator community which can supplement more specific measures of the pollinator community, such as those offered by ecological networks.

Another limitation of this study is that it was conducted over a single year. Whilst I can conclude that floral improvement increased pollinator persistence in the study year, this may not be consistently true across multiple years. Furthermore, studying each orchard for a single year does not allow pollinator populations to be tracked between years to assess whether impacts on the pollinator population propagate from one year to the next. This question would be best addressed using molecular techniques to track family lineages of pollinators between years (e.g. Carvell et al. (2017)) when exposed to different levels of resource provision and volatility, which was outside the scope of this study. However, as molecular techniques become cheaper and more available, this approach should be prioritised.

3.4.2 Supporting pollinator persistence at a local scale

Adding non-crop floral resources can be an effective way to increase local-scale pollinator abundances (Carvell et al., 2004, 2007, 2015, 2017; Haaland and Gyllin, 2010; Kennedy et al., 2013; Morandin and Kremen, 2013; Cole et al., 2015; Feltham et al., 2015; Kremen and M'Gonigle, 2015; M'Gonigle et al., 2015) and, in some cases, pollination services to crops (Carvalheiro et al., 2012; Blaauw and Isaacs, 2014; Barbir et al., 2015; Feltham et al., 2015; Campbell et al., 2017; Dainese et al., 2017; Häussler et al., 2017; however, the results of such interventions are variable, with some studies finding no impact on wild pollinator communities (Williams et al., 2015; Wood et al., 2015; Campbell et al., 2017). This variability could be because additional floral resources are aggregating pollinators from the surrounding habitat (e.g. Kohler et al. (2008)), rather than promoting population-level increases (Scheper et al., 2013).

This chapter demonstrates that, by filling gaps in floral resource provision through the season, floral improvement of apple orchards can increase pollinator activity later in the season, even when resources later in the season are not enhanced. This strongly suggests that the improved orchard habitat is allowing pollinators to persist through the season, independent of resources in the surrounding landscape. This finding is in line with the findings of Chapter 1, which suggested that additional floral resources form chronosequences of desirable resources, supporting pollinators through the season.

Providing continuous floral resources is crucial for supporting diverse pollinator populations as less mobile pollinators, such as solitary bees, may only be able to use floral resources at a local scale (Albrecht et al., 2007; Williams et al., 2010; Winfree et al., 2011; Marini et al., 2012; Jönsson et al., 2015; Sardiñas and Kremen, 2015). By providing continuous floral resources, improved apple orchards are therefore more likely to result in population-level changes in these pollinator communities, resulting in a more diverse pollinator community.

3.4.3 Economic value of orchard improvement

By providing more continuous floral resources, improved apple orchards showed increased pollinator activity later in the season. This manifested itself as an increase in the pollination and quality of strawberries, a high value crop, later in the season. This demonstrates that functionally important pollinator communities were being supported by the intervention.

Floral enhancement has been shown to increase crop pollination in a wide range of crops (Carvalheiro et al., 2012; Blaauw and Isaacs, 2014; Barbir et al., 2015; Feltham

et al., 2015; Campbell et al., 2017; Dainese et al., 2017; Häussler et al., 2017), which it may do by increasing the abundance and diversity of pollinator communities (Carvell et al., 2004, 2007, 2015, 2017; Haaland and Gyllin, 2010; Kennedy et al., 2013; Morandin and Kremen, 2013; Cole et al., 2015; Feltham et al., 2015; Kremen and M'Gonigle, 2015; M'Gonigle et al., 2015). Whilst I have no direct measure of pollinator abundance, there is evidence that improved orchards had a greater propensity to increase the abundance of pollinator populations by lengthening the window of opportunity for many pollinator species to reproduce. This could increase the number of overwintering reproductive pollinators available to pollinate apple flowers in the following year (Carvell et al., 2017). Orchard improvement could also increase pollinator diversity by providing for a wider range of pollinating species, including those with narrower phenophase or lower mobility, which are often the pollinators most vulnerable to decline (Albrecht et al., 2007; Jönsson et al., 2015; Marini et al., 2012; Cresswell et al., 2000; Williams et al., 2010; Öckinger et al., 2010; Winfree et al., 2011). By doing this, floral improvement could increase the quality and robustness of pollination services, which have been linked to the diversity of pollinator populations (Garibaldi et al., 2016).

3.4.4 Future Directions

This study has focused on the structure and function of the flower-pollinator community through the season. However, there are several properties of orchard networks that could not be analysed within the small sample size of this study. In particular, the functional diversity of flowers through the season could impact heavily on the temporal structure of flower-pollinator networks. This is because pollinator species require that nectar is not only abundant but also provided in flowers that are accessible, and the accessibility of floral nectaries will vary between pollinator species.

Within my data, there is anecdotal evidence that this factor affects the persistence of pollinator species and the network structure through the season. I tentatively explore this idea in Figure 3.6 and Table 3.3. Figure 3.6 depicts the plant-pollinator networks through time for three orchards. Orchards B.St and T.S are the improved orchards with the highest and lowest phytometer pollination, respectively. Orchard T.W is a representative unimproved orchard for comparison. By comparing these orchards, I highlight the potential importance of functional diversity for supporting chronosequences of functionally similar pollinators. In particular, I suggest that a greater diversity of floral resources at each point through the season can allow a wider range of pollinator species to persist through the season (Table 3.3). It would be highly beneficial to conduct large-scale studies in which the nectar abundance and diversity of the plant community are varied independently through the season. Such studies could provide a better understanding of the relative importance of these aspects of the plant community in supporting pollinator populations.





Potential Strawberry Pollinators



Figure 3.6: Chronosequences of plant-pollinator interactions throughout the season. Each plant and pollinator species is denote the start or end of a chronosequence of plant-pollinator interactions. Plants are labelled with numbers, and a key represented by a coloured rectangle. Grey lines between these nodes represent links, the thickness of which is proportional provided for each diagram separately. The plant species that occur in the network between the end of apple flowering and to the number of interactions (a scale is provided on each diagram). Links going into or leaving month nodes (e.g. Apr) the placement of strawberry buckets are pictured in the top-right of each diagram.
)	4
	Improved orchard with highest phy- tometer pollination: B.ST	Improved orchard with lowest phytometer pollination: T.S	Representative example of unimproved orchard: T.W
	Fewer chronosequences are ending each	More chronosequences are end-	More chronosequences are ending each
	month than forming.	ing each month than forming,	month than forming, particularly in
		particularly in June and July,	June and July. There is an almost com-
		but some chronosequences per-	plete bottleneck into August.
		sist into August.	
	There are several flower species present	There is a small range of floral	There is a single flowering type attract-
_	in the network, across multiple families	species, but they do not cover	ing pollinators (hogweed, family Api-
	(including Rosaceae, Ranunculaceae,	the families Rosaceae, Aster-	aceae). This provides large quantities
	Fabaceae, and Apiaceae, members of	aceae and Apiaceae, which are	of nectar (Baude data) but may not be
	which are prevalent in the network in	prevalent in the network earlier	a preferred resource for all pollinators.
	April and May).	in the season.	
	Pollinators are feeding from phenolog-	Pollinators with a preference for	At the start of the season, plant species
	ically distinct flower species that, to-	particular plant families may	in the network are primarily from the
	gether, provide resources throughout	be unable to find floral re-	families Rosaceae, Ranunculaceae and
	the season. This is possible because dif-	sources throughout the entire	Fabaceae. The pollinator community
	ferent plant families are present at each	season. More generalist polli-	associated with these plants may be un-
	point in time, creating continuity for	nator species may be supported	supported immediately after apple flow-
	pollinators of a wide range of dietary	throughout the season, as there	ering, when no plants from these fam-
	specialisms. This results in a larger and	is a continuous supply of flo-	ilies are present. The network has to
	more diverse pool of potential phytome-	ral resources, but more specialist	build almost from scratch in August,
	ter pollinators.	species may not be. The pool of	with hogweed as a central resource.
		potential phytometer pollinators	The pool of potential phytometer polli-
		may be smaller and less diverse.	nators is small and not very diverse.

Table 3.3: A summary of key features of the networks shown in Figure 3.6 that are not otherwise considered in this chapter.

3.4.5 Conclusions

By combining novel network tools (Chapter 2) with other ecological measures, I have demonstrated that orchards with additional non-crop floral resources have the propensity to support more abundant, diverse and effective pollinator populations. This highlights the potential benefit of improving floral resources in apple orchards to promote both conservation and food-production objectives. Fundamental to this is the ability of improved orchards to support pollinator populations throughout the season. Future work considering restoration of pollinator populations in agricultural habitat should therefore endeavour to take a temporal perspective to identify periods of vulnerability for pollinators.

Chapter 4

Increasing the quantity, stability and diversity of nectar provided by floral management regimes in a mass-flowering crop

4.1 Introduction

Insect pollinators are responsible for increasing the yield and quality of over 75% of crops globally (Klein et al., 2007); accordingly, the pollination services provided by managed and wild pollinators have been valued at between EUR153 billion (Gallai et al., 2009) and US\$235-577 billion (Lautenbach et al., 2012) annually. There is increasing evidence that wild and managed pollinators work synergistically to deliver more effective and robust pollination services than managed pollinators alone (Winfree et al., 2007; Garibaldi et al., 2013; Mallinger and Gratton, 2015), making wild pollinators economically valuable targets for conservation.

Despite being targeted, the abundance and diversity of pollinator populations have sharply declined (Biesmeijer, 2006; Bommarco et al., 2012a; Cameron et al., 2011; Carvalheiro et al., 2013; Potts et al., 2016) such that yields of crops with a higher pollinator dependence are increasing at a lower rate and showing more variability than those of less pollinator dependent crops (Garibaldi et al., 2011). If pollination services were lost entirely, so would an estimated 5-8% of global crop production (Aizen et al., 2009), including a wide range of fruits, legumes, nuts and some commodity crops. Given that within Europe at least 9% of bees and butterflies are threatened, and up to 50% of bee species are threatened in the UK (Potts et al., 2016), insect pollinator declines are both of conservation and economic concern.

