Characterizing the pollinator communities & pollination sustainability of four economically important crops in Great Britain.

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Declaration of original authorship

I confirm that this is my own work and the use of all material from other sources has been properly and fully acknowledged.

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Abstract

Bees provide a critical ecosystem service for agricultural production by contributing to the pollination of the majority of leading global crops. A growing body of research indicates that species rich pollinator communities benefit the yields and stability of insect-pollinated crops. Additionally, species rich communities may promote more resilient crop pollination services, which is particularly imperative due to increasing rates of anthropogenic induced environmental changes. However, this ecosystem service is being compromised due to declines in bee species, driven by a loss of floral and nesting resources due to agricultural land expansion and intensification. Whilst agri-environment schemes have been implemented across Europe to halt biodiversity losses, recent evidence suggests that they predominantly benefit common bumblebee species, and are of limited value to solitary species, which also provide important crop pollination services. Currently there is limited information on which species provide crop pollination services to guide management and monitoring, and preserve pollination services. Identifying crop pollinating bee species, monitoring their populations in agricultural landscapes and understanding how crop pollinator communities vary across time and space have recently been identified as key research objectives for national and international policy and monitoring programmes.

Focusing on Great Britain, which has comprehensive data on its bee fauna, and considering four of its most economically important crops – apples, field bean, oilseed rape and strawberries – this thesis aimed to address key knowledge gaps in our understanding of bee crop pollinator communities. The first objective of this thesis was to produce national lists of bee pollinators for each of the four focal crops. Building upon this information the second objective was to evaluate the capacity of different survey methods to sample bee species in each of these crops. The final objective was to investigate how pollinator community composition, and pollinator species richness, may affect the stability of crop pollinator occurrence.

The results of chapter 2 indicate that whilst a small suite of common species may make a disproportionate contribution to flower visitation to our focal crops, at least a quarter of bee species in Great Britain, including some rare and specialist ones, could act as potential pollinators of these crops. These findings indicate that current agri-environment schemes, which have been predominantly developed around the needs of bumblebees, may not be as effective at supporting pollination service in crops such as apples and oilseed, which are also visted by a diverse range of solitary bees.

Chapter 3 revealed that different survey methods sample distinct components of crop pollinator communities, and that the efficacy of different survey methods to sample bee crop pollinators may be contingent upon the guild and crop being targeted. Transect walks were superior at measuring both abundance and richness of bumblebees in all crops, and may be sufficient to sample bee pollinators in crops such as field bean, which are almost exclusively visited by bumblebees. Pan traps, notably yellow ones, detected the greatest abundance and species richness of solitary bees in apple, oilseed and strawberry crop sites, and may be an essential complementary sampling technique in crops for which solitary bees are key pollinators. These findings can be used to inform national pollinator monitoring schemes which aim to sample crop pollinators in agricultural areas.

Finally, the results of chapter 4 indicate that bee crop pollinator communities composed of a small number of closely related species, such as field bean, are likely to exhibit more synchronized inter-annual occupancy dynamics, and show a greater variance in mean occupancy, compared to crop pollinator communities comprised of a more diverse set of bee species, such as oilseed. Additional analyses also indicate that more species rich pollinator communities may result in greater stability of crop pollinator occurrence over time, which could have positive benefits for the resilience of crop pollination services under future environmental changes.

The outcomes of this thesis show that agri-environment schemes need to be adapted to cater for the resource requirements of a wider diversity of bee species than at present, and strategies to achieve this are discussed within the context of the wider literature. The implications of differences in the capacity of different survey methods to sample and monitor crop pollinating bee species are also discussed. Additionally, a consideration of how management in agricultural landscapes can promote stable bee populations in and around cropped areas is also provided. Together these recommendations provide an overview of how species-rich and stable bee crop pollinator populations could be protected and promoted in agricultural landscapes in order to safeguard production of insect pollinated crops.

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1. Introduction

1.1 Pollination services

1.1.1 Ecosystem services

The natural world underpins both the existence and quality of human life through the provision of goods and services that sustain human well-being (Daily 1997; IPBES 2019). The benefits that people obtain from natural ecosystems have been termed ‘Ecosystem Services’ (MEA 2005; Figure 1.1), and the components of ecosystems which provide goods and services (e.g., air, soil, water and living organisms), referred to as ‘Natural Capital’ (Guerry et al. 2015; Science for Environment Policy 2020). There is now growing recognition of the critical role of natural capital for sustaining economic and social wellbeing (Bateman & Mace 2020). However, complexities in assigning economic valuations to natural resources, and misconceptions of an inherent conflict between environmental conservation and economic development, have meant that ecosystem services have not been routinely integrated into land management and policy decision-making (Costanza et al. 1997; De Groot et al. 2010; Guerry et al. 2015). This failure to incorporate ecosystem services, and the stocks of natural capital that provide them, into public and private decision-making, and their subsequent unsustainable exploitation, has resulted in significant biodiversity losses (Rands et al. 2010). The first formal assessment of the status of ecosystem services, conducted for the ‘Millennium Ecosystem Assessment’ report, found that an estimated 60% were being degraded or used unsustainably (MEA 2005). More recently the IPBES ‘Global Assessment Report on Biodiversity and Ecosystem Services’ warned that despite significant increased understanding of the importance of biodiversity and ecosystems to human quality of life:

"biodiversity is still being lost, ecosystems are still being degraded and many of nature's contributions to people are being compromised" (IPBES 2019).

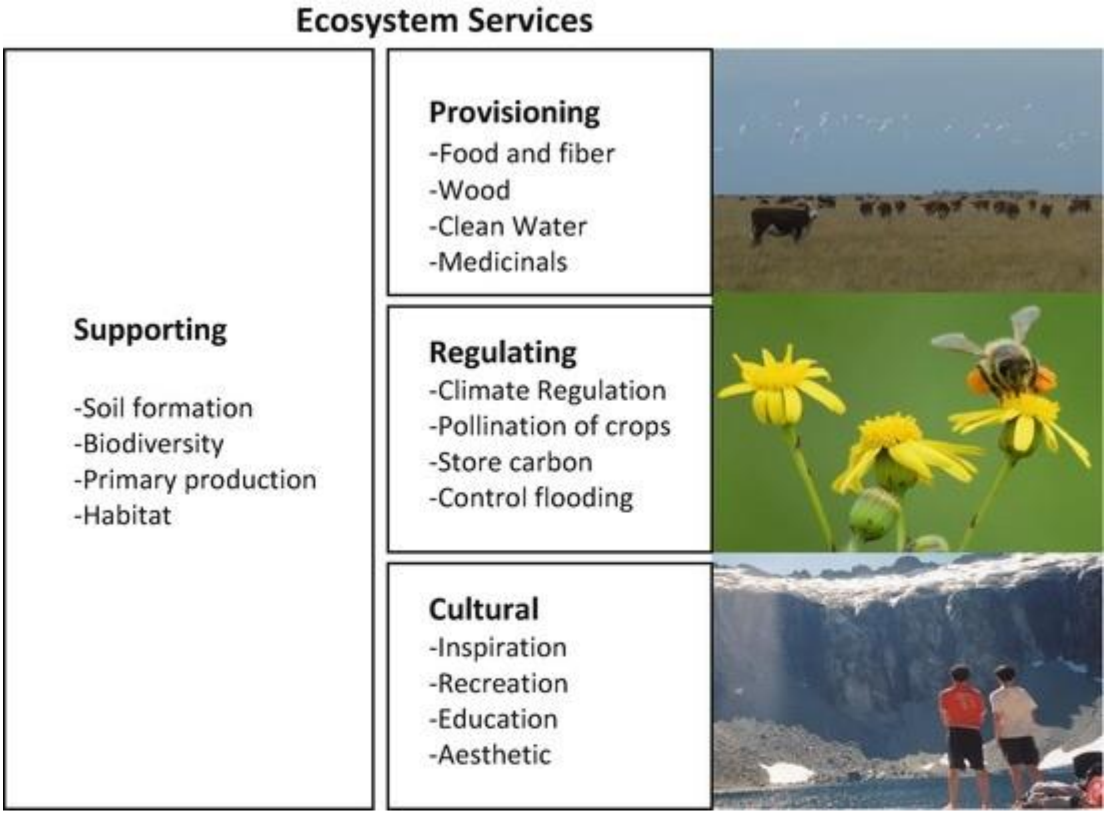


Figure 1.1: Four categories of ecosystem services as classified by the Millennium Ecosystem Assessment (Sala et al. 2005).

1.1.2 Crop pollination

Animal pollinators, including birds, mammals and insects, provide a key ecosystem service for human well-being by contributing to the pollination of agricultural crops (Ollerton, Winfree & Tarrant 2011; Dicks et al. 2021). Animal pollinators facilitate plant reproduction, and contribute to increased fruit and seed set of cultivated plants, by transferring male gametes (contained within pollen) from the stamen (male part) of one flower to the pistil (female part) of another flower (Ollerton 2017; Figure 1.2). Fruit, vegetable and seed production from the majority of leading global food crops are dependent to some degree upon biotic pollination, with over a third of global production accounted for by crops that benefit from animal-mediated pollination (Klein et al. 2007). Additionally, many crops grown for farmed animal feed and biofuel production rely in part upon biotic pollination (Science for Environment Policy 2020). Animal pollinated crops are disproportionately more important from an economic and nutritional perspective than pollinator-independent staple crops (Vanbergen et al. 2014; Ollerton 2017). Pollinator-dependent crops are of considerably higher value per-hectare than pollinator-independent crops (Gallai et al. 2009). Furthermore, whilst non-animal pollinated staple crops constitute the bulk of human food production, animal pollinated crops provide the majority of micronutrients that are essential to human health (Eilers et al. 2011; Vanbergen et al. 2014). Rises in average wealth have led to increased demand for fruit, vegetables and oils (Godfray & Garnett 2014), and considerable growth in global crop production has been driven by a disproportionate expansion in land cultivated for pollinator-dependent crops compared to pollinator-independent ones (Aizen et al. 2019). As such, animal pollinators play an important role in agricultural production and food security (Science for Environment Policy 2020). This ecosystem service is being increasingly degraded, however, due to declines in pollinator diversity (IPBES 2016; IPBES 2019).

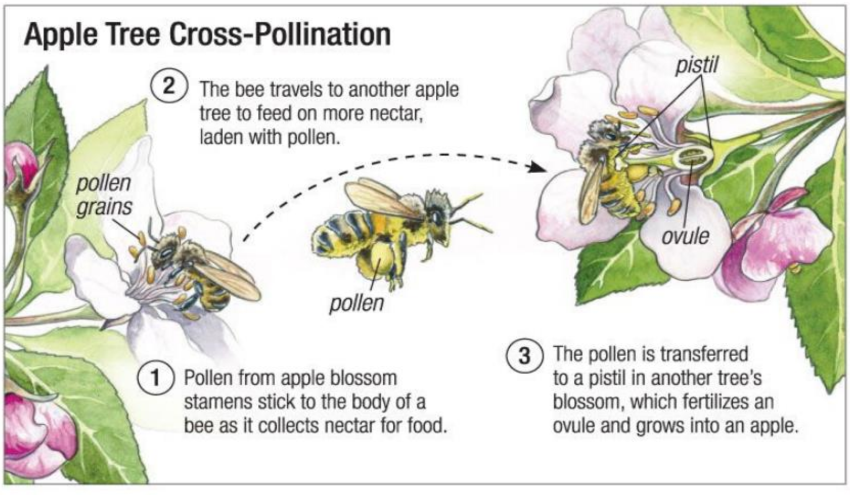


Figure 1.2: Process by which insect pollinators facilitate the pollination of apple trees (Philadelphia Orchard Project 2019).