A key driver of pollinator decline is habitat loss (Aguilar et al., 2006; Potts et al., 2010a; Vanbergen and Garratt, 2013; Ferreira et al., 2015), which can reduce both habitat connectivity and the availability of nesting sites and floral resources for pollinators (Roulston and Goodell, 2011; Wallisdevries et al., 2012; Scheper et al., 2014; Goulson and Hughes, 2015; Baude et al., 2016). Floral resources in a habitat structure the pollinator community at both a local and landscape scale, with increased abundance and diversity of nectar leading to increased pollinator abundance and species richness (Potts et al., 2003) and promoting pollinator health (Alaux et al., 2010; Goulson and Hughes, 2015). However, the quantity and diversity of floral resources available to pollinators have seen sharp declines (Goulson and Hughes, 2015; Baude et al., 2015; Baude et al., 2016).

Adding floral resources to agricultural areas could bolster local pollinator populations and give agricultural habitat greater independence from the surrounding landscape. The addition of non-crop floral resources can increase the abundance and diversity of pollinator populations (Carvell et al., 2004, 2006, 2015, 2017; Haaland and Gyllin, 2010; Williams et al., 2012; Kennedy et al., 2013; Cole et al., 2015; Feltham et al., 2015) and pollination services (Carvalheiro et al., 2012; Blaauw and Isaacs, 2014; Barbir et al., 2015; Feltham et al., 2015; Campbell et al., 2017; Häussler et al., 2017). Similarly, floristically diverse hedgerows can provide preferred forage for pollinators (de Vere et al., 2017; Wood et al., 2017), increase pollinator abundance, diversity and colonisation (Morandin and Kremen, 2013; Kremen and M'Gonigle, 2015; M'Gonigle et al., 2015) and enhance pollination services (Dainese et al., 2017). Accordingly, in many countries farmers and growers are now offered financial incentives to increase the availability of floral resources for pollinators; however, the results of such interventions are variable (Williams et al., 2015; Wood et al., 2015; Campbell et al., 2017). If ecologically-motivated payments to farmers are to be effective, it is important that this this inconsistency is minimised.

One reason for this variability could be that additional floral resources simply aggregate the pollinators that are already present in an area (e.g. Kohler et al. (2008)), rather than promoting population-level increases (Scheper et al., 2013). Whilst pollinator aggregation can, in some cases, increase crop visitation (Pereira et al., 2015), it is unclear to what extent it influences the size and stability of the underlying pollinator populations (Williams et al., 2012). Moreover, while large pollinators such as bumblebees (*Bombus* spp.) are sufficiently mobile to use floral resources throughout a landscape, smaller and less mobile pollinators, such as solitary bees, may only be able to use floral resources at a more local scale (Cresswell et al., 2000; Albrecht et al., 2007; Williams et al., 2010; Winfree et al., 2011; Marini et al., 2012; Jönsson et al., 2015; Sardiñas and Kremen, 2015). This suggests that, in order to have a consistent, positive impact on a wide range of pollinating species, floral resources need to meet the local nutritional demands of less mobile species too.

For this to be achieved, there must be a continuous supply of locally-available floral resources throughout the season, which will ensure that pollinators can find food during their entire lifecycle, regardless of their phenology (Mayfield and Belavadi, 2008; Rundlöf et al., 2014; De Palma et al., 2015; Wood et al., 2017). However, floral management regimes currently vary in their ability to provide continuous forage for pollinators (Carvell et al., 2006; Havens and Vitt, 2016; Wood et al., 2017). This could be particularly important in landscapes dominated by mass-flowering crops (Blitzer et al., 2012; Kennedy et al., 2013; Scheper et al., 2013), which can only provide significant floral resources for short periods throughout the year (Riedinger et al., 2015). The presence of mass-flowering crops can increase the abundance of pollinators (Westphal et al., 2003; Diekötter et al., 2010; Jauker et al., 2012; Crone, 2013; Holzschuh et al., 2013; Grab et al., 2017), especially when those with different phenologies are combined in a landscape (Rao and Stephen, 2010; Riedinger et al., 2014). However, pollinators depend on wild flowers and weeds to add diversity to their diet and provide resources between the crop flowering periods (Kovács-Hostyánszki et al., 2013; Requier et al., 2015) without which they may be negatively affected by the presence of mass-flowering crops (Holzschuh et al., 2016). Adding floral resources to these areas through either hedgerow management or the addition of floral strips provides a means to harness the significant nectar and pollen resources provided by mass-flowering crops to promote sustainable pollinator population growth.

In this chapter, I assess the ability of floral areas managed under existing agrienvironment schemes to support the nutritional demands of pollinators in the massflowering crop apple (*Malus domestica*). Specifically, I consider the quantity and stability of nectar that different surveyed areas provide throughout the season and compare this to floral compositions that have been optimised *in silico*. I then consider how we might tailor floral compositions to support specific key pollinator groups in apple orchards. Finally, I consider how we might increase the quantity and stability of nectar provision without sacrificing the diversity of nectar available to pollinators.

Apple, an early-season mass-flowering crop, has a global value of USD\$51.7 billion annually (FAO, 2014) and, given that apple production would be reduced by an estimated 40-90% in the absence of pollinators (Klein et al., 2007), insect pollination of apples has

an estimated value of at least USD\$20.7 billion. Solitary bees are key pollinators of apple (Garratt et al., 2016), but the short, early-season flowering phenology of apple is insufficient to cover the entire flight period of most species (García and Miñarro, 2014); therefore these species are likely to be reliant on other, locally-available floral resources outside the crop flowering period. Apple orchards therefore provide a highly relevant system in which to study pollinator resource needs through the season.

To ensure that the nutritional demands of pollinators can be met by local-scale floral resources, ecologists and land managers need a robust approach for identifying suitable and complimentary flowering species that can support pollinator populations throughout the year. However, whilst there is a growing body of literature evaluating plants based on their desirability to specific pollinator groups (e.g. Fussell and Corbet (1992); Carvell et al. (2006); Connop et al. (2010); Wood et al. (2017), the quality of resources they provide (Somme et al., 2015) and their phenology relative to the crop (Russo et al., 2013; Robson, 2014), there is limited research on how flowering plants should be combined to best promote the quantity and continuity of floral resources in agricultural habitats.

In one of the very few studies that does this M'Gonigle et al. (2017) produced a tool that optimises plant mixes for pollinator visitation, richness, and phenology. Whilst this is a valuable start, their analysis considers floral phenology in a binary manner (presence or absence of any flowers) such that a mix scores highly if it provides continuous flowering for a greater number of pollinating species. Their tool is therefore unable to distinguish more subtle, yet important, nuances of floral provision such as the quantity of available floral resources throughout time, the extent of gaps in floral provision or the trade-off between increasing nectar quantity and stability.

By considering the nectar production of common British plants (Baude et al., 2016), I aim to evaluate floral mixes based on the amount and stability of nectar they provide throughout the season and, in doing so, identify opportunities for improving the quality of floral resource provisioning for pollinators.

A useful framework for incorporating rewards (i.e. nectar supply) and volatility (i.e. fluctuations in nectar supply) of different floral resources is the portfolio optimisation framework of economics. This approach is underpinned by the concept that an investor can reduce their exposure to risk whilst maintaining a given average return by selecting assets that vary differently through time. Similarly, by selecting flowering plants with different phenologies, we can reduce the volatility of the overall flowering portfolio for a given average nectar supply. Optimal flowering portfolios are those with the highest average nectar supply across the season for a given volatility (Figure 4.1).



Figure 4.1: An illustration of the reward-volatility profile for hypothetical floral portfolios. Each point on the graph represents a hypothetical floral portfolio, where each portfolio represents an area of planted flowers, which will produce a certain amount of nectar throughout the year. Right: The flowering phenology of two of the floral portfolios, where each line represents the nectar production through the season of a single flowering species. Left: The reward and volatility of these two portfolios (blue and yellow points) relative to other hypothetical portfolios (grey points). The blue portfolio is deemed optimal as there are no portfolios with a higher reward and lower volatility (blue box). The yellow portfolio is sub-optimal as there are several other portfolios with a higher reward and lower volatility (grey points within yellow box). In what follows, I use a portfolio optimisation framework to address 5 objectives: 1) Determine which flower combinations (including flowering hedgerows, weeds and wild-flowers) maximise nectar reward and stability through the season in an apple orchard; 2) Determine whether existing floral management options provide high nectar reward and stability through the season relative to floral portfolios optimised *in silico*; 3) Evaluate the potential of flowering hedgerows to increase nectar reward and stability in an apple orchards; 4) Determine which floral combinations (including flowering hedgerows, weeds and wildflowers) provide the highest and most stable nectar supply for eight key apple-pollinating bee species (genera: *Bombus* and *Andrena*); 5) Investigate the trade-off between providing a high quantity and stability of nectar whilst maintaining nectar diversity.

4.2 Methods

4.2.1 Collecting field data

To determine a suitable pool of flowering species from which to construct floral portfolios, and the pollinators they could support, I conducted floral abundance and flower-visitor surveys across twenty-one apple orchards.

Field sites

Orchards across the South West of England were visited for up to two seasons (mid-March to mid-September) between 2014 and 2016. These sites covered a wide range of floral management strategies including the addition of floristically diverse hedgerows and flowering strips, and unmown grassland and were representative of the typical breadth of modern, commercial apple orchards.