1.2 Insect pollinators

1.2.1 Bee pollinators

Insects, including ants, beetles, flies, moths and wasps, represent the most significant group of crop pollinators (Rader et al. 2016). Bees, in particular, are an important pollinating taxon (Potts et al. 2010; Ollerton 2017), encompassing 20,000 species worldwide (Figure 1.3); many of which are prolific pollinators of a wide diversity of crop plants (Wilson-Rich et al. 2014). Domesticated honeybees have long been attributed as the most important crop pollinators (Morse 1991; Carreck & Williams 1998). However, a continual decoupling of honeybee stocks and pollinator-dependent crop trends (Aizen & Harder 2009; Breeze et al. 2014a; Aizen, Garibaldi & Harder 2022) bolsters growing consensus that their role has likely been overestimated (Westerkamp & Gottsberger 2000; Ollerton 2017), and that wild bees' make a more significant contribution to crop pollination than previously thought (Potts et al. 2010; Breeze et al. 2011). Growing evidence suggests that whilst honeybees can supplement wild insect pollination, they cannot substitute for it (Garibaldi et al. 2011a; Garibaldi et al. 2013). Honeybees are extensively used for crop pollination due to their large colony sizes and relatively low rental costs (Isaacs et al. 2017), but distinctive aspects of their behaviour and ecology mean that they are often poor pollinators of many crops (Westerkamp & Gottsberger 2000). Conversely, wild insects, including a variety of bee species, have been evidenced as efficient pollinators of a wide variety of different crop types (Figure 1.3), including many orchard, soft fruit and leguminous crops, as well as those which are buzz-pollinated (Westerkamp & Gottsberger 2000; Garibaldi et al. 2013; Khalifa et al. 2021). The integration of farm practices that support wild pollinator populations, alongside the management of domesticated species – known as Integrated Crop Pollination – therefore presents the best solution to maximise crop pollination service delivery (Isaacs et al. 2017; Garratt et al. 2018).

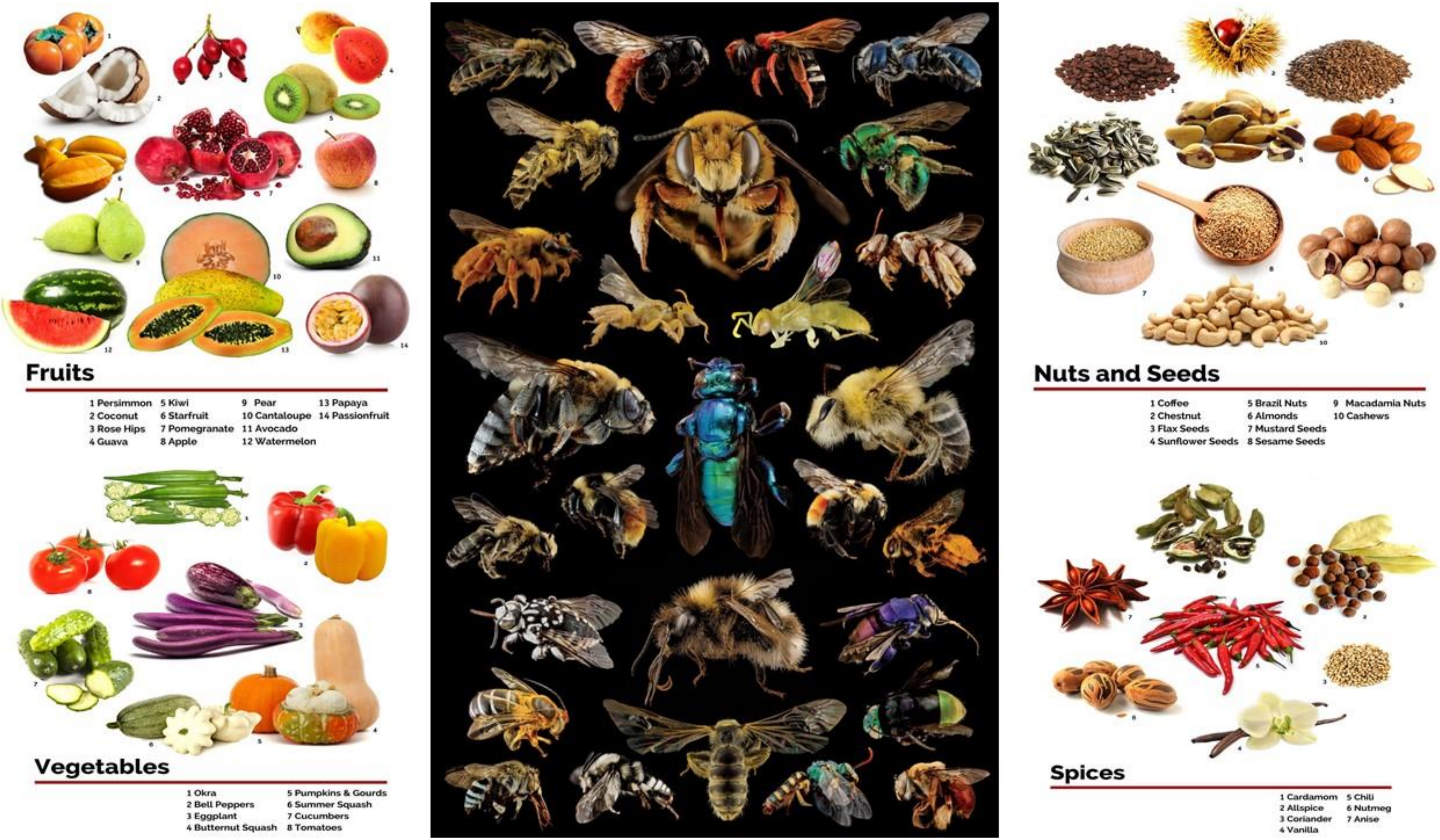


Figure 1.3: A selection of the 20,000 bee species found worldwide and some of the crops that they pollinate (Museum of the Earth 2019).

1.2.2 Wild bees

Wild bee pollinators can make an important contribution to crop pollination in four main ways (Kremen & Chaplin-Kramer 2007). Firstly, where their ecological needs are met in agricultural landscapes, wild bees have the capacity to fully and consistently pollinate crops (Kremen, Williams & Thorp 2002; Rader et al. 2012; Isaacs et al. 2017), mitigating the risks associated with heavy reliance upon managed pollinators (Winfree et al. 2007). Second, most economically valuable self-compatible crops still benefit from insect pollination, yet pollination of such crops is rarely managed for (e.g., by hiring honeybees). As such, improvements in productivity from insect-mediated pollination is generally provided by wild pollinators (Kremen & Chaplin-Kramer 2007). For example, many economically important field-produced crops are self-pollinating, but have been demonstrated to benefit from increased fruit set and size as a result of cross-pollination by wild bee species (Klein, Steffan-Dewenter & Tscharntke 2003; Greenleaf & Kremen 2006). Thirdly, wild pollinators can increase the pollination efficiency of managed species through behavioural interactions. For example, wild bees have been demonstrated to increase the movement of honey bees between flowers. This is particularly critical in crops with separate male and female flowers, or strong self-incompatibility mechanisms, such as many orchard crops (Kremen & Chaplin-Kramer 2007). Finally, wild bees can pollinate many crops which are not effectively, or at all, pollinated by honey bees, including alfalfa and tomatoes (Klein et al. 2007; Andersson et al. 2014). A synthesis of global crops found universal positive associations between fruit set and flower visitation by wild insects, but significant fruit set increases from honey bee visitation in just 14% of systems surveyed (Garibaldi et al. 2013).

1.3 Pollinator declines

1.3.1 Bee declines

Pollinator declines, and the associated risks to human well-being (Dicks et al. 2021), have been cited as one of the most significant crises of the Anthropocene (Marshman, Blay-Palmer & Landman 2019). The 'European Red List of Bees' (Nieto et al. 2014) assessed the status of all European bees and estimated that almost 15% of species are threatened, or near threatened. There was insufficient data however to estimate the status of over half of species. Where data is available, however, it points to severe declines amongst many bee species (Biesmeijer et al. 2006; Williams & Osborne 2009; Potts et al. 2011; Powney et al. 2019). Declines in bee abundance and species richness have been linked to habitat degradation, pathogens, pesticides and climate change (Potts et al. 2010; Vanbergen et al. 2013; Goulson et al. 2015; Figure 1.4). Whilst the interaction of these multiple pressures poses the greatest overall threat to bee populations (Vanbergen et al. 2014), changes in land use and land management represent the most significant cause of pollinator declines (Dicks et al. 2021). In particular habitat loss and fragmentation, due to increasing agricultural land expansion and intensification, are primary drivers of declines in wild pollinators (Brown & Paxton 2009; Senapathi et al. 2017).

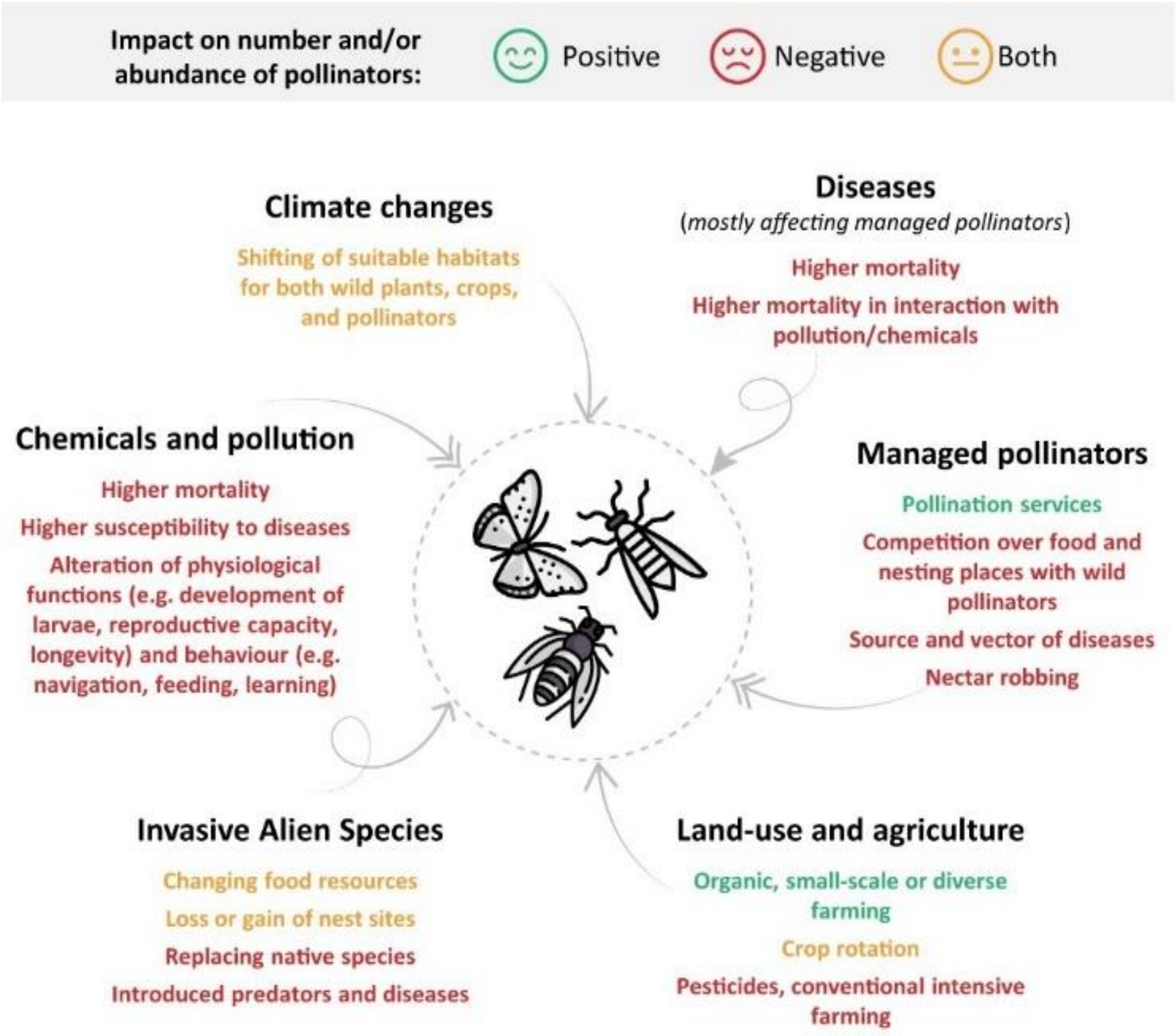


Figure 1.4: The impacts of different pressures on pollinating insects, including bee species (European Court of Auditors 2020).