In 2014, a single, organic apple orchard was visited between mid-March and mid-September. In 2015, twenty orchards, across four geographical blocks, were visited between early-April and mid-September. Sixteen of these orchards were commercial apple orchards, whereas four were organic, ancient orchards. In 2016, twelve of the orchards visited in 2015, the details of which are given in Section 2.2.2, were re-visited between mid-March and early-September. For site locations, see Appendix A.

Floral abundance surveys

The number of open floral units were counted in randomly positioned quadrats (see Section 2.2.3 for details). The number and size of quadrats and the sampling frequency varied between years. In 2014, a single site was surveyed using twelve 0.5 x 0.5m quadrats, 3 times a week. In 2015, 20 sites were surveyed using ten 1 x 1m quadrats, once each fortnight. In both of these years, quadrats were placed randomly within each site, where a site was defined as the apple trees, grassland understorey and associated hedgerows. In 2016, 12 of these sites were further sampled using twenty-five 1 x 1m quadrats placed randomly in each of the ground and hedgerow flora.

Flower-visitor surveys

At each site, interactions were observed between flower-visiting insects and open flowers. In 2014, all interactions were observed 1m either side of randomly placed transects, with apple tree, hedgerow and grassland understorey areas sampled proportionally to their area. Three times per week, two 25m transects were completed in the grassland understorey, two 5m transects were completed in the adjacent hedgerows and ten 5m transects were completed in apple trees.

In 2015, two 50m transects were completed in each of the ground (grassland understorey and apple trees) and hedgerow areas, once per fortnight.

In 2016, interactions were observed along two 25 minute random walks, one covering the ground flora (grassland understorey and apple trees) and the other covering the hedgerow area (see Section 2.2.3 for details).

4.2.2 Constructing random floral portfolios

Selecting plants

I define a floral portfolio as mixes of flowering species, where the area of each species is defined in terms of $1m^2$ blocks. To represent apple flowers, each portfolio was populated with 25,000 blocks of apple (2.5 hectares). This area was the average size of all cropped areas in the study to the nearest half a hectare. From a total plant list of 124 surveyed species, 120 species occurred in at least 2 of the surveyed orchards and hence had the demonstrated potential to grow in apple orchards. Grass species do not produce nectar and so were not considered. Nectar production data was not available from Baude et al. (2016) for one of these plant species, hemlock water dropwort (*Oenanthe crocata*), so this species was excluded. Portfolios were constructed by randomly selecting 250 x $1m^2$ blocks of single flowering species to populate a total area of 250m. This area was chosen as it is the minimum area of improved land that meets the requirements of the Wild Pollinators and Farm Wildlife Mid-Tier Countryside Stewardship Package,

a frequently adopted agri-environment scheme option that has been evaluated for its ability to support pollinators (Dicks et al., 2015).

Measuring portfolio nectar reward

Portfolio nectar reward was calculated using estimated annual nectar production per area and flowering phenology for the UK's most common flowering plant species using the data available in Baude et al. (2016). This paper provides direct and modelled annual nectar production, per grown area, for many of the UK's most common flowering plant species. In line with Baude et al. (2016), the floral abundance of each plant in each *in silico* orchard was assumed to follow a triangular distribution, increasing at a linear rate from the flowering start date to the flowering peak date and decreasing at a linear rate from the peak date to the end date. The daily nectar production per unit area was then calculated from the annual nectar production for each plant as follows:

$$N_{dp} = \frac{AN_p \times FA_{dp}}{\sum_{n=1}^{d=1} FA_{dp}}$$

(4.1)

where AN_p = annual nectar production per unit area for plant p FA_{dp} = floral abundance at day d for plant p

For each portfolio, the total daily nectar production was calculated by summing daily nectar production for each $1m^2$ flowering block for each day. The mean of this daily nectar production from 1st March to 30th September was used as the measure of portfolio reward.

Two measures of portfolio nectar volatility were used: the standard deviation of daily nectar production (standard deviation model) and the number of days where total nectar production fell below 6.5% of the nectar produced by the 2.5ha apple crop at peak flowering (shortfall model) between 1st March and 30th September. The threshold value of 6.5% was chosen as it resulted in the most normal distribution in shortfall across 10,000 randomly generated portfolios (see Figure 4.2 and Appendix D for details) and hence was best able to distinguish between portfolios with different consistency of nectar supply.

For brevity, results presented here are for the shortfall measure of volatility as this is more representative of pollinator exposure to periods of risk; however, both metrics give qualitatively similar results.



Figure 4.2: Three potential threshold values demonstrated for two hypothetical floral portfolios. If the threshold is too high (pale blue) then the nectar production of portfolios will rarely exceed the threshold whereas if the threshold is too low (darkest blue) then the nectar production of portfolios will frequently exceed the threshold. More suitable threshold values (e.g. medium blue) will more readily distinguish between different nectar profiles because some portfolios will have nectar production that is mostly below the threshold (higher shortfall) whereas other will have nectar production that is mostly above the threshold (lower shortfall). The best threshold value will result in a roughly symmetrical (in this case, normal) distribution of higher shortfall and lower shortfall portfolios.

4.2.3 Objective 1: Determine which flower combinations maximise nectar reward and minimise nectar volatility through the season

Superior floral portfolios are those with the highest reward for a given volatility, meaning that near-optimal floral portfolios will be those with higher mean daily nectar provision and lower nectar volatility. The relative optimality of randomly generated portfolios was determined using an iterative algorithm that identified the portfolio with the highest reward before successively identifying the next most rewarding portfolios of lower volatility (Appendix E).

One-thousand random portfolios were generated using the 119 chosen plant species (i.e. 120 species minus hemlock water dropwort). Random portfolios were then split equally into ten optimality bands, henceforth referred to as portfolio ranks, where a rank of 1 is allocated to the 10% of portfolios that were most optimal. To identify any relationship between portfolio rank and plant composition, the area of each plant species in a portfolio was regressed against portfolio rank. Plants with a greater area in more optimal portfolios and a lower area in less optimal portfolios will have a negative correlation in this regression; therefore, plants with a significant negative correlation were those that occurred more frequently in highly ranked portfolios. This analysis was repeated 1,000 times to establish 95% confidence intervals for each plant species.

4.2.4 Objective 2: Determine whether existing floral management options provide high nectar reward and low nectar volatility through the season relative to floral portfolios optimised *in silico*

The nectar reward and volatility was calculated for areas of land managed under four existing agri-environment options: sown with nectar mix, sown with bird-seed mix, enhanced margins, and unmown grassland. Nectar production was calculated from data on the floral abundance of different plant species within thirty-nine managed patches (26 sown with a nectar mix, 4 sown with a bird seed mix, 5 areas of enhanced margins and 4 of unmown grassland) provided by Mathilde Baude from Baude et al. (2016). These data were from replicate sites in the UK and floral counts had been conducted at least twice during patch-flowering.

To estimate the start and end flowering date for each flowering species in each patch, I used phenology data from the online EcoFlora database, as compiled by Baude et al. (2016), as this data was not available from the field trials. A LOESS smoothing function was used to estimate floral abundance throughout the season for each constituent plant species which was then used to calculate nectar reward and volatility. To check that the estimated start and end dates did not have a large influence on the analysis, the analysis was repeated with these dates shifted by 20% of the total flowering duration (simulating an early shift, late shift and shortening of the flowering period).

With 119 potential flowering species, there are 119,250 possible portfolio configurations. As such, random portfolio generation could only capture a small portion of all possible floral portfolios, and is unlikely to capture the most extreme (i.e. very best and worst) portfolios. To identify floral portfolios with higher reward:volatility ratios than those constructed using random plant selection, I created an optimisation algorithm that iteratively removed plants from the available pool of species prior to portfolio construction. As the objective of this analysis was to identify more-optimal floral mixes that could be utilised as part of agri-environment schemes, I began the optimisation process with a reduced pool of 96 plant species, including only those species that were observed growing as part of the ground flora during orchard surveys; this removed hedgerowspecific plant species that would be unsuitable in a flowering strip. In each iteration, one-thousand portfolios were randomly generated and the plant species with the greatest over-representation in the lowest-ranked portfolios was removed. This process is nondeterministic and hence will not necessarily identify the same optimal portfolios across multiple runs, but is useful for investigating the potential for improving floral mixes.

4.2.5 Objective 3: Determine the extent to which areas of flowering hedgerow influence the nectar reward and volatility of floral portfolios

To evaluate the contribution of hedgerow and ground flora to portfolio reward and volatility, portfolios were constructed with varying areas of hedgerow flora. Each portfolio was constructed as before but the area of non-crop flowering plants was populated with fixed proportions of hedgerow and ground flora. Portfolios were constructed with 0% to 100% of the non-crop area as hedgerow, at 10% increments. In each case, the area of crop was not reduced; rather, the composition of the additional floral resources within the floral portfolio were reduced. For example, portfolios with 100% hedgerow area represent an orchard populated with apple trees and an area of flowering hedgerow, but lacking any flowering ground plants.

Hedgerow plants were defined as plants that were seen exclusively in hedgerows during field surveys and included hedgerow shrubs, such as willows (*Salix* spp.) and hawthorn (*Crataegus monogyna*), as well as climbing plants, such as bittersweet (*Solanum dulcamara*) and bramble (*Rubus fruticosus* agg.), but did not include plants that grow at the base of hedgerows such as deadnettle (*Lamium* spp.). This is because hedgerow specialist plants require a different management input (i.e. the planting of flowering hedgerows) whereas other species were seen to exist in flowering meadow areas and could possibly be introduced in the absence of hedgerows. This allowed me to evaluate whether proactive planting of hedgerows is a worthwhile element of agri-environmental management.

As there were fewer hedgerow plants than ground plants, the plant selection process was standardised such that the number of plant species chosen from the ground and hedgerow flora was proportional to that habitats' area in the portfolio and summed to a maximum of 25 plant species (the total number of hedgerow plants). For example, when 20% of the area of the portfolio was hedgerow, a maximum of 5 hedgerow species and 20 ground species could be used to form a portfolio.

4.2.6 Objective 4: Determine how floral portfolios differ when optimised to support different key pollinating bee species

Bombus terrestris, Bombus hortorum, Bombus pascuorum, Bombus lapidarius, Andrena nitida, Andrena cineraria, Andrena dorsata and Andrena haemorrhoa were chosen as focal pollinator species. These species were chosen as they are important pollinators of a range of crops (Dicks et al., 2015) including apple (Garratt et al., 2016) and all were found in my orchard surveys. Portfolios specific to each pollinating species were constructed using only flowers each species was observed foraging on in the 21 orchards. However, in reality pollinators will be able to use a wider range of plants than observed in these orchards, so forage plants listed for each pollinator species by Falk and Lewington (2015) were also included in their potential forage plants.

To investigate the optimal portfolio for each of the bee species, the nectar reward and volatility of each portfolio was evaluated separately for each of their flight seasons. The flight season of each pollinating species was found in Falk and Lewington (2015), as the alternative (using the first and last dates that a pollinator was seen in the surveyed orchards) would likely underestimate phenological breadth.

4.2.7 Objective 5: Determine whether a trade-off exists between maximising nectar quantity and nectar diversity and whether this can be reconciled by optimising portfolios using both criteria

Optimising floral portfolios could have the side effect of decreasing the diversity of nectar available, which could have adverse effects on pollinator populations (Scheper et al., 2014; Goulson and Hughes, 2015). To evaluate this, Shannon's Diversity Index of the amount of nectar contributed by each plant was calculated for each day using the *vegan* package (Oksanen et al., 2015) within R statistical software (Yan et al., 2011), the average of which was used as a third portfolio selection criteria. Portfolios were then optimised to maximise the product of nectar abundance and nectar diversity whilst minimising nectar volatility. These floral portfolios were then compared to those generated without considering nectar diversity.

4.3 Results

4.3.1 Field Results

Consistent with the work of Garratt et al. (2016), the most frequent wild pollinators of apple were *Bombus* spp. and *Andrena* spp., which formed 61% of the total visits to apple and 14% of all flower visits when considering all sites. *Andrena* spp. and *Bombus* spp. were observed visiting 22 and 43 different flowering species within all surveyed orchards, respectively. (For complete lists of observed flowers and the interaction partners of the focal *Bombus* spp. and *Andrena* spp., please see F).

4.3.2 Objective 1: Determine which flower combinations maximise nectar reward and minimise nectar volatility through the season

At the 95% confidence level, there was as significant negative correlation between the planted area in the portfolio and portfolio rank for 22 plant species (Zone A, Figure 4.3), indicating that the presence of these flowers will significantly increase the quality of nectar provision for pollinators (by increasing the abundance and/or stability of nectar provision). These species included hedgerow shrubs (e.g. willows (*Salix* spp.), hawthorn (*Crataegus monogyna*), *Buddleja davidii*), wild flowers (e.g. *Centaurea nigra, Leucanthemum vulgare, Lamium album, Trifolium* spp.), and agricultural weeds (e.g. *Cirsium* spp., *Senecio jacobaea*). Plant species in the most optimal portfolios had a significantly higher total nectar production ($\mu = 187.7 \text{ g/m}^2/\text{y}$) than those in random portfolios ($\mu = 41.3 \text{ g/m}^2/\text{y}$)(t_{95.3} = 14.4, p < 0.001) but no significant difference in flowering duration (t_{31.5} = -1.87, p = 0.0715) or the distance between their flowering peak and that of the apple crop (t_{24.7} = 0.331, p = 0.744) relative to plant species in random portfolios.

Ten plant species were, on average, more likely to occur in more optimal floral portfolios, but not consistently so (*Taraxacum officinale* agg., *Salvia pratensis*, *Myosotis arvensis*, *Hedera helix*, *Succisa pratensis*, *Leontodon autumnalis*, *Chamaerion angustifolium*, *Prunella vulgaris*, *Vicia sativa*, *Acer campestre*), suggesting that these species are not sufficient to ensure high or stable nectar supply but do make positive contributions relative to other plant species (Zone B, Figure 4.3).

The remaining eighty-seven species were more likely to occur in less-optimal portfolios, on average, indicating that they do not contribute to the quantity and stability of nectar provision as well as other plant species (Zone C, Figure 4.3). This included several species that were frequently observed in surveyed agri-environmental patches (*Epilobium montanum, Galium verum, Lotus corniculatus, Medicago lupulina, Ranun*culus acris, Ranunculus repens, Silene dioica, Sonchus arvensis) suggesting that these plants make poor contributions to nectar provision.187.7

4.3.3 Objective 2: Determine whether existing floral management options provide high nectar reward and low nectar volatility through the season relative to floral portfolios optimised *in silico*

Thirty of the 39 surveyed patches (nectar seed mix, enhanced margins, unmown grassland and wild-bird seed mix) were less optimal (had lower mean daily nectar production and higher volatility) than random floral portfolios, whereas only 3 were more optimal



portfolio, for all plant species. A negative coefficient indicates plant species that occur frequently in optimal portfolios and occurred more frequently in more-optimal portfolios at least 95% of the time, those in Zone B occurred more frequently in hence should be included in planting regimes. Error bars indicate 95% confidence intervals such that plants in Zone A more-optimal portfolios 1-94% of the time and those in Zone C occurred more frequently in less-optimal portfolios.

(Figure 4.4). These three patches were all sown with nectar seed mix and were the only mixes in which 20% of the flowers recorded were from at least 4 of the following: *Centaurea nigra, Senecio jacobaea, Trifolium pratense, Cirsium arvense* and *Leucanthemum vulgare*. All patches of enhanced margins, unmown grassland or wild-bird seed mix had lower mean daily nectar production and higher nectar volatility than all random *in silico* portfolios.

When creating optimised floral portfolios in silico, there was a significant, positive linear relationship between mean nectar production and optimisation step ($R^2 = 0.953$, $F_{2,10997} = 1.13e+05$, p < 0.001) and a significant negative linear relationship between shortfall and optimisation step ($R^2 = -0.872$, $F_{2, 10997} = 1.02e+05$, p < 0.001), indicating that floral portfolios can be improved to increase both the amount and stability of nectar provided to pollinators. However, even optimised portfolios were not able to provide the threshold level of nectar (6.5% of that produced by the apple crop at peak flowering) for 19% of days.

Patches managed under existing agri-environment schemes were all less optimal than optimised mixes with an equivalent number of flowering species. Nectar seed mix provided the highest quantity and stability of nectar; however, optimised floral portfolios provided 57% more nectar across the season whilst exposing pollinators to only 46% of the volatility when compared to the best nectar seed mix.

4.3.4 Objective 3: Determine the extent to which areas of flowering hedgerow influence the nectar reward and volatility of floral portfolios

Hedgerow-only portfolios had significantly greater mean nectar production ($t_{1884} = 16.8$, p < 0.001, Figure 4.5) than ground-only portfolios without significant differences in mean seasonal nectar volatility ($t_{1975} = 0.588$, p = 0.557, Figure 4.5), even when controlling for the number of species permitted in each portfolio type. However, the least volatile ground-only portfolios exposed pollinators to 40% of the nectar volatility compared to the least volatile hedge-only portfolios, suggesting that some ground flora mixes can offer a more stable nectar supply than areas of hedgerow. Including hedgerow plants in random portfolios to create mixed hedge/ground portfolios significantly increased mean nectar production ($t_{1820} = 15.8$, p < 0.001, Figure 4.5) without significantly altering seasonal nectar volatility ($t_{1946} = 0.346$, p = 0.729, Figure 4.5) relative to ground-only random portfolios.



Figure 4.4: The nectar reward and volatility for areas under different floral management regimes versus random and optimised floral portfolios. Hedgerow plants were not included in this simulation of agri-environment mixes.



Figure 4.5: The nectar reward and volatility for ground-only, hedge-only and mixed floral portfolios of an equivalent area.

4.3.5 Objective 4: Determine how floral portfolios differ when optimised to support different key pollinating bee species

Willows (Salix spp., common knapweed (Centaurea nigra), thistles (Cirsium spp.) and white dead-nettle (Lamium album) were consistently found in optimised portfolios for all 119 of the focal pollinator species. Of the plants commonly found in surveyed agrienvironment scheme patches, only ox-eye daisy (Leucanthemum vulgare), clovers (Trifolium spp.), ragwort (Senecio jacobaea) and yarrow (Achillea millefolium) consistently ranked within the top 20 plants for all of the pollinator species. Apart from clovers (Trifolium spp., common vetch (Vicia sativa) was the only Fabaceae flower to rank within the top twenty plants, and only for a single species (Bombus terrestris). Whilst floral portfolios optimised for bumblebee species contained many flowers from the families Lamiaceae and Dipsacaceae, those optimised for solitary bees typically contained higher numbers of hedgerow shrubs from the Rosaceae family, as well as members of the Apiaceae family (Figures 4.6 and 4.7).

4.3.6 Objective 5: Determine whether a trade-off exists between maximising nectar quantity and nectar diversity and whether this can be reconciled by optimising portfolios using both criteria

There was a significant, negative quadratic relationship between seasonal nectar diversity and optimisation step ($R^2 = 0.590$, $F_{2,10997} = 7919$, p < 0.001; Figure 4.8), showing that nectar provision in optimised portfolios was dependent on a smaller subset of plants than random portfolios. However, portfolios containing the twenty most optimal plants are only slightly less nectar diverse than random portfolios ($\mu = 1.78$ compared to $\mu = 1.86$) but have considerably higher mean daily nectar production (= 236 gm-2 compared to = 92 gm-2), indicating an opportunity for increasing nectar provision without significantly impacting nectar diversity. An average of nine flowering plant species grew in the 39 surveyed agri-environment patches but an average of 34 plant species were recorded in each of the surveyed apple orchards (range: 20 to 52), including hedgerow and ground flora, suggesting that even low diversity sites are able to meet this recommendation.