1.3.2 Agricultural intensification

Agricultural ecosystems represent the largest and most important land use of the earth’s terrestrial surface (Bennett et al. 2021). Concomitantly modern agricultural practises also represent the most significant driver of biodiversity losses (Raven & Wagner 2021), primarily through the conversion of natural ecosystems into intensively managed farming systems (Dudley & Alexander 2017). Paradoxically, modern intensive agricultural practises to increase crop production are eroding critical ecosystem service provision (Fijen et al. 2018), including pest regulation and pollination services (Zhang et al. 2007), by acting as a major contributor to insect declines (Benton et al. 2002; Tscharnkte et al. 2005; Potts et al. 2010; Vanbergen et al. 2014; Ollerton et al. 2014). Valuable heterogeneous semi-natural habitats have been degraded and replaced by homogeneous habitats at both the local and landscape scale (Stoate et al. 2001; Tscharntke et al. 2005; Kovács-Hostyánszki et al. 2017). In many countries, hedgerows, and other woody linear features, have been destroyed to amalgamate and enlarge fields, and arable plant diversity has been reduced through crop specialization, monocultures, and herbicide application (Tscharntke et al. 2005; Kremen et al. 2007; Raven & Wagner 2021). The subsequent erosion of food, nesting, and hibernation resources have been extensively linked to reductions in both bee diversity (Klein et al. 2007; Carre et al. 2009; Le Feon et al. 2010; Kennedy et al. 2013; Vanbergen et al. 2014) and crop pollination service delivery (Kremen & Chaplin-Kramer 2007; Gill et al. 2016; Kovács-Hostyánszki et al. 2017), and have occurred concurrently with the increasing pollinator-dependence of agriculture (Aizen et al. 2008; Aizen, Garibadi & Harder 2022). As such, there have been growing concerns that losses in bee diversity could impair future crop pollination services (Aizen, Garibaldi & Harder 2022), and potentially threaten future food security (Reilly et al. 2020) and human health (Smith et al. 2015).

1.4 Food security

1.4.1 Crop production

Insect pollination benefits crop yield, quality, market value and yield stability (Klein et al. 2007; Bonmarco, Marini & Vaissière 2012; Klatt et al. 2014; Garratt et al. 2014a; Vanbergen et al. 2014; Ollerton 2017). As such, concerns have grown over potential yield losses (Leonhardt et al. 2013) and future pollination deficits (Gill et al. 2016) due to increasing reliance on dwindling pollinator populations (Aizen et al. 2008; Holland et al. 2020). Pollinator-dependent crops have been demonstrated as having lower relative yield growth and stability than less-dependent crops (Garibaldi et al. 2011a; Dicks et al. 2021). Furthermore, threats to future food security may no longer be a theoretical future concern (Aizen et al. 2008), given recent empirical evidence of pollinator limitation across a variety of crops in Europe and North America (Holland et al. 2020; Reilly et al. 2020). Whilst there is evidence that bee declines have become less accentuated in recent decades (Carvalheiro et al. 2013), the tenuous growth and stability of pollinator-dependent crops has led to calls for more active conservation and monitoring of wild pollinators in agricultural habitats (Garibaldi et al. 2011a; Adamson et al. 2012; Garibaldi et al. 2013; Dicks et al. 2016; Potts et al. 2016) to protect future food security.

1.4.2 Ecological intensification

Historically increased food production has been accomplished by employing new technologies and converting natural habitats to cultivated land (MEA 2005; Garibaldi et al. 2011a; Vanbergen et al. 2014). Meeting future crop demands in this way would require further extensive land clearance and cause significant greenhouse gas emissions (Tilman et al. 2011; Bahadur et al. 2018). Furthermore, declining pollinator availability, and associated growth stagnation in pollinator-dependent crop yields (Garibaldi et al. 2011a; Reilly et al. 2020), cannot be compensated for by agronomic advances alone (Aizen et al. 2008; Kovács-Hostyánszki et al. 2017; Fijen et al. 2018). Many now argue that future crop production increases need to come from ‘ecological intensification’, whereby higher crop yields are produced on the same, or less, land area, by managing service-providing organisms (Bonmarco, Kleijn & Potts 2013; Garibaldi et al. 2019; Kleijn et al. 2019), whilst simultaneously reducing environmental degradation (Royal Society of London 2009; Godfray et al. 2010; Wezel et al. 2015). Integrating wild insect pollinators into agronomic management has been heralded as a means to sustainably produce food and conserve biodiversity (Pywell et al. 2015; Fijen et al. 2018). Currently, however, the large-scale integration of ecosystem services, such as insect pollination, into farm management is largely lacking (Fijen et al. 2018). Whilst ecological intensification, notably through a diversification of vegetation at the field, farm and landscape scales (Figure 1.5), has been shown to enhance pollinating insect biodiversity, and in turn crop pollination services (Gemmill-Herren et al. 2021), uptake of such practises has generally been low (Cole et al. 2020). Protecting crop pollination services will therefore require substantial institutional innovation in local structures and food system governance to secure a wholescale transition to more pollinator friendly agricultural practices (Gemmill-Herren et al. 2021).

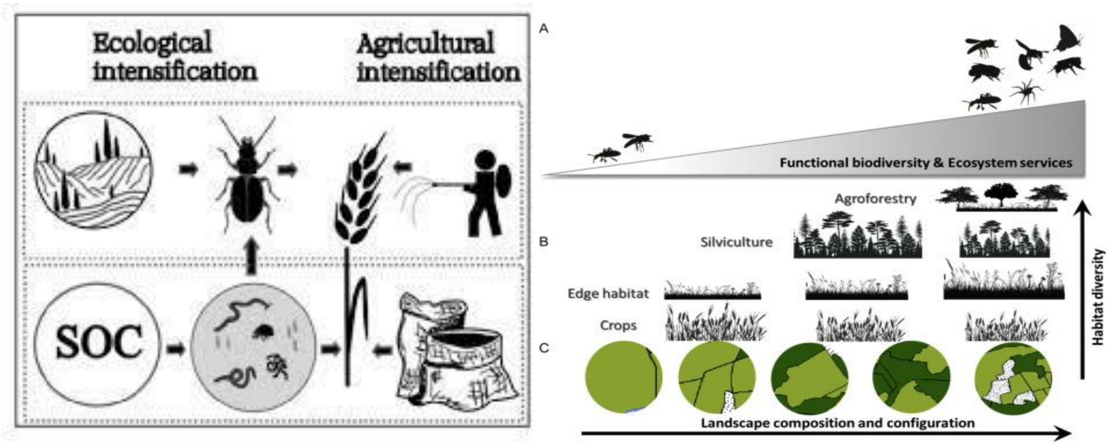


Figure 1.5: Left - Ecological intensification, whereby beneficial landscape (e.g., landscape hetereogenity) and management (e.g., high soil organic carbon (SOC)) aspects enhance ecosystem service providing organisms, and pesticide and fertilizer inputs utilized by intensive agricultural practises are reduced (Redlich 2020).

Right - The relationship between the functional biodiversity of ecosystem providing organisms (e.g., pollinators) and the diversity of vegetation and habitat complexity at the field, farm and landscape scale (Vanbergen et al. 2020).

1.5 Species Diversity

1.5.1 Species richness

Compelling experimental evidence from plant communities has established a generally positive relationship between biodiversity and ecosystem function (Eisenhauer et al. 2016). Recent research in agricultural systems also indicate a positive relationship between pollinator diversity and crop yields, likely due to niche complementarity and functional redundancy (Vasiliev & Greenwood 2020). However, there are considerable financial costs associated with implementing real-world conservation policies (McCarthy et al. 2012). It has therefore been postulated that cost-effective management should target the small proportion of bee species found to deliver the majority of flower visits (Kleijn et al. 2015). However, this approach may not ensure sufficient and stable crop pollination delivery over large temporal or spatial scales (Fijen et al. 2018; Winfree et al. 2018; Garibaldi et al. 2019). There is increasing evidence of the importance of species diversity, including rare species, for adequate and stable crop pollination service delivery at both the farm and landscape scale, due to species turnover (Martins et al. 2018; Winfree et al. 2018). Pollinator diversity, rather than an abundance of common species, has increasingly been demonstrated to positively benefit crop yield quantity, quality and stability (Vasiliev & Greenwood 2020). Bee populations undergo significant temporal and spatial fluctuations (Roubik 2001; Williams, Minckley & Silveira 2001) and exhibit marked community variation across crop fields and years (Adamson et al. 2012; Kremen, Williams & Thorp 2002). Thus, targeting management at a narrow subset of common, dominant pollinating bee species (Kleijn et al. 2015) will not promote resilient crop pollination service delivery if it fails to incorporate species which can supplement pollination when dominant species are performing sub optimally (Fijen et al. 2018; Vasiliev & Greenwood 2020).

1.5.2 Response diversity

Food security depends not only on the magnitude of crop yields, but also the stability and resilience of crop pollination services (Senapathi et al. 2015). In ecological terms resilience can be defined as “the degree to which an ecosystem function can resist or recover rapidly from environmental perturbations” (Oliver et al. 2015a). Biodiversity can provide ‘insurance effects’, whereby ecosystem services are maintained in the face of environmental fluctuations because some species will contribute at times others do not (Yachi & Loreau, 1999). Biodiversity is likely to become increasingly critical for resilient crop pollination services in the future due to the increasing rate and intensity of environmental perturbations such as land use and climate change (Oliver et al. 2015a; Oliver et al. 2015b). Bee species show variable responses to environmental stressors - i.e., response diversity – because of differences in response traits that mediate their sensitivity to environmental drivers (Oliver et al. 2015a; Senapathi et al. 2015). For example, difference in traits, including body size, nesting type, niche breadth, phenology and reproductive strategy, can influence bee sensitivity to climate and land use change (Williams et al. 2010; Rader et al. 2013; De Palma et al. 2015; Kammerer et al. 2021). High bee diversity has been linked to more stable and resilient crop pollination delivery due to varying responses to changes in weather (Brittain, Kremen & Klein 2013; Rogers, Tarpy & Burrack 2014) and landscape disturbance (Winfree & Kremen 2008). Protecting biodiversity and ecosystem service providers are often seen as contrasting objectives (Sutter et al. 2017), requiring distinct conservation measures (Kleijn et al. 2015). However, there is significant overlap between the flowering plants visited by many dominant crop pollinating bees and rarer species, and there is scope to develop measures to conserve a wide range of bee species within farmland and safeguard pollination services (Sutter et al. 2017).

1.6 Pollinator Management

1.6.1 Farm practices

Whilst landscape configuration, notably the presence of high quality, heterogenous habitats is vital for preserving pollinator populations (Senapathi et al. 2017; Dicks et al. 2021), there is growing evidence that farm management, which dictates foraging and nesting resources at the local level (Kovács-Hostyánszki et al. 2017), is also an important determinant of pollinator persistence in agricultural landscapes. Farm practises can potentially offset the negative impacts of surrounding habitat loss, safeguarding bee diversity and improving productivity, even in heavily degraded landscapes (Kennedy et al. 2013). Wildlife friendly farming, whereby conservation measures are integrated into farmland (Green et al. 2005), has been demonstrated to sustainably boost crop yields through the provision of nesting habitat and floral resources for key pollinators (Pywell et al. 2015). There is, however, a distinct lack of information and guidance available to growers and land managers on the best strategies to support wild pollinators and meet their crop pollination requirements (Isaacs et al. 2017). Part of this likely stems from a lack of information on those species which are delivering pollination service to advise management. Very little is known about the overall contribution of wild species to the pollination of individual crops, nor which, or how many, species, are delivering this service (Kremen & Chaplin-Kramer 2007), due to a paucity of studies. To date the only large-scale study seeking to identify bee species visiting crop flowers provided only a global overview of a small percentage of dominant species (Kleijn et al. 2015). Growing evidence suggests that individual crops exhibit differences in their pollinator communities and pollination service benefits (Garratt et al. 2014b). Identifying the pollinating bee species of different crops would allow for their biological and ecological needs to be incorporated into management interventions aimed at improving pollination service delivery (Isaacs et al. 2017).

1.6.2 Agri-environment schemes

One of the earliest initiatives to embed biodiversity conservation into agricultural policy was the European Union implementation of agri-environment schemes. Initially developed to provide financial remuneration to farmers for adopting practises that protect threatened habitats, they are now also targeted at conserving ecosystem service providing organisms, including farmland birds and arable plants (Batary et al. 2015). From a pollinator perspective, measures have been commonly aimed at boosting floral resources - the main factor limiting bee populations (Roulston & Goodell 2011). However, their success has been highly variable, due to a lack of consistently appropriate and diverse flowering plant mixtures that provide forage throughout the year (Scheper et al. 2013; Scheper et al. 2015; Albrecht et al. 2020). Many of the measures evidenced as most beneficial to pollinators have had low uptake (Cole et al. 2020) due to farmer resistance (Burton 2012), and uncertainties over the costs and benefits of management for wild pollination services (Breeze et al. 2016). Furthermore, many measures preferentially benefit a limited suite of species (Campbell et al. 2017; Wood, Holland & Goulson 2015; 2016a). Most measures to boost floral diversity have been designed around the foraging requirements of bumblebees, and are of limited value to solitary bees, which largely rely on non-sown plant species (Wood, Holland & Goulson 2016a). Additionally, bees are central place foragers and encompass a diverse range of nesting guilds (Tscharntke et al. 2005). Suitable nesting sites and resources within their foraging range play a significant role in determining community composition, abundance and persistence within farms (Tscharntke et al. 2005; Lonsdorf et al. 2009). However, little is known about many species' ecological requirements (Winfree et al. 2007) and engineering 'optimal' farm habitats to boost pollinator diversity and crop yields has thus far proved elusive (Gill et al. 2016).

1.6.3 Pollinator traits

One way in which diverse pollinator communities may benefit crop production is through niche complementarity (Vasiliev & Greenwood 2020), whereby different architectural, behavioural, spatial and temporal use of floral resources by pollinators (Blüthgen & Klein 2011; Albrecht et al. 2012; Mallinger & Gratton 2015) could lead to increased yields and crop quality. However, evidence indicates that bee declines are biased towards species with particular traits. For example, small and specialist solitary species, with short flight periods appear to be more susceptible to agricultural intensification than many large bodied and social bumblebee species (Williams et al. 2010; De Palma et al. 2015). Increasingly homogenised crop pollinator communities in agricultural landscapes have been linked to reduced crop yield and quality (Carre et al. 2009; Grab et al. 2019). However, whilst greater species diversity can increase ecosystem productivity, the range of bee species which can effectively pollinate some crop flowers can be limited by the accessibility of floral resources (Garibaldi et al. 2014). A meta-analysis of global crop systems determined that the best predictor of fruit set was achieved by incorporating trait matching between flower visitors and crops (Garibaldi et al. 2015). Whilst most crops are adapted for pollination by a range of species, some bees are better adapted to certain flowers (Westerkamp & Gottsberger, 2000; Figure 1.6). Long-tongued species, such as bumblebees, are the most efficient pollinators of deep tubular flowers (Fontaine et al. 2005). Conversely short tongued species are more efficient at pollinating shallow, open flowers (Garibaldi et al. 2015).

Management to improve crop yields may therefore also benefit from crop specific strategies aimed at key pollinating taxa (Garratt et al. 2014a).

Figure 1.6: Long-tongued Anthophora bee taking nectar from a deep, tubular flower and a short-tongued Colletes taking nectar from an open, shallow flower (Held 2013).

1.7 Pollinator trends

1.7.1 Identifying pollinators

Crucial to developing conservation strategies to maximise crop pollination productivity is to match resource management with target taxa (Kremen 2005; Murray, Kuhlmann & Potts 2009). The identification of crop flower visitors is vital to guide management that can improve and sustain crop pollination and production (Garratt et al. 2016). Employing the most appropriate survey methods for wild bees in agricultural settings is critical to capture representative samples of crop pollinator communities (Templ et al. 2019) and to assess the effectiveness of management practices on populations (Gill & O’Neal 2015). Sampling methods fall into two broad categories - active (observation plots, transect walks) and passive (e.g., pan traps, trap nests) (Westphal et al. 2008). Whilst there is now a wide breadth of research comparing different sampling methods, many have provided conflicting results (Templ et al. 2019). It is unclear, for example, to what degree factors such as guild or colour preferences impact upon the relative efficiency of different methods to sample bee communities (McCravy et al. 2019; Connelly et al. 2015). Increasing evidence suggest individual survey methods sample different components of pollinator communities (Westphal et al. 2008; O'Connor et al. 2019). Recent studies indicate that active methods may be biased towards large social species, such as bumblebees, compared to trapping methods, which may more comprehensively sample solitary bee species (Krahner et al. 2021; Thompson et al. 2021). Critically, assessments of sampling techniques are rarely carried out in crop areas (McCravy 2018) or fail to account for the possible impacts of crop type on results. Thus, the potential to develop crop specific mitigation strategies that can boost yields and meet future crop production demands (Garratt et al. 2014a) is currently hampered by a lack of information on the best means to inventory crop pollinator communities.

1.7.2 Monitoring programmes

Alongside gathering information on the bee species providing crop pollination service delivery, there also remains a critical need to monitor their populations (Potts et al. 2016; O'Connor et al. 2019). Despite their critical importance for crop pollination, the status of wild bee species is largely unknown due to a lack of standardised and systematic monitoring data (IPBES 2016; Carvell et al. 2017; Powney et al. 2019). Whilst there is growing evidence of bee declines, current knowledge is often deficient and fragmented (Potts et al. 2010; Vanbergen et al. 2013). Information on bee trends is almost exclusively based upon ad-hoc records (Powney et al. 2019), which tend not to be collected in intensively cultivated agricultural landscapes (Garratt et al. 2019). Long-term and standardized data on species abundances and distribution are vital to identify drivers of declines, target conservation resources and evaluate the impacts of implemented measures (Moussy et al. 2022). Existing monitoring schemes for insects, often citizen science-based projects, tend to sample all groups simultaneously or focus on non-bee taxa, and frequently employ protocols such as malaise and light traps that are not always appropriate for bees (Montgomery et al. 2021). Whilst concerns over pollinator declines have begun to result in policy efforts to gather information on the status and trends of bee species (Breeze et al. 2021), response actions have thus far failed to keep pace with the threats facing them (Potts et al. 2016). Existing schemes currently focus upon entire bee species communities (Carvell et al. 2017; O'Connor et al. 2019). Whilst such national level monitoring schemes are undoubtedly critical for wider biodiversity conservation, more refined focus, specifically upon crop pollinating species in agricultural settings, is vital to inform management that can improve and sustain crop production (Garratt et al. 2016; Potts et al. 2021), and ensure resilient crop pollination service delivery (Carvell et al. 2017).

1.7.3 Occupancy models

Traditionally, measuring population variability, has been contingent upon long-term abundance data (Lundberg et al. 2000), but this is only available for a very limited number of taxa with dedicated monitoring schemes (Outhwaite et al. 2018). In contrast distribution records i.e., records of a species at a given time and place, are available for a wide range of species (Mason et al. 2018); although the nature of their collection process means that they contain inherent biases, such as uneven recording intensity (Powney & Isaac 2015). Occupancy models, however, now represent a robust statistical technique to overcome the challenges presented by unstructured biological records, by accounting for the likelihood of pseudoabsences and uneven recording effort (Isaac et al. 2014). As well as providing information on trends in the distribution of species, occupancy model data have now been used as a surrogate for abundance across a wide range of taxa (Stauffer et al. 2021). A recent study on butterflies in the UK demonstrated that there is a strong correlation between mean inter-annual changes in citizen science collected distribution records and abundance (Mason et al. 2018). Employing hierarchical Bayesian Occupancy Models the UK Centre for Ecology and Hydrology has utilised biological records collated by the Bees, Wasps and Ants Recording Society (BWARS 2020a) to measure species-specific trends of wild bee species in Great Britain (Powney et al. 2019). This data opens up opportunities to examine population trends in British bee species.

1.8 UK crop pollination

1.8.1 UK agriculture

UK crop agriculture is highly pollinator dependent (Schulp, Lautenbach & Verburg 2014). Insect pollination underpins key sectors of UK agriculture (Garratt et al. 2014a) with service provision heavily dependent upon wild pollinators (Breeze et al. 2011; Breeze et al. 2014a). Between 2014 and 2016 pollination services in the United Kingdom were estimated to increase agricultural productivity by ~£630 M per year (Breeze et al. 2021). Insect pollinated crops grown in the UK include apples, field bean, oilseed rape and strawberry, which represent the most economically important orchard, fodder, oil and soft fruit crops cultivated in the UK, respectively (Table 1.1).

Table 1.1: Summary of the pollinator dependence and economic benefits of pollination service for apples, field bean, oilseed rape and strawberry crops in the United Kingdom (2014-2016 average) (information taken from Breeze et al. 2021).

Crop	**Pollinator Dependence**	**Total Production**
Apples	57 – 69%*	£200.2 M
Field Bean	25%	£90.8 M
Oilseed Rape	25%	£662.0 M
Strawberry	45%	£334.3 M

Pollinator dependence = the proportion of yield lost in the absence of pollination.
Total production = the total market sale price of all UK production of the crop.
*Apple data based upon 3 different varieties (Cider, Culinary and Dessert).