When portfolios were optimised to maximise the product of mean nectar production and diversity whilst minimising nectar volatility, portfolios had significantly higher mean nectar diversity ($t_{1902.1} = 109.15$, p < 0.001) but significantly lower mean nectar production ($t_{1996.4} = -156.73$, p < 0.001) and significantly higher volatility ($t_{1954.9} =$ 100.96, p < 0.001) than when nectar diversity was not considered in the optimisation. However, these differences had low absolute magnitude (3.80% higher nectar diversity,









7.16% lower mean nectar production, 0.856% higher volatility). This indicates a small trade-off between promoting high, stable nectar supply and ensuring a diversity of plants at any given time point.



Figure 4.8: The abundance, volatility and diversity of nectar provided from randomly generated portfolios (dark blue) through to fully-optimised portfolios (dark red), shown from two different angles. A sharp decline in nectar diversity can be seen in the final optimisation stage, where the maximum number of species in the portfolio is reduced from 20 to 10.

4.4 Discussion

Mass-flowering crops can provide large quantities of nectar but do not flower for long enough to support the lifecycle of most pollinating species. Adding floral resources to agricultural habitat can be an effective way of filling these gaps to support pollinating insects. In this study, I successfully developed a new computational framework, based on the portfolio optimisation framework of economics, to evaluate the quantity and stability of nectar provided by different floral portfolios throughout the season. I found considerable variation in the quantity and stability of nectar offered by different floral portfolios, which may influence how effectively different floral portfolios can sustain pollinator populations. This could explain why adding floral resources to agricultural habitat is not always an effective way to increase pollinator populations (Williams et al., 2015; Wood et al., 2015; Campbell et al., 2017) and highlights the potential to design floral mixes that better support key pollinators in apple orchards.

Of four existing agri-environment strategies (nectar seed mix, bird seed mix, enhanced margins, unmown grassland), areas sown with nectar seed mix provided the highest quantity and stability of nectar; however, floral portfolios optimised *in silico* provided an estimated 50% more nectar across the season whilst exposing pollinators to half the nectar volatility when compared to the best nectar seed mix. Hedgerow species such as willow (*Salix* spp.) were found disproportionately often in the most nectar-rich and nectar-stable floral portfolios, far outperforming common hedgerow species such as blackthorn (*Prunus spinosa*), whilst agricultural weeds such as dandelion (*Taraxacum agg.*), ragwort (*Senecio jacobaea*) and thistles (*Cirsium* spp.) outperformed most popular constituents of existing floral mixes.

Optimising the quantity and stability of nectar provided by floral portfolios reduced the diversity of nectar providers, decreasing the redundancy of nectar provision whilst also limiting pollinator diet breadth; however, by including a minimum of 20 plant species in a floral portfolio, large gains in nectar quantity and stability can be achieved without significantly compromising the diversity of nectar available throughout the season.

Overall, these results highlight the value of quantifying the amount and stability of nectar offered by different floral management options, rather than merely identifying flowering gaps, when planning restoration efforts. In this section I first consider the limitations of my approach, before outlining key results and practical recommendations for land managers. I finish by discussing potential future avenues for developing a better understanding of pollinator restoration in agricultural habitats.

4.4.1 Limitations

A key limitation of my approach is that it remains untested in the field; in reality, the quantity and phenology of flowers produced by a particular management regime, and the amount of nectar each flower produces, may not be accurately reflected by model estimates.

Establishing a particular ratio of flowers, with a particular flowering phenology, demands a greater understanding of how floral abundance and phenology relate to the composition and management of the floral community. As well as uncertainty over floral abundance and phenology estimates, we cannot be sure that the realised nectar production of a given floral community will reflect modelled estimates. For example, growth conditions, such as soil type, water availability or light conditions (Petanidou et al., 1999), and regional genetic variation (Leiss and Klinkhamer, 2005) can influence the rate of nectar production of individual flowers. In addition, nectar production may depend heavily on how frequently a flower is visited by the pollinator population, such that popular flower species might be depleted more rapidly than others.

These limitations do not invalidate my approach, however, as there is an order of magnitude difference in nectar production between flowering plant species, suggesting that relative nectar availability of each floral portfolio is unlikely to change significantly even with changes in absolute nectar availability.

4.4.2 Key Findings

There are four key findings, which are discussed in turn below.

1) Floral communities should be evaluated based on the stability of nectar they provide

Floral communities vary greatly in their ability to provide pollinators with nectar; however, to my knowledge, this is the first study to consider two key elements of nectar provision - quantity and stability - simultaneously. Evaluating these components of nectar provision showed that floral compositions vary greatly in their ability to provide nectar consistently throughout the season. This is particularly pertinent when considering mass-flowering crops, which can have narrow flowering windows, leaving pollinators vulnerable to food shortages before and after crop flowering (Tscharntke et al., 2005; Blitzer et al., 2012; Kennedy et al., 2013; Scheper et al., 2013).

Bombus spp. and *Andrena* spp. are key pollinators of apple, but queens of most of these species will be active for several weeks before apple flowers (Falk and Lewington,

2015). During this period, queens will be highly active, prospecting for nest sites and/or provisioning offspring (Falk and Lewington, 2015) and so having locally-available nectar prior to apple flowering may promote the establishment of these pollinator populations. Similarly, in temperate climates, bumblebees are active for the majority of the year and so require floral resources well beyond the flowering period of apple. In particular, bumblebee colonies need plentiful resources in late summer when the rate of larval rearing is at its highest (Dicks et al., 2015).

However, the phenology of nectar availability should also be considered alongside the total quantity of nectar provided by a floral community. Notably, the threshold I used to evaluate nectar volatility of floral portfolios was a mere 6.5% that of the total nectar produced by apple at peak flowering; despite this, even optimised floral mixes did not produce this much nectar on 20% of days (Figure 4.4). This demonstrates that small areas of locally-restored floral resources may never be able to stabilise nectar production to the level of the crop throughout the season. Instead, managing existing floral populations, such as agricultural weeds and flowering hedgerows, or systematically combining mass flowering crops with different phenologies might better maximise the amount of nectar provided throughout the season by providing larger areas of floral cover.

2) Existing floral mixes can be improved

Existing floral management options mostly provided low or inconstant nectar supplies, as has been highlighted in other studies (Carvell et al., 2006; Havens and Vitt, 2016; Wood et al., 2017); however, a small number of nectar seed mixes were more optimal than random portfolios. In general, nectar seed mixes provided a greater supply and consistency of nectar than wild bird seed mix, unmown grass or enhanced margins; however, optimised floral portfolios far surpassed the nectar provision of these mixes whilst also providing a more stable nectar supply.

Several plants were frequently found in the most optimal portfolios; these included those that offer high nectar reward (e.g. thistles (*Cirsium* spp.), common knapweed (*Centaurea nigra*)) and/or fill key phenological gaps (e.g. willow (*Salix* spp.), ivy (*Hedera helix*)). Thistles are frequently recognised as important floral resources for bees and butterflies (Andrada et al., 2004; Carvell et al., 2006; Wallisdevries et al., 2012) as they produce large quantities of nectar.

Willows are already documented as an important early-season nectar source for pollinators, especially queen bumblebees (Rowe et al., 2011; de Vere et al., 2017), whereas ivy has been identified as an important late-season nectar source that may increase the viability of overwintering pollinator populations (Garbuzov and Ratnieks, 2014). Willows also produce large quantities of high quality pollen which provides an important source of early-season protein for a range of pollinator species (Moerman et al., 2015).

Interestingly, in line with existing research showing the importance of weeds for pollinators (Hicks et al., 2016), many of the most valuable plants in our analysis were considered agricultural weeds (e.g. dandelion (*Taraxacum agg.*), ragwort (*Senecio jacobaea*), thistles); discouraging the removal of these plants could therefore be an effective way to support pollinators.

Hedgerows have also frequently been identified as valuable habitat for pollinators providing both food, nesting sites and navigation across the landscape (Cranmer et al., 2011; Morandin et al., 2011; Kovács-Hostyánszki et al., 2013; Kremen and M'Gonigle, 2015; Morandin et al., 2016; de Vere et al., 2017). In our study, flowering hedgerow significantly increased portfolio mean daily nectar production. This is unsurprising given that hedgerows typically contain a high proportion of perennial climbing plants and shrubs which are able to produce higher quantities of nectar (Hicks et al., 2016). Adding hedgerow plants to floral portfolios did not significantly lower the nectar volatility; this is probably because, apart from willow and ivy, many of the most prolific nectar providers in hedgerows appear in spring when the apple crop is already providing a large quantity of nectar (e.g. blackthorn (*Prunus spinosa*)). This highlights the importance of selecting hedgerow plants based not only on their floral display but also their floral phenology.

Combining areas of flowering hedgerow with areas of sown with standard nectar seed mixes increased the quantity and stability of nectar provision of the overall management option, suggesting that whilst nectar-rich flowering strips are a good way of increasing nectar provision, they could work more effectively when combined with hedgerow management practises that promote flowering species.

3) Floral mixes can be tailored to pollinators

By optimising portfolios we were able to identify planting regimes that outperformed random portfolios for all pollinator species. Several plant species (common knapweed (*Centaurea nigra*), thistles (*Cirsium* spp.), willows (*Salix* spp.), white deadnettle (*Lamium album*)) consistently formed part of the most optimal portfolios across all pollinator groups, suggesting that these species should always form part of planting regimes in apple orchards but the exact composition of floral portfolios varied between pollinators.