Wild bees are believed to be the most important pollinators of all four of these crops in the UK (Garratt et al. 2016; Garratt et al. 2014b; Feltham et al. 2015). Although evidence suggests that they may exhibit differences in their bee pollinator communities (Figure 1.7), likely related to corresponding differences in crop floral phenology and morphology (Garibaldi et al. 2015). Apple flowers appear to be commonly visited by *Andrena* species (Campbell et al. 2017). Field bean and strawberry are predominantly visited by bumblebees, with long-tongued species, such as *Bombus pascuorum* cited as common visitors to bean (Garratt et al. 2014a), and shorter-tongued species, such as Bombus terrestris, identified as frequent visitors to strawberry flowers (Felthham et al. 2015). Oilseed appears to have the most diverse bee pollinator community, and as well as being visited by both *Andrena* and *Bombus* species, can also be commonly visited by *Lasioglossum* species (Woodcock et al. 2016).

Andrena spp.
Apple

Bombus pascuorum
Field bean

Lasioglossum spp.
Oilseed rape

Bombus terrestris agg.
Strawberry

Figure 1.7: Bee species/genera believed to be amongst the predominant flower visiting pollinators to apple (RSPB 2015), field bean (Torres et al. 2015), oilseed rape (Benton 2015) and strawberry (NRI 2021).

1.8.2 British bees

Approximately 270 bee species have been recorded in Britain and Ireland, encompassing 28 different genera (Falk, 2019). Great Britain has some of the best data available on bee populations through biological records collated by the Bees, Wasps and Ants Recording Society (BWARS 2020a). These have permitted assessments of changes in pollinator diversity (Biesmeijer et al. 2006) and long-term population trends (Powney et al. 2019). Both show significant bee declines, likely linked to agricultural policy and practises (Ollerton et al. 2014). The devolved countries of Great Britain are also currently the only regions in Europe to have developed both national pollinator initiatives (DEFRA 2015; The Scottish Government 2017; Welsh Government 2013) and set up a national pollinator monitoring scheme (Carvell et al. 2016). Objectives of these schemes include developing strategies to protect crop pollination service delivery (DEFRA 2015) and monitoring the trends of crop pollinating species (Carvell et al. 2020). As such Great Britain is an ideal case study to explore how information on crop pollinating bee species can be utilised to inform management and monitoring (Underwood, Darwin & Gerritsen 2017).

1.9 Thesis aims

This thesis aims to address gaps in knowledge around species-specific bee pollinator communities and monitoring of bee crop communities using four of the most economically important orchard, fodder, biofuel and soft fruit crops in Great Britain - apple, field bean, oilseed rape and strawberry - as case studies. All derive benefits to crop quantity, quality and/or market value from insect pollination (Woodcock et al. 2013; Garratt et al. 2014a; Garratt et al. 2014b; MacInnis & Forrest 2019), but most show evidence of insufficient pollination at present (Garratt et al. 2014a; Garratt et al. 2014b). This thesis aims to address the following research questions:

1. Which bee species are visiting, and potentially contributing to the pollination of apple, field bean, oilseed rape and strawberry crops in Great Britain?
2. Are there differences in the capacity of survey methods to sample bee communities of crops and how might this information be used to improve sampling and monitoring of crop pollinator communities?
3. How does pollinator community composition, and pollinator species richness, affect the stability of crop pollinator occurrence?

1.10 Thesis structure

Whilst the importance of wild bees for crop pollination is now well established, much less is known about which species contribute to service delivery to inform agricultural management, monitoring and conservation. Chapter two uses a novel approach of combining field survey and ecological trait data to produce lists of potential bee pollinators for each of our four focal crops in Great Britain. Additionally, dominant crop pollinating species are identified for all four crops, as well as an estimation of the contribution of wild bees compared to honey bees to flower visitation for each crop.

An increasing number of studies have reported declines in bee abundance and diversity, including in Great Britain. As such there is an urgent need to inventory and monitor bee populations. Yet evaluations of methods to inventory and monitor bees are rarely carried out in crops, nor do they consider potential differences amongst crop types or focus specifically upon crop pollinating species. Using the lists of bee species identified as potential crop pollinators in the preceding chapter, chapter three evaluates the most commonly employed sampling methods (transects, observation plots, pan traps) to assess wild bees in crop sites. The results are then used to consider how this information could be used to inform protocols to effectively sample and monitor the bee communities of crops.

Food security depends on not only the amount, but also the stability and resilience of agricultural crop production. An understanding of how crop pollinator community composition and species richness could influence crop pollination services has previously been untested, in part due to a lack of standardised data. Chapter four utilises the lists of crop pollinating bee species compiled in chapter two to compare the occupancy dynamics of the pollinator communities of the four focal crops. Using data from recently developed Bayesian occupancy detection models' chapter four investigates to what extent crop pollinator community composition, and pollinator species richness, affect the stability of crop pollinator occurrence.

1.11 Focal crops and taxa

Apples, field bean, oilseed and strawberries were chosen as the focal study crops as they represent the most economically valuable examples of the four main categories of crops grown in Great Britain – orchard, protein, oil and soft fruit, which are insect pollinated (DEFRA 2022a; Image 2022). These crop types are different in terms of growing conditions, as well as floral phenology and morphology (Garibaldi et al. 2015), which is likely to translate into differences in their pollinator communities (Garratt et al. 2014a), making them good case studies for other similar crops. In addition the University of Reading has a considerable number of datasets focused on their the pollinator communities (University of Reading 2018).

Wild bees formed the focus of this thesis as they are the primary pollinators of many agricultural crops (Khalifa et al. 2021), including apples, field beans, oilseed rape and strawberries in Great Britain (Campbell et al. 2017; Garratt et al. 2014a; Feltham et al. 2014). Additionally, there is now considerable crop field survey, distribution, and traits data (Kleijn et al. 2015; Powney et al. 2019) available for wild bees to address the questions covered in this thesis. Whilst other insect groups, notably flies, are important pollinators of many crops, including apples, oilseed rape and strawberries (Rader et al. 2016), there is a general lack of crop field studies and traits data available for most other taxa (Rader et al. 2020). As such, there was insufficient data to expand the research work to other key insect crop pollinators at this time, but other insect groups could form the basis of similar future work.

1.12 Thesis Papers

The experimental chapters (2 – 4) in this thesis are based upon the following publications:

Paper 1 (Chapter 2):

Hutchinson *et al.* (2021). Using ecological and field survey data to establish a national list of the wild bee pollinators of crops. *Agriculture, Ecosystems and Environment*, 315, 107447. https://doi.org/10.1016/j.agee.2021.107447

Paper 2 (Chapter 3):

Hutchinson *et al.* (2021). Inventorying and monitoring crop pollinating bees: Evaluating the effectiveness of common sampling methods. *Insect Conservation and Diversity*, 15, 299-311. https://doi.org/10.1111/ICAD.12557

Paper 3 (Chapter 4):

Hutchinson *et al.* (2022). Bee occupancy dynamics: The influence of pollinator community composition and species richness on crop pollinator occurrence. *Frontiers in Sustainable Food Systems*, 313.

https://doi.org/10.3389/fsufs.2022.943309

I declare that I conducted all the research for these publications and was the principal author of each paper. My supervisors, and other co-authors, who also provided data or technical support for data analyses, assisted with editing the content.

Minor changes have been made to the versions presented here compared to the published versions, all of which are outlined in the title page for the relevant chapter.

Chapter 2: Using ecological and field survey data to establish a national list of the wild bee pollinators of crops.

This chapter is a modified version of the following publication:

Hutchinson, L. A., Oliver, T. H., Breeze, T. D., Bailes, E. J., Brünjes, L., Campbell, A. J., Erhardt, A., de Groot, G. A., Foldesi, R., García, D., Goulson, D., Hainaut, H., Hambäck, P. A., Holzschuh, A., Jauker, F., Klatt, B. K., Klein, A-M., Kleijn, D. Kovács-Hostyánszki, A., Krimmer, E., McKerchar, M., Miñarro, M., Phillips, B. B., Potts, S. G., Pufal, G., Radzevičiūtė, R., Roberts, S. P. M., Samnegård, U., Schulze, J., Shaw, R. F., Tscharntke, T., Vereecken, N. J., Westbury, D. B., Westphal, C., Wietzke, A., Woodcock, B. A. & Garratt, M. P. (2021). Using ecological and field survey data to establish a national list of the wild bee pollinators of crops. *Agriculture, Ecosystems and Environment*, 315, 107447. https://doi.org/10.1016/j.agee.2021.107447

Author contributions: Conceptualisation: LH, MG, TB, TO; study design: LH, MG, TB, TO; data curation: LH; formal analysis: LH; writing – original draft preparation: LH; writing – review and editing: all authors.

This chapter is based upon the above publication. The methodology and findings remain unchanged from the published version. However, some alterations have been made to the following version for completeness and to improve clarity and readability of the thesis:

- Additional information has been added to the abstract to more comprehensively summarise the key findings.
- Additional information and references, and edits, have been added to the introduction and discussion sections.
- Some of the supplementary material from the published version has been incorporated into the main text, and has resulted in minor textual changes to the methods and results sections.
- Some small changes have been made throughout the chapter to correct minor textual errors in the published version.

2.1 Abstract

The importance of wild bees for crop pollination is well established, but less is known about which species contribute to service delivery. Using sites in Great Britain as a case study, we used a novel qualitative approach combining ecological trait information and field survey data to establish a national list of crop pollinating bees for four economically important crops (apple, field bean, oilseed rape and strawberry). A traits data base was used to establish potential pollinators, and combined with field data to identify both dominant crop flower visiting bee species, and other species that could be important crop pollinators, but which are not presently sampled in large numbers on crops flowers. Additionally, we approximated the contribution of wild bee species to flower visitation relative to that of the managed honeybee in all four crops. We found evidence of variation in the bee communities of different crops. Additionally, whilst the majority of total crop flower visits were attributable to a small number of common and generalist species, many other bee species were identified as potential pollinators, including rare and specialist ones. Furthermore, we found that collectively wild bee species make a more substantial contribution to crop flower visits relative to that of honeybees in all crops. Establishing a national list of crop pollinators is important for practitioners and policy makers to inform targeted management approaches for improved ecosystem services, conservation and species monitoring. Data can be used to make recommendations about how pollinator diversity could be promoted in agricultural landscapes. Our results suggest agri-environment schemes need to support a higher diversity of solitary species than at present. Management would also benefit from targeting specific species to enhance crop pollination services to particular crops. Whilst our study is focused upon Great Britain, our methodology can be applied to other countries, crops and insects.

2.2 Introduction

Insect pollination is key to global agricultural productivity (IPBES 2016) due to growing demand for entomophilous crops (Godfray & Garnett 2014; Aizen et al. 2019). The nutritional and economic importance of insect pollinated crops (Vanbergen et al. 2014), and the inability of managed pollinators (e.g., Apis mellifera) to meet service demand, mean agriculture is highly dependent upon wild pollinators (Aizen & Harder 2009; Breeze et al. 2014a). Yet, conventional agricultural practices are a key driver of pollinator declines (Senapathi et al. 2015), including wild bee species, the primary pollinators of many insect pollinated crops. (Klein et al. 22007; Potts et al. 2010). Whilst agri-environment scheme options have had positive impacts (Tonietto & Larkin 2018), most benefit a limited suite of common species (Scheper et al. 2013; Wood et al. 2015; Wood, Holland & Goulson 2015, 2016a, 2016b). Associated reductions in phylogenetic diversity amongst bee species in agricultural landscapes have therefore led to increasingly homogeneous pollinator communities, and in turn reduced crop yields and quality (Grab et al. 2019).

There is now a growing consensus amongst the scientific community of a positive link between biodiversity and ecosystem service provision (Hagan, Vanschoenwinkel & Gamfeldt 2021), including biodiversity-mediated benefits of species rich pollinator communities for crop production (Dainese et al. 2019). Whilst the majority of crop flower visitation is carried out by a small proportion of common and generalist bee species (Kleijn et al. 2015), species-rich communities have been shown to positively influence crop yields and pollination service stability (Hoehn et al. 2008; Garibaldi et al. 2011a; Martins et al. 2015; Woodcock et al. 2019). Protecting biodiversity and ecosystem service providers are, however, often seen as contrasting objectives (Sutter et al. 2017), requiring distinct conservation measures (Kleijn et al. 2015). Yet, management that only targets dominant crop pollinators will not safeguard production if it fails to encompass ‘insurance’ species (Yachi & Loreau 1999) that can supplement pollination services at times when dominant species are performing suboptimal (Fijen et al. 2018).

High species turnover across fields and years means that diverse pollinator communities, including rare and specialist species, are required to maintain crop pollination service at the landscape scale (Martins et al. 2018; Winfree et al. 2018). Additionally, evidence of climate change induced declines in some wild bee species (Soroye, Newbold & Kerr 2020), may mean that supporting wider species diversity is crucial for crop pollination service stability and resilience under the substantial future environmental changes that are predicted (Oliver et al. 2015a; Dainese et al. 2019). Historically agri-environment measures to boost pollinator populations in farmland have focused on enhancing floral diversity within field margins (Carvell et al. 2007). Such flower mixes are principally created with leguminous (*Fabaceae*) species, which preferentially provide forage for bumblebees (Wood et al. 2015), and are of limited value to other bee species (Wood, Holland & Goulson 2015, 2016a, 2016b). Yet solitary bee species are more important pollinators of some crops (Woodcock et al. 2013; Campbell et al. 2017).

Additionally, different crops may have distinct pollinator communities (Garratt et al. 2014a). As such, current agri-environment schemes are often not optimally designed to increase pollination services to many crops (Wood, Holland & Gouslon 2015, 2016a; Image et al. 2022). Identifying key pollinating species to individual crops, and ones which may provide additional pollination and insurance against declines in other species, would help inform agricultural management for bee pollinators (Garratt et al. 2014a). Yet there is insufficient information on bee communities for many crops (Kremen & Chaplin-Kramer 2007) and no studies have attempted to establish a ‘national list’ of crop pollinators to ensure that management and monitoring programmes include important crop pollinating species (Carvell et al. 2017; Garratt et al. 2019).

In order to inform pollinator management and monitoring, and using sites in Great Britain as a case study due to the comprehensive data available on its bee fauna (Powney et al. 2019), we aimed to compile the bee species visiting four crops:

1. Apple (*Malus domestica*);
2. Field bean (*Vicia faba*);
3. Oilseed rape (*Brassica napus*);
4. Strawberry (*Fragaria x ananassa*).

Insect pollination has been shown to enhance yield quantity and quality in all four crops (Bartomeus et al. 2014; Garratt et al. 2014b). Additionally, these crops differ in flower phenology and morphology (Garibaldi et al. 2015), and likely show corresponding differences in their pollinator community composition (Garratt et al. 2014a). We compiled a list of all British bee species and their available ecological traits, and combined these with field survey data in order to devise an approach to generate lists of:

(i) Definite flower visitors to each crop;

(ii) Likely flower visitors, which are expected to also contribute to crop pollination;

(iii) Possible crop flower visitors whose contribution to pollination is not well understood and merits further investigation;

(iv) Dominant crop pollinating species.

In addition, we also assessed the contribution of wild bees compared to honey bees for crop flower visitation.

Our aim was to compile these lists for reference purposes, but not to statistically compare pollinator communities between crops, due to the unstandardized nature of the datasets used to generate the lists of bee species.

2.3 Methods

2.3.1 Potential crop pollinators

First, a species database of all extant, resident wild bee species in Great Britain was established using the most recent checklist of UK species (Else et al. 2016). For each species, data on the following were collated: flight period (months); sociality (cleptoparasite, eusocial or solitary (regarded as applying to all non-*Bombus* species)); lecty (oligolectic or polylectic, including if any of the target crop plant families are visited for pollen and/or nectar), tongue length (short/long) and geographic coverage (distribution and habitat) based on trait information compiled by Stuart Roberts for the EU- FP6 ALARM-project and information taken from species accounts generated by the Bees, Wasps and Ants Recording Society (BWARS 2020a). The most up to date information on species with a designated conservation status was also sourced from the 'Pantheon' invertebrate database (Webb et al. 2018).

Potential crop pollinators, as defined here, are those bee species which, based upon these ecological traits could pollinate our target crops. Habitat specialists that are not coincident with cropland were initially excluded i.e., primarily coastal, heathland species, as were species with particularly restricted geographical distributions i.e., confined to the north coast of Scotland. The known floral ecology of each species was then used to refine lists for each crop. Cleptoparasitic species, species that are oligolectic on plant families other than the target crop or polylectic, but not documented in the literature as foraging on the relevant plant family for pollen or nectar, were excluded. Species whose flight period does not overlap with the relevant crops main flowering period (Apple: April – May; Bean: May – Jun; Oilseed: April – June; Strawberry: April – July) were also excluded. For field bean, only 'long-tongued' species (Michener 2000) were considered as its flowers have deep corollas and most visits by 'short-tongued' species involve nectar robbing rather than legitimate visitation (Garratt et al. 2014a). Oilseed datasets were from a mixure of spring and winter sown, but all were from fields surveyed between April and June.

Establishing potential pollinators based upon ecological traits, as described above, permitted us to identify species caught in pan traps only that could potentially pollinate our crops. Additionally, for species only recorded as a single visit to crop flowers it allowed us to distinguish between species that were potential pollinators and those that could be misidentifications or errant species that, for example, may have emerged early or been observed on flowers but not necessarily foraging from it and contributing to pollination.

2.3.2 Field survey data

Field studies from across Great Britain and Europe were sourced through literature searches in google scholar and, alongside existing datasets held by the authors, were combined with the potential crop pollinator lists in order to establish shortlists of crop flower visitors. All field studies utilised in analyses had been conducted in orchards and crop fields in agricultural farms.

Fifty-seven datasets from across England, Scotland and eight other European countries (Figure 2.1) were available to combine with the potential crop pollinator lists in order to establish shortlists of crop flower visitors.

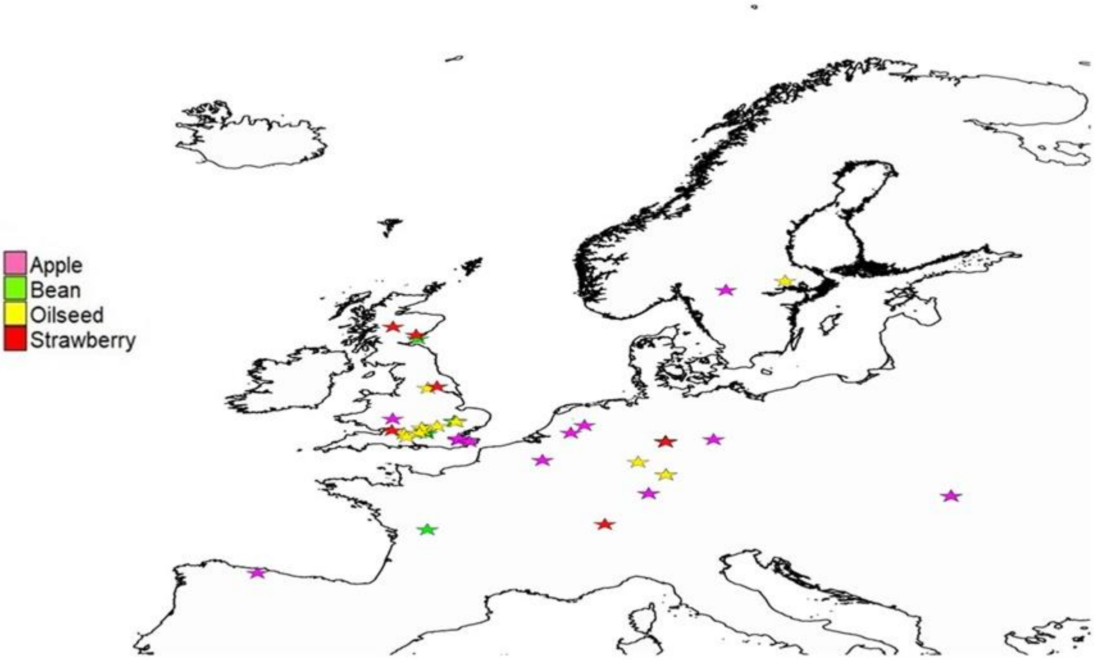


Figure 2.1: Map of Europe, showing the countries from which field studies were sourced for each crop.

Lists of bee species recorded in crop fields were compiled using three types of survey data:

i) British flower visitation studies (e.g., transect walks, observation plots);

ii) British pan trap studies in crop fields;

iii) Other European flower visitation studies (used to validate crop flower visitation for species sampled in British pan traps only).

For every bee species the total number of reported legitimate flower visits and the number of studies in which they were recorded in was calculated for each crop. If studies did not include quantitative data, then a conservative approach was taken whereby each bee species listed was taken as representing a single crop flower visit. As pan trap catches do not provide information on floral associations (Westphal et al. 2008), these data were used, in combination with trait data and European field data, to generate the lists of likely and possible pollinators only (see next section).

2.3.3 Crop flower visitors

The lists of potential crop pollinators were combined with the field survey data to categorize bee species into one of three flower visitor categories (Figure 2.2) as follows:

1. ‘Definite’ flower visitors:
   a. Species recorded visiting crop flowers in British studies.
   b. Species only recorded as a single visit were –
      i. Retained if they were recorded in at least one other European crop flower visitor study.
      ii. Retained but downgraded to a likely flower visitor if they did not appear in another European study but were classified as a potential crop flower visitor.
      iii. Excluded if they did not meet the above criterion.
2. ‘Likely’ flower visitors:
   a. Species recorded in British pan trap crop studies only and recorded as making at least two flower visits in other European studies.
   b. Species recorded visiting once in a single European study were –
      i. Retained in the likely flower visitor category if they were classified as a potential flower visitor for that crop.
      ii. Excluded if they did not meet the above criteria.

3. ‘Possible’ flower visitors:
    a. Species only recorded in British pan trap studies, or in other European flower visitor studies only, and classified as a potential crop flower visitor.
    b. Species only recorded as a single flower visit in European studies were excluded.