A lot of attention has been given to leguminous plant mixes (Fabacea), which are

deemed attractive to bumblebees (Carvell et al., 2006; Orford et al., 2016) and provide floral resources throughout summer. Our analysis showed that, with the exception of clovers (*Trifolium* spp.), these species were not found frequently in optimal floral portfolios, with common knapweed (*Centaurea nigra*), thistles (*Cirsium* spp.), willows (*Salix* spp.) and white deadnettle (*Lamium album*) all ranking above the most-highly ranking member of the Fabaceae family for all bumblebee species analysed. This is in line with national surveys of floral use by bumblebees (Fussell and Corbet, 1992) in which the genera *Lamium, Buddleija, Cirsium, Symphytium, Centaurea*, and *Stachys* were frequently visited.

Nevertheless, Fabacea flowers may be more energetically favourable forage for longertongued pollinators such as bumblebees because their nectaries can only be accessed by a small subset of pollinating species and so might be depleted less frequently. This is not reflected in my analysis and so I may have underestimated the value of less accessible plant species, including members of the Fabaceae. However, there are alternative flowering species that are not only frequently found in optimal portfolios but also offer some exclusivity to longer-tongued pollinators, such as members of the Lamiaceae family. These species could provide good alternative to Fabaceae flowers such as bird's foot trefoil (*Lotus corniculatus*), and vetch (*Vicia* spp.) for supporting larger pollinating insects. In addition, current evidence suggests that members of the Lamiaceae provide higher quantities of amino acids per flowers than members of the Fabaceae and are particularly good providers of the amino acids phenylalanine and lysine (Petanidou et al., 2006).

Early-season pollinators, including Andrena nitida, A. cineraria and A. haemorrhoa, are less exposed to nectar volatility in apple orchards as a large portion of their lifecycle occurs within the flowering period of the apple crop. However, the lower mobility of these species may make them more dependent on local scale resources (Cresswell et al., 2000; Biesmeijer, 2006; Albrecht et al., 2007; Jönsson et al., 2015). Floral portfolios optimised for these species included a greater proportion of spring flowering hedgerow plants such as *Prunus* spp., as well as a range of *Apiaceae*. This is in line with previous research showing the preference of bees for arable weeds and hedgerow flowers over sown flowers (Wood et al., 2015; de Vere et al., 2017) and highlights the importance of often overlooked resources in agricultural habitats.

4) Including at least twenty flowering species maintains nectar diversity

Maximising nectar production whilst minimising nectar volatility reduces the nectar diversity of floral portfolios. This has three implications: firstly, there will be less redundancy such that nectar provision will be more vulnerable to environmental disruption. Having redundancy is particularly important when floral resources are being provided by a wide taxonomic range of flowering species, the phenologies of which could respond differently to environmental stressors. Secondly, pollinators will be provided with a less varied diet, which may compromise their health (Alaux et al., 2010; Goulson and Hughes, 2015). Thirdly, lower nectar diversity is likely to support less pollinator functional diversity (Williams et al., 2015), which may reduce the quality of pollination services (Hoehn et al., 2008; Klein, 2009; Winfree and Kremen, 2009). We found that floral portfolios consisting of twenty of the most optimal flowering species offered the best trade-off between maximising the stability and abundance of nectar whilst maintaining nectar diversity. Given that even low-diversity orchard sites contained at least 20 plants species, this should be a practical target. However, it may be more readily achieved by encouraging farmers to reduce removal of weeds (e.g. thistles, ragwort), or allowing low-lying plants (e.g. dandelion, clover) to grow in the grass strips between rows of apple trees.

4.4.3 Future directions

Other pollinator groups

I chose to focus on wild bees as they are key pollinators of a wide range of crops (Klein et al., 2007; Roulston and Goodell, 2011) including apple (Garratt et al., 2016) and are centrally-placed foragers, making them vulnerable to local-scale nectar shortages. This does not detract from the conservation or service-provision value of other pollinating insect species such as flies and butterflies; however, we have a much poorer understanding of the feeding requirements of these groups and their propensity to use resources across a landscape (Dicks et al., 2015). From a conservationist's perspective, it is important that we establish the feeding requirements and habits of non-Hymenopteran pollinating insects so that floral portfolios can be designed to promote a wider range of pollinating species.

Other resource needs for pollinators

Nectar provides energy to fuel metabolic processes but most pollinators also require pollen as a source of protein (Müller et al., 2006; Dicks et al., 2015). In a previous study of food provision by floral mixes, Hicks et al. (2016) found that relatively few species were both good nectar and pollen providers. In the same study, common knapweed and ox-eye daisy produced an order of magnitude more pollen per floral unit per day than white clover or oregano, yet all of these species featured heavily in floral portfolios optimised for nectar provision. A lack of available data on pollen production prevented consideration of this important floral reward; however, it is a factor that could and should be incorporated into this type of analysis as more data on the quantity and quality of pollen becomes available.

For pollinator species to establish in an agricultural habitat, they must not only be provided with adequate nutrition, but also adequate nesting resources. For example, Grundel et al. (2010) found that bee species richness was related to both plant richness and abundance of potential nesting resources. Nesting requirements vary between pollinator species (Falk and Lewington, 2015) such that, in order to support a diverse pollinator community, agricultural habitats must provide a range of appropriate nesting habitats. For example, Potts et al. (2005) found that whilst the availability of bare ground and potential nesting cavities were the two primary factors influencing the structure of the bee community, several other nesting resources (steep and sloping ground, plant species providing pithy stems, and pre-existing burrows) also had an influence. These studies highlight the importance of combining the provision of diverse floral and nesting resources to support pollinators in agricultural habitats.

Other ecosystem services

Adding floral resources has the potential to influence other ecosystem service providers. For example, plants provide nectar to parasitoid wasps which may promote natural pest control. Conversely, plants can provide refuge and food sources for pests which may increase the ecosystem disservice of herbivory. With the emergence of the novel, highly-damaging pest *Drosophila suzukii* (Walsh et al., 2011; Calabria et al., 2012), this is particularly important where apples are grown alongside stone fruit crops; *D. suzukii* is a highly generalist pest that oviposits in a range of berry-producing plants, including honeysuckle (*Lonicera* spp.), *Prunus* spp. and ivy (*Hedera helix*). Given the recent and potentially continued loss of a range of valuable plant protection products for managing pests (The Andersons Centre, 2014), future work should focus on the trade-off between ecosystem services and disservices.

4.5 Conclusions

Adding floral resources to agricultural habitats has the potential to be mutually beneficial for pollinators and land managers but it is important that the needs of pollinators are met throughout the season. We have shown that flowering mixes can be optimised to support the nutritional demands of pollinators in specific crops by increasing the quantity, stability and diversity of nectar throughout the season. Plant species that are prolific nectar producers and/or fill key phenological gaps should be core plants when restoring food for pollinators in apple orchards but additional plants should be used to promote specific pollinator groups, attract a wider range of pollinator guilds and/or to maximise the redundancy of the system, as well as providing other resources such as pollen and nesting sites. However, these decisions cannot be made without considering entire portfolios of flowers, rather than individual plant species. Doing so is crucial if we want to provide pollinators with nectar throughout the season, a pre-requisite for stable, population-level change.

Chapter 5

Discussion

Restoring healthy pollinator communities to agricultural habitats could benefit both wildlife and food production. Increasing the availability of floral resources through targeted management can be an effective way to restore pollinator communities (Albrecht et al., 2012; Blaauw and Isaacs, 2014; Carvalheiro et al., 2012; Carvell et al., 2007; Williams et al., 2012); however, such interventions currently provide inconsistent results (Williams et al., 2015; Wood et al., 2015, 2017). This could be because we rarely consider how floral resources are partitioned through the season. I argue that habitats are more able to support pollinator communities if they provide continuous resources at a local scale, but such continuity is often lacking in landscapes dominated by mass-flowering crops (Benedek, 1997; Bernardino and Gaglianone, 2008; Menz et al., 2011).

The objective of this thesis was to develop new tools to identify and address periods of vulnerability through the season for pollinators, with a view to informing restoration efforts in agricultural habitats. In this chapter, I draw together my key findings to highlight the exposure of pollinators to food instability in the mass-flowering crop, apple, before evaluating existing restoration efforts in this crop. I finish by outlining key limitations of my research and worthwhile future avenues in the field of restoration ecology.

5.1 Vulnerability of pollinators

Pollinators require resources throughout their entire lifecycle (Falk and Lewington, 2015), but this is rarely considered in restoration ecology. To redress this imbalance, I explored the provision and utilisation of floral resources through the season in an early-flowering crop, apple, and revealed that pollinators can experience a volatile food supply in this system. The availability of nectar following crop-flowering varied significantly between orchards (Chapter 3) which was reflected in the extent to which pollinators interacted with flowers through the season (Chapter 2). This was such that focal pollinators were feeding from flowers for almost twice as long through the season, on average, in strawberry farms, where the crop flowers continuously through the season, than in apple orchards. These results highlight an opportunity to support pollinators in apple orchards by improving floral resource availability.

5.2 Restoration of pollinators

There is a large body of evidence demonstrating that floral restoration can be an effective way to support pollinator communities (Albrecht et al., 2007; Carvell et al., 2007) and increase crop pollination (Carvalheiro et al., 2012; Blaauw and Isaacs, 2014; Feltham et al., 2015; Pywell et al., 2015; Orford et al., 2016; Häussler et al., 2017). I found consistent evidence that the addition of floral resources can support pollinators in apple orchards. Key apple pollinators were feeding from flowers for almost 20% more of their potential phenophase, on average, in apple orchards with improved floral resources than those without (Chapter 2). Furthermore, by analysing the structure of the flower-pollinator network through the season, I found that pollinators were more likely to fulfil a functionally important network role in improved apple orchards (Chapter 3). By combining field and modelling techniques, I was also able to demonstrate that increased pollinator persistence in improved apple orchards was likely due to local-scale increases in pollinator persistence, rather than pollinators aggregating from the surrounding habitat (Chapter 3). These data suggest that improving floral resources in apple orchards could support local and landscape scale conservation objectives, whilst increasing the persistence of crop pollinators in agricultural habitats.