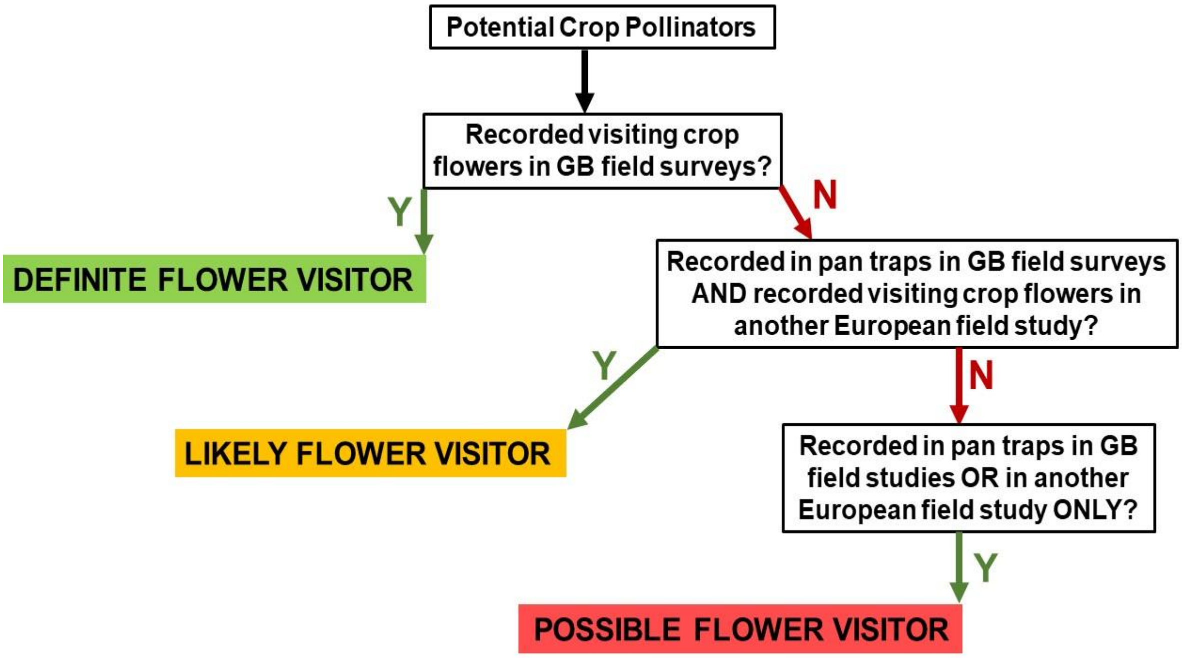


Figure 2.2: Methodology by which bee species deemed to be potential crop pollinators were assigned to different flower visitor categories; Definite, Likely and Possible.

2.3.4 Dominant crop flower visitors

As visitation rate to crop flowers is a good proxy of relative contribution to pollination service delivery (Vazquez´, Morris & Jordano 2005), we identified the dominant British flower visiting bee species per crop by approximating the species attributed with a combined total of 80% of flower visits, the proportion identified as corresponding to the dominant flower visitors by Kleijn et al. (2015). Only British flower visitation datasets where bee species were either all identified to species or genus were included in the analysis.

We calculated the proportion of flower visits attributed to every bee species at each site per dataset. This was done to negate the potential biases of different sampling effort and intensity between field studies and to account for the fact that some species may have an unusually high abundance within a given site or individual dataset but not make a significant contribution to flower visitation overall. Any flower visits for bees only identified to genus were allocated to bees identified to species level at the same percentage as those bees accounted for overall flower visits i.e., if a given *Andrena* species accounted for 20% of flower visits then 20% of the total flower visits by unidentified *Andrena* were added to that species total flower visits. For each crop the total average proportion of flower visits per species across all datasets was then calculated to determine the species corresponding to a combined total of 80% of all flower visits.

The majority of studies recorded all, or most, *Lasioglossum* species to genus only, so visits to crop flowers had to be aggregated to *Lasioglossum* spp. for all crops, except strawberry. Additionally, it was not possible to get individual site data for one strawberry field study dataset, but as all sites were within the same region of Scotland, the datum was considered as one site for analysis. Finally, one oilseed data set had largely qualitative data, and it was only possible to assign bee species a number of flower visits between one and four.

2.3.5 Contribution of wild bees and honey bees to crop flower visitation

Finally, we calculated the average proportion of visits to crop flowers attributed to wild bees compared to honey bees for all crops. To do so we repeated the analysis described above, but this time aggregated visits by wild bee species and included data for honeybee visits to crop flower visits for all datasets in which they were also recorded.

2.4 Results

2.4.1 Potential crop pollinators

A preliminary list of 229 extant, permanent resident British wild bee species was compiled (Appendix 1). Of those 132 species were excluded due to ecological and lecty traits that were deemed incompatible with these bees being present in crop fields and/or crop flower visitors (Appendix 2). Four species were treated as an aggregate – *Bombus terrestris aggregate* (hereafter referred to simply as *B. terrestris*) – due to the difficulties of separating their workers in the field (Wolf, Rohde & Moritz 2010; Bossert 2015). Therefore, a total of 97 species were initially identified as potential crop pollinators. Accounting for their documented foraging ecology and flight period, the following number of species were considered as potential pollinators per crop: apple- 81, bean- 27, oilseed - 60, and strawberry – 88 (Appendix 3).

2.4.2 Field survey data

The total number of studies sourced per crop were as follows: apple – 17; bean – 10; oilseed – 19; strawberry – 11 (Table 2.1; Full details of all crop studies are given in Appendix 4).

Table 2.1: Number of field studies per survey type that were sourced for each crop (total number of sites are provided in brackets).

Crop	**Survey Type**			**Total**
	British Flower Visitor	**British Pan Trap**	**European Flower Visitor**	
Apple	5	2	10	17 (162)
Field Bean	5	3	2	10 (41)
Oilseed Rape	9	4	6	19 (183)
Strawberry	5	1	4	10 (41)

2.4.3 Crop flower visitors

Seventy-three species from ten genera where categorised as flower visitors of one or more crops, 63 of which were recorded in British crop field studies (Table 2.2; Figure 2.3). Fourteen species were included in flower visitor categories that were not initially identified as potential crop pollinators. Ten of those were widely polylectic *Bombus* or *Lasioglossum* species, all recorded in oilseed datasets, but not documented in the literature as foraging on *Brassicaceae*. The remaining species were three short-tongued *Andrena* species recorded visiting bean flowers, two of which are oligolectic on *Fabaceae,* and a *Colletes* species, recorded in a single strawberry dataset, that is documented as being oligolectic on another plant family. The majority of species identified as potential pollinators, but not recorded in crop field surveys were either rare species or polylectic species documented as having distinct preferences for plant families other than the target crop. The remaining species were overwhelmingly smaller species from the genera *Lasioglossum* or cavity nesting *Hylaeus or Megachilidae* species. Most species identified as crop flower visitors were geographically widespread and polylectic species. However, a quarter (n = 18) of species included in flower visitor categories currently have a designated conservation status in Britain. Full lists of all bee species identified as crop flower visitors for all four crops are provided in tables 2.3a – 2.3d. All bee species recorded in crop field studies but either downgraded in their status as a crop flower visitor, i.e., definite to likely (as per the methodology in section 2.3.3.) or excluded entirely as potential pollinators are provided in Appendix 5.

Table 2.2: Number of bee species, based upon field datasets and trait information that were assigned to each category of flower visitor per crop.

	Flower Visitor Category			
Crop	**Definite**	**Likely**	**Possible**	**Total**
Apple	19	13	23	55
Field Bean	11	0	3	14
Oilseed Rape	37	10	3	50
Strawberry	9	6	18	33

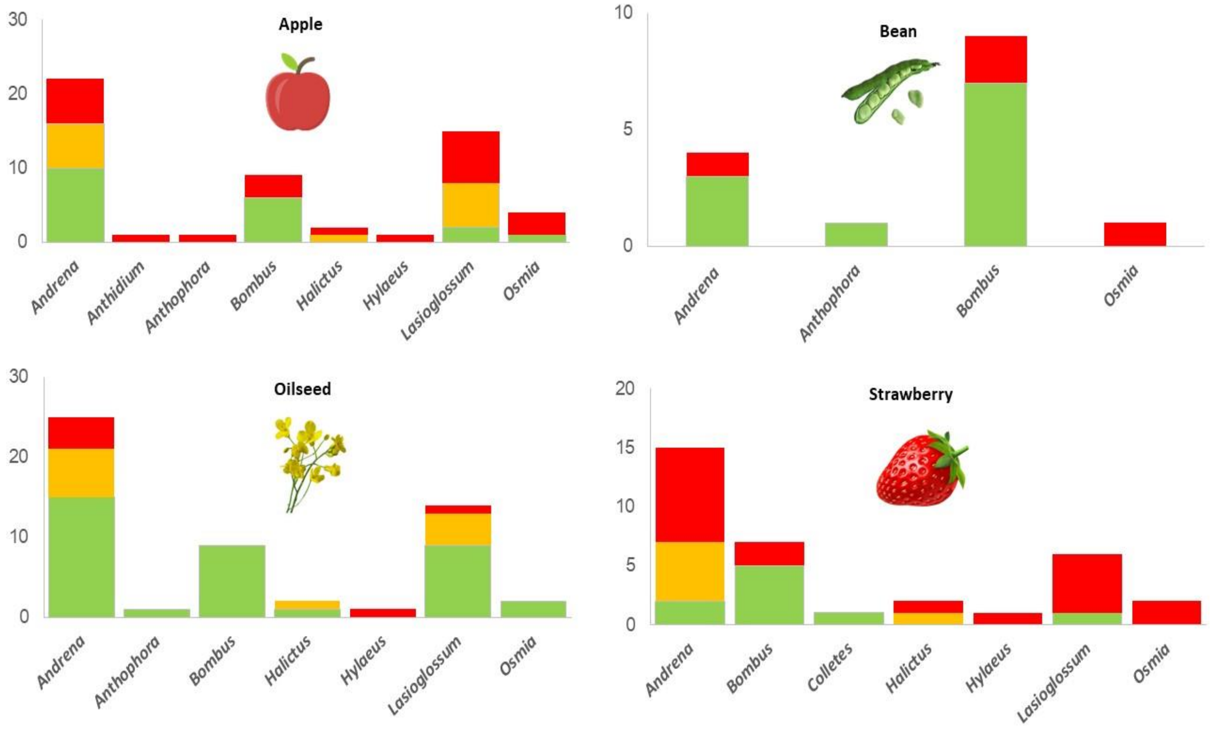


Figure 2.3: The number of bee species from each genus which were categorised as definite (green), likely (orange) or possible (red) flower visitors per crop.

2.4.3.1 Apple

All five British apple flower visitor studies recorded every bee to species level. *Andrena* were the most speciose genus of flower visitor, both overall (n = 21) and in the definite flower visitor category (n = 10). *Bombus* species were the next most commonly represented genus in the latter category (n = 6), but were less frequent overall (n = 9) than *Lasioglossum* species (n = 16). Within the definite flower visitor category 80% of flower visits were attributed to eight species (four *Andrena* and four *Bombus*), only half of which were recorded in all studies. Most likely and possible flower visitors were *Andrena* or *Lasioglossum* species.

2.4.3.2 Bean

Three of the five British bean flower visitor studies recorded all bee to species level, the remainder only recorded *Bombus* to species, which was both the most common genus overall (n = 9) and in the definite flower visitor category (n = 7). Three short-tongued *Andrena* sp. were identified as definite flower visitors, but all were recorded as very low numbers of flower visits (≤ 10). Four *Bombus* species and *Anthophora plumipes* accounted for 95% of all visits recorded in British flower visitation studies. However, all the *A. plumipes* records derived from one older study (Bond & Kirby 1999) carried out at a single site. The four *Bombus* were the only species recorded in four or more studies. No species met the criteria for the likely flower visitor category. The possible flower visitor category included two *Bombus* and one *Osmia* species.

2.4.3.3 Oilseed

Six of the nine British oilseed flower visitor studies recorded bees to species level, but only two included quantitative data on all bee species. *Andrena* was the most speciose genus of bee, both overall (n = 24) and within the definite flower visitor category (n = 15). *Bombus* and *Lasioglossum* species were equally represented in the definite flower visitor category (n = 9), but *Lasioglossum* were more frequent overall (n = 12). Within the definite flower visitor category 80% of recorded flower visits were attributed to six species (three *Andrena* and three *Bombus*), only two of which were recorded in all nine studies, with the remainder only recorded in between five and eight studies, despite all being large *Andrena* or *Bombus* species, generally identified and quantified in all field studies. The likely and possible visitor categories were entirely comprised of *Andrena* or *Halictidae* species, two of which are oligolectic on *Brassicaceae*.

2.4.3.4 Strawberry

Two British strawberry flower visitor studies recorded all bees to species level. The remaining three only recorded a group of large *Andrena* and *Bombus* to species. *Bombus* species were the most common genus of bee within the definite flower visitor category (n = 5), and the second most frequent genus overall (n = 7), with *Andrena* species being the most prevalent genus across all categories (n = 14). Within the definite flower visitor category 80% of recorded flower visits were attributed to just two *Bombus* species, which along with two other *Bombus*, were the only species recorded in more than two studies. The likely visitor category was almost exclusively represented by *Andrena* species. The possible visitor category was largely comprised of solitary bees from five different genera.

Table 2.3a: List of bee species identified as potential pollinators of apple, including flower visitor category (definite, likely or possible), conservation status (if applicable), type of study recorded in (British flower visitor, British pan trap, European flower visitor), number of visits recorded (V) or abundance sampled (A), and number of studies (S) recorded in. Conservation status: Na = Notable A; Nb = Notable B; RB1 = Endangered; RDB2 = Vulnerable; RDB3 = Rare; S41 = Priority Species

			British Flower Visitor		**British Pan Trap**		**Europe Flower Visitor**	
Species	**Category**	**Conservation Status**	**V**	**S**	**A**	**S**	**V**	**S**
Andrena nigroaenea	Definite	-	172	3	37	2	33	2
Bombus terrestris agg.	Definite	-	113	5	4	1	836	10
Andrena haemorrhoa	Definite	-	96	5	67	1	354	10
Bombus lapidaries	Definite	-	59	5	5	1	242	9
Andrena cineraria	Definite	-	41	3	20	1	33	6
Andrena nitida	Definite	-	35	5	29	1	27	8
Andrena scotica	Definite	-	24	3	5	2	66	4
Bombus pascuorum	Definite	-	20	4	2	1	160	10
Andrena dorsata	Definite	-	14	1	18	1	38	6
Bombus hortorum	Definite	-	10	4	4	1	21	5
Bombus pratorum	Definite	-	10	5	4	1	41	6
Bombus hypnorum	Definite	-	9	5	1	1	29	5
Andrena fulva	Definite	-	5	1	-	-	47	6
Lasioglossum calceatum	Definite	-	4	1	11	2	64	6
Osmia bicornis	Definite	-	4	3	5	1	76	8
Andrena flavipes	Definite	-	2	2	262	2	246	8
Andrena chrysosceles	Definite	-	1	1	42	1	36	3
Andrena minutula	Definite	-	1	1	44	1	27	4

Species	**Category**	**Conservation Status**	**British Flower Visitor**		**British Pan Trap**		**Europe Flower Visitor**	
			V	**S**	**A**	**S**	**V**	**S**
Lasioglossum pauxillum	Definite	Na	1	1	129	1	29	3
Halictus tumulorum	Likely	-	-	-	22	1	33	3
Lasioglossum malachurum	Likely	Nb	-	-	192	2	15	3
Andrena bicolor	Likely	-	-	-	2	1	7	3
Lasioglossum morio	Likely	-	-	-	105	1	7	3
Andrena helvola	Likely	-	-	-	5	1	6	3
Lasioglossum fulvicorne	Likely	-	-	-	1	1	6	3
Lasioglossum punctatissimum	Likely	-	-	-	1	1	5	2
Andrena gravida	Likely	RDB1	-	-	1	1	2	2
Andrena labiate	Likely	Na	-	-	2	1	2	1
Andrena trimmerana	Likely	Nb	-	-	1	1	1	1
Lasioglossum leucopus	Likely	-	-	-	3	1	1	1
Lasioglossum parvulum	Likely	-	-	-	2	1	1	1
Andrena subopaca	Likely	-	1	1	1	1	-	-
Andrena angustior	Possible	-	-	-	4	1	-	-
Andrena fucata	Possible	-	-	-	10	2	-	-
Andrena semilaevis	Possible	-	-	-	1	1	-	-
Bombus humilis	Possible	-	-	-	1	1	-	-
Halictus rubicundus	Possible	-	-	-	2	1	-	-
Lasioglossum albipes	Possible	-	-	-	6	1	-	-
Lasioglossum minutissimum	Possible	-	-	-	89	2	-	-
Lasioglossum smeathmanellum	Possible	-	-	-	1	1	-	-
Lasioglossum villosulum	Possible	-	-	-	1	1	-	-
Andrena varians	Possible	Nb	-	-	-	-	65	3

Species	Category	Conservation Status	British Flower Visitor		British Pan Trap		Europe Flower Visitor	
			V	S	A	S	V	S
Lasioglossum sexstrigatum	Possible	-	-	-	-	-	50	1
Anthopora plumipes	Possible	-	-	-	-	-	37	6
Osmia bicolor	Possible	Nb	-	-	-	-	14	3
Bombus sylvarum	Possible	Nb, S41	-	-	-	-	8	2
Hylaeus communis	Possible	-	-	-	-	-	8	1
Lasioglossum zonulum	Possible	-	-	-	-	-	5	3
Bombus jonellus	Possible	-	-	-	-	-	2	1
Lasioglossum lativentre	Possible	-	-	-	-	-	2	2
Osmia aurulenta	Possible	-	-	-	-	-	2	2
Andrena barbilabris	Possible	-	-	-	-	-	1	1
Anthidium manicatum	Possible	-	-	-	-	-	1	1
Lasioglossum leucozonium	Possible	-	-	-	-	-	1	1
Osmia caerulescens	Possible	-	-	-	-	-	1	1

Table 2.3b: List of bee species identified as potential pollinators of bean, including flower visitor category (definite, likely or possible), conservation status (if applicable), type of study recorded in (British flower visitor, British pan trap, European flower visitor), number of visits recorded (V) or abundance sampled (A), and number of studies (S) recorded in.

			British Flower Visitor		**British Pan Trap**		**Europe Flower Visitor**	
Species	**Category**	**Conservation Status**	**V**	**S**	**A**	**S**	**V**	**S**
Bombus hortorum	Definite	-	1379	5	37	2	120	2
Bombus pascuorum	Definite	-	1184	5	3	1	42	2
Anthophora plumipes	Definite	-	618	1	-	-	-	-
Bombus terrestris agg.	Definite	-	411	5	58	3	284	2
Bombus lapidaries	Definite	-	207	4	33	3	66	2
Andrena wilkella	Definite	-	10	2	9	2	-	-
Bombus ruderatus	Definite	Nb, S41	15	2	-	-	?	1
Bombus pratorum	Definite	-	8	2	4	2	7	1
Bombus hypnorum	Definite	-	5	1	2	1	-	-
Andrena haemorrhoa	Definite	-	2	1	26	2	-	-
Andrena labialis	Definite	-	2	1	1	1	-	-
Bombus ruderarius	Possible	S41	-	-	1	1	-	-
Osmia bicolor	Possible	Nb	-	-	1	1	-	-
Bombus sylvarum	Possible	Nb, S41	-	-	-	-	12	1

Table 2.3c: List of bee species identified as potential pollinators of oilseed, including flower visitor category (definite, likely or possible), conservation status (if applicable), type of study recorded in (British flower visitor, British pan trap, European flower visitor), number of visits recorded (V) or abundance sampled (A), and number of studies (S) recorded in.

			British Flower Visitor		**British Pan Trap**		**Europe Flower Visitor**	
Species	**Category**	**Conservation Status**	**V**	**S**	**A**	**S**	**V**	**S**
Andrena cineraria	Definite	-	685	6	3	3	68	5
Bombus lapidaries	Definite	-	572	8	48	3	259	6
Bombus terrestris agg.	Definite	-	496	8	118	3	265	6
Andrena scotica	Definite	-	229	5	7	2	3	2
Andrena nitida	Definite	-	211	6	18	2	22	5
Andrena nigroaenea	Definite	-	204	7	38	5	35	4
Andrena haemorrhoa	Definite	-	171	8	39	4	148	5
Bombus pratorum	Definite	-	54	4	44	3	11	4
Bombus pascuorum	Definite	-	51	7	35	3	54	5
Andrena fulva	Definite	-	51	6	19	3	13	3
Bombus hortorum	Definite	-	37	4	116	3	15	3
Andrena dorsata	Definite	-	31	5	2	2	3	2
Bombus hypnorum	Definite	-	27	4	-	-	1	1
Andrena chrysosceles	Definite	-	26	5	17	3	54	5
Andrena bicolor	Definite	-	15	4	39	4	6	3
Andrena flavipes	Definite	-	13	6	4	3	48	4
Osmia bicornis	Definite	-	7	3	-	-	23	3
Lasioglossum calceatum	Definite	-	4	2	12	4	11	4

Species	Category	Conservation Status	British Flower Visitor		British Pan Trap		Europe Flower Visitor	
			V	S	A	S	V	S
Lasioglossum pauxillum	Definite	Na	4	3	1	1	43	3
Andrena subopaca	Definite	-	3	2	-	-	5	2
Bombus jonellus	Definite	-	3	2	5	1	-	-
Lasioglossum malachurum	Definite	Nb	3	2	28	3	20	3
Lasioglossum morio	Definite	-	3	3	1	1	9	3
Osmia bicolor	Definite	Nb	3	2	1	1	46	2
Andrena helvola	Definite	-	2	2	-	-	18	4
Andrena labiate	Definite	Na	2	2	-	-	3	1
Bombus muscorum	Definite	S41	2	1	1	1	-	-
Lasioglossum fulvicorne	Definite	-	2	2	2	2	15	2
Lasioglossum parvulum	Definite	-	2	2	-	-	2	1
Lasioglossum pauperatum	Definite	RDB3	2	1	-	-	-	-
Lasioglossum puncticolle	Definite	Nb	2	2	-	-	1	1
Andrena fucata	Definite	-	1	1	-	-	4	2
Andrena minutula	Definite	-	1	1	9	2	21	3
Anthophora plumipes	Definite	-	1	1	1	1	6	2
Bombus soroeensis	Definite	-	1	1	-	-	3	1
Halictus tumulorum	Definite	-	1	1	-	-	16	2
Lasioglossum xanthopus	Definite	Nb	1	1	2	1	51	3
Andrena angustior	Likely	-	1	1	-	-	-	-
Andrena congruens	Likely	Na	1	1	-	-	-	-
Andrena nigrospina