5.3 Refining restoration efforts

Both field and modelling results suggested that floral improvements can vary significantly in the extent to which they provide an abundant and stable food supply for pollinators. Pollinator persistence was three times as high in the best versus worst floristically improved apple orchards (Chapter 2) and nectar provision after crop-flowering varied by an order of magnitude between improved orchards (Chapter 3). These data suggest pollinators could still be left vulnerable to food shortage even following efforts to increase food provision. In an attempt to address this variability, I developed a new tool to evaluate floral enhancements based on their ability to provide continuous, diverse and abundant floral resources (Chapter 4). Using this, I demonstrated that habitat patches managed in line with existing agri-environment options were poor nectar-providers, both in terms of nectar quantity and stability. Floral portfolios optimised *in silico* provided 57% more nectar across the season whilst exposing pollinators to only 46% of the volatility when compared to the best agri-environmental habitat patches. In line with existing research, agricultural weeds (Bretagnolle and Gaba, 2015; Carvalheiro et al., 2011; Requier et al., 2015; Pocock et al., 2012; Morandin et al., 2011) were identified as valuable resources for pollinators. This is heartening, as encouraging the growth of weeds may be more feasible and cost-effective for growers than sowing areas of wild flowers; however, there is a need to raise the perceived value of pollinators in the farming community to overcome the negative perceptions of weediness.

5.4 Limitations

There are three key limitations of this thesis: the focus on a single crop, the lack of model testing, and the lack of direct measures of crop value. Many of my conclusions could be given more breadth, certainty and value were these limitations addressed.

5.4.1 Breadth: considering a wider range of mass-flowering crops

In this thesis, I have focused on a single species of early-flowering crop: apple. This was due to the time-intensive nature of the field work conducted. However, there is reason to believe that different mass-flowering crops affect pollinator populations in different ways (Kallioniemi et al., 2017). Therefore, we need to study a wider range of crop types to determine the best way to support pollinators in different contexts.

Crop flowering phenology, for example, could strongly affect the appropriateness of different floral management options for supporting pollinators. Pollinators in areas of early flowering crops could benefit from floral mixes currently promoted under agri-environment schemes, which typically provide high quantities of floral resources in summer. However, these mixes can be poor at providing resources in spring (Havens and Vitt, 2016; Carvell et al., 2007) such that pollinators in areas of late flowering crop might receive greater benefit from the addition of shrubs or perennial species, such as *Salix sp.* or *Prunus sp.*, which flower earlier in the year. There is a need to evaluate the vulnerability of pollinators across a much wider range of crop phenologies and to consider how pollinators are best supported in each scenario.

In addition to this, the practical and economic feasibility of different management strategies will vary between crop types. For example, fruit trees are grown within areas of permanent grassland understorey which can be florally diverse throughout the season (García and Miñarro, 2014). Conversely, in annual crops these areas are unavailable, so hedgerow improvement and set-aside land may provide more practical alternatives. Establishing feasible and effective management strategies for different crop types should be prioritised but requires collaboration between researchers and land managers so that sufficiently broad crop types can be evaluated.

5.4.2 Validation: testing model conclusions

Modelling is an extremely valuable tool in ecology as it gives access to questions that are too time-consuming or expensive to address using field approaches. However, modelbased conclusions gain further value when they can be validated in field trials.

In Chapter 4, I highlighted floral combinations that offer the highest quantity and stability of nectar resources for pollinators. These mixes could provide effective alternatives to existing agri-environment seed mixes. However, there is a need to trial different floral-mixes over multiple years to evaluate whether 'optimised' floral mixes do indeed offer higher nectar quantity and stability and whether this results in increased pollinator abundance and diversity. There is also the need to develop effective management strategies to establish and maintain chosen floral communities, which is not trivial given the different growth habits and lifecycles of plants.

In Chapter 2, I developed a novel approach to increase the temporal resolution of ecological networks. This could be a valuable tool when considering pollinator restoration in habitats with inconsistent floral resource provision (e.g. mass-flowering crops). However, there is a need to evaluate the accuracy of reconstructed networks. This could be achieved by rarefying highly-resolved networks to reduce their temporal resolution, before applying the reconstructed networks to be compared to observed networks to check for similarities in structure and composition.

5.4.3 Relevant currency: assessing the economic benefits of restoration

The broad economic value of pollinators is now widely recognised (Klein et al., 2007; Lautenbach et al., 2012), but there are few studies considering the financial costs and benefits of specific management options for pollinators. In this project, I speculate
that floral enhancement could increase apple pollination by increasing the abundance of overwintering apple pollinators. However, to evaluate whether floral enhancement is an effective and economical way to increase crop pollination, it would be necessary to determine changes in crop value following floral enhancement and the cost of different floral enhancement options. For example, Blaauw and Isaacs (2015) studied floral enhancements in highbush blueberry fields and showed that the resultant increase in pollination services would counteract the cost of the intervention within 3-5 years. Such studies are inherently challenging and expensive as they demand broad data sets and skill sets, which are best achieved in larger, interdisciplinary teams. However, they can provide a relevant currency with which to engage policymakers and land managers and can allow agri-environment initiatives to direct money in a more cost-efficient manner.

5.5 Future directions

"The search for truth is in one way hard and in another way easy, for it is evident that no one can master it fully or miss it wholly. But each adds a little to our knowledge of nature, and from all the facts assembled there arises a certain grandeur."

– Aristotle

The work in this thesis contributes to the rapidly developing fields of restoration and network ecology. In this section, I highlight what I believe are key areas of missing knowledge in these fields. I then go on to discuss the importance of developing breadth in ecological research and the tools that can be used to do this. I finish by discussing the importance of engaging relevant stakeholders in what is, ultimately, a highly applied field of science.

5.5.1 Knowledge: relating network properties to ecosystem function

There is a general understanding that network properties can relate to network functioning (Olesen et al., 2007; Bascompte, 2010; Thebault and Fontaine, 2010). However, if this concept is to be a useful tool in restoration ecology, it is crucial that we gain a better understanding of this relationship, as well as how network structure can be manipulated effectively.

In particular, it would be beneficial to know how different network structures, including the temporal role distribution of species (Chapter 2), affect network growth and stability through the season, and how this influences the provision and stability of pollination services. For example, I have speculated that *party hub* plant species increase the propensity of a network to grow throughout the season, which could promote biodiversity. However, it is impossible to say for certain which features of a network are desirable without first studying the relationship between different elements of network structure and function either *in silico* or across a larger number of orchards.

Following on from this, it would be beneficial to understand how specific network properties can be achieved in practise. Understanding the determinants of species network roles could facilitate this. However, it is currently unclear whether network role is more dependent on species' traits, species' abundance or on the ecological context in which a species is placed. This information could inform the identity and quantity of plant species that should be encouraged in an area to encourage a particular distribution of plant roles. Crucially, this could allow ecologists to develop simple, generalisable guidance to help growers manipulate their plant communities effectively.

5.5.2 Breadth: combining network types

Ecologists have traditionally compartmentalised complex processes into more manageable parts. However, there is growing evidence that we cannot fully understand ecological processes that are broken up in this way; that is, the study compartments are never truly independent. Accordingly, ecological networks are increasingly being combined to include multiple interaction types (Pocock et al., 2012).

This is particularly appropriate in agricultural habitats as manipulating floral communities is likely to influence a wide range of insect species and this will affect the provision of both ecosystem services and disservices (Zhang et al., 2007). A frequent concern of growers is that floral resources may harbour pests (personal communication). However, by using knowledge of plant-pollinator and plant-herbivore interactions, it may be possible to develop bespoke management regimes that provide continuous floral resources for pollinators whilst minimising the opportunity for plant-pest interactions. A greater understanding of the temporal structure of plant-herbivore and plant-pollinator networks could offer insight into management schedules that modify resource availability for pollinators, pests and pest-controllers through the season, for example by selective mowing. Given the potential importance of the pest-pollinator trade-off, I collected plantpollinator, plant-insect herbivore and insect herbivore-parasitoid networks in 20 apple orchards across the South West of England. Whilst I invested considerable effort in this process, I was unable to use the plant-herbivore and herbivore-parasitoid networks due to challenges with rearing herbivores in an unfamiliar laboratory environment and a lack of time for taxonomic identification of parasitoid species. Ultimately, the task proved infeasible for only a single person to complete. Despite this, I believe there is huge potential in the study of multi-guild ecological networks, which may give insight into the dynamics and robustness of a system (Pocock et al., 2012; Thebault and Fontaine, 2010), whilst also providing a relevant tool for asking practical questions.

5.5.3 Tools: adopting molecular techniques

Collecting ecological networks is an intensive process which is inherently expensive. Molecular techniques, which are becoming cheaper, more accurate and more widely available, could revolutionise the study of ecological networks by providing a faster and more reliable way to identify interactions. This could offer the opportunity for researchers to establish increasingly complex multi-guild networks and/or integrate population ecology into network studies.

In the past decade, molecular techniques have been increasingly applied in studies of predator-prey interactions, where prey DNA detected within the gut of predators can be used to infer interactions (Sheppard and Harwood, 2005), and seed-dispersal networks, where micro-satellite markers can be used to identify the source of seeds carried by different seed-dispersers (Jordano et al., 2007). More recently, molecular techniques have been used to genetically identify species of pollen collected by honey bees (de Vere et al., 2017).

Such studies can teach us how pollinators are using the landscape, as they are not limited to interactions observed within a specific boundary. Furthermore, analysing the pollen carried by individual pollinators could provide a useful tool for monitoring the movement and foraging behaviour of different species, which may have implications for crop pollination, pollinator conservation, and gene transfer within the plant community. Finally, molecular tools may capture a larger proportion of a species' interactions than field sampling, especially where the species is rare or interacts with rare species, and so could provide a valuable tool in the field of conservation ecology, where rarer species are often of greatest interest.

Molecular techniques can also be used to measure the impact of restoration efforts on

the size and dynamics of pollinator populations. For example, Goulson et al. (2010) used molecular markers to track the survival of bumblebee colonies through a season. Using a similar approach, Herrmann et al. (2007) demonstrated that increased abundance of bumblebees in areas of mass-flowering crop was due to an increase in colony size, rather than an increase in the number of nests. More recently, Carvell et al. (2017) used microsatellite markers to track over 1,600 families of bumblebees across a farmed landscape, and found that colonies produced more daughter queens that survived to the following year when they were located within 250-1,000 metres of habitats with high-quality floral resources. It would be exciting to use this approach in an orchard system to track the survival of pollinator species within a manipulative study in which floral resources were removed at specific points in the season. This could help to identify key period of vulnerability for pollinators.

5.5.4 Tools: citizen science and the technological era

Citizen science is the involvement of volunteers in the collection and/or analysis of data (Pocock et al., 2015; Silvertown, 2009). Aided by modern developments in communication technology, citizen science "offers a means of doing substantial, thoughtful public outreach and of tackling otherwise intractable, laborious or costly research problems" (Gura, 2013). More specifically, it can allow for cost-efficient data collection at large spatio-temporal scales, whilst also giving the public and/or growers insight into key conservation issues and the scientific method (Dickinson et al., 2010; Hochachka et al., 2012; Miller-Rushing et al., 2012).

Citizen science can be a valuable approach for monitoring species or ecosystems (e.g. the UKs Breeding Bird Survey, Harris et al. (2016)) but can also be used to quantify ecosystem service provision. For example, Birkin and Goulson (2015) monitored pollination services in gardens and allotments by asking participants to grow *Vicia faba* plants and manipulate the pollination environment. In addition, there have been recent efforts to use citizen science approaches to construct ecological networks at large spatial scales (Deguines et al., 2012, 2016; Smith and Roy, 2008; Silvertown et al., 2015). For example, Deguines et al. (2016) used a nation-wide dataset to demonstrate that urbanisation results in functional homogenisation of flower-visitor communities.

Citizen science is not without limitations; there is a need to develop resources, skills and experience within academic organisations so projects can be delivered effectively. Furthermore, statistical techniques need to be developed to address some of the inherent bias within citizen science data. However, if these limitations can be addressed, citizen science could have huge potential to expand the scale of ecological network studies whilst engaging stakeholders in key environmental and ecological issues.

5.5.5 Sharing: knowledge exchange

A key but frequently overlooked element of applied ecological research is sharing findings with relevant practitioners. Given that pollinators are supported by floral resources in gardens, allotments, parks and nature reserves (Baldock et al., 2015) as well as both arable and pastoral farms (Klein et al., 2007; Andersson et al., 2012; Holzschuh et al., 2013), practitioners of restoration ecology include not only growers of pollinator dependent crops but also pastoral farmers, councils, conservation groups and the general public. Knowledge exchange needs to be at the forefront of restoration ecology, and science more generally. There are many ways this can be encouraged by funding bodies and research establishments including offering training at an undergraduate and postgraduate level, forming partnerships with relevant organisations and non-academic institutions and providing funding to put theory into practise. The benefits can be mutual to both parties in the knowledge exchange process: applied research will remain relevant to the needs of practitioners and practitioners will have the best information with which to put theory into action.

5.6 Final remarks

No individual study can master the complexity of natural systems completely. In this thesis, I have contributed new tools and new insight into how apple orchard ecosystems change through a season, which I believe is a valuable contribution to our understanding of ecological restoration in agricultural habitats. However, this is only a small part of an exciting whole. In a stimulating era of interdisciplinary work between ecologists, molecular biologist, mathematicians and practitioners, now is the time to begin assembling our knowledge to expose the true grandeur of ecological systems.

Appendices

Appendix A

Orchard Field Site Details

Site	Latitude	Longitude
B.Ra	51.964188	-2.4239016
B.Mo	51.959944	-2.4268413
B.Ba	51.955369	-2.4223566
B.St	51.956413	-2.4303603
D.A	51.804138	-2.2306752
D.M	51.810692	-2.2263622
D.T	51.810559	-2.2349238
D.K	51.816383	-2.2212982
T.N	51.344320	-2.8385282
T.E	51.337014	-2.8240013
T.S	51.340500	-2.8323054
T.W	51.335044	-2.8392792

Table A.1: Site locations for each site, surveyed in 2016, for blocks B, D and T.

Appendix B

Network reconstruction approach

mpling due to dependency on the weather. in at least one window.		ē	lates. Identify the earliest and latest date that each plant species was identified, across all sites. This represents the <i>faasible</i> phenophase of each species in the network. Ithis	e the Remove any unfeasible interactions (i.e. those occurring interactions (i.e. those occurring in a time slice where the plant is not flowering)
Divide the entire season for each site into slices of a chosen length. Identify the central date in each time slice, which will be the date i prediction dates. This is necessary to ensure evenly spaced (and hence comparable) time slices, which cannot be ensured during sar Networks were predicted at fortnightly intervals as this resolution was sufficient to capture all flowering species	•	Data: Floral abundance survey dat	Calculate the vegetation similarity between prediction dates and sampling c Use foess smoothing (smoothing coefficient = 0.75) of floral abundance per spec date to estimate floral abundance for each day through the season. $FA_{da} =$ vector containing abundance of flower i at day d. $FA_{da} =$ vector containing abundances of all flower i at day d. Calculate the difference between overall floral composition for prediction date sampling dates, VD_{psi} as one minus the Kulczynski similarity index for all pairwi comparisons (implemented using the vegdist function, Vegan Package, R) one, then multiply TD_{ps} by VD_{ps} to create and overall weighting matrix W. Entries ir	e estimated similarity between a site across given days. alculated by averaging the observed network, N _o , from each <i>sampling date j</i> , wher edicting a given N _s is given by the corresponding similarity estimate, W _{jj} .
	•	Data: List of <i>prediction dates</i> and <i>sampling dates</i>	Calculate the time difference between prediction dates and sampling dates. $TD_{ps} = e^{-\frac{ dp-ds }{k}}$ Where dp is the prediction date and ds is the sampling date. Higher values of k increase the weighting of more distant time slices. Results here are presented for $k = 5$ but all results are robust to changes in k ($k = 2.5$, $k = 7.5$). Scale matrices such that each matrix has a sum of	matrix represent th The predicted network, N _s for <i>prediction date i</i> is c weighting given to each No when pr

Figure B.1: Explicit outline of network prediction method.

Appendix C

Role-role connectivity profiles





Appendix D

Threshold selection as portfolio optimisation volatility criteria

A threshold value of 0.065 times the maximum daily nectar production of apple as this resulted in the most normal distribution of the shortfall nectar volatility measure.



Figure D.1: The distribution of the 'shortfall' nectar volatility measure, given different threshold values, where, for each individual graph, the x-axis represents 'shortfall' and the y-axis represents mean daily nectar production.

Appendix E

Optimality bands for portfolio optimisations



Figure E.1: Optimality bands shown for 10,000 random portfolios, where dark red denotes the most optimal portfolios. The shortfall (top) and standard deviation (bottom) models of volatility are shown.

Appendix F

Interactions of focal pollinator species

Andrena cineraria

Heracleum sphondylium Malus domestica, Oenanthe crocata, Ranunculus repens, Salix cinerea, Symphoricarpos albus, Taraxacum agg.

Andrena dorsata

Malus domestica, Rubus fruticosus agg., Taraxacum agg.

Andrena haemorrhoa

Heracleum sphondylium, Malus domestica, Ranunculus ficaria, Rubus fruticosus agg., Pyrus communis, Salix alba, Salix cinerea, Taraxacum agg., Trifolium pratense

Andrena nitida

Heracleum sphondylium, Malus domestica, Oenanthe crocata, Prunella vulgaris, Prunus spinosa, Ranunculus ficaria, Ranunculus repens, Rubus fruticosus agg., Taraxacum agg.

Bombus hortorum

Calystegia sepium, Cirsium vulgare, Galeopsis tetrahit agg., Glechoma hederacea, Lamium album, Leucanthemum vulgare, Malus domestica, Ranunculus repens, Rosa canina agg., Rubus fruticosus agg., Taraxacum agg., Trifolium pratense

Bombus lapidarius

Cirsium arvense, Cirsium vulgare, Glechoma hederacea, Lamium album, Malus domestica, Ranunculus repens, Rubus fruticosus agg., Salix cinerea, Symphoricarpos albus, Taraxacum agg., Trifolium pratense, Trifolium repens

Bombus pascuorum

Calystegia sepium, Centaurea nigra, Cirsium arvense, Cirsium palustre, Cirsium vulgaris, Epilobium hirsutum, Geranium robertianum, Glechoma hederacea, Lamium album, Lamium purpureum, Lotus corniculatus, Malus domestica, Oenanthe crocata, Ranunculus repens, Rubus fruticosus agg., Taraxacum agg., Trifolium pratense, Trifolium repens, Vicia hirsuta, Vicia sativa, Vicia sepium

Bombus terrestris

Angelica sylvestris, Calystegia sepium, Cirsium arvense, Cirsium vulgare, Convolvulus arvensis, Digitalis purpurea, Galeopsis tetrahit agg., Glechoma hederacea, Heracleum sphondylium, Lamium album, Lamium purpureum, Malus domestica, Ranunculus repens, Rubus fruticosus agg., Salix cinerea, Taraxacum agg., Trifolium repens

Appendix G Link to R Code

All code used in the production of this thesis can be found at: https://github.com/seardin/sam.ardin.supporting.code

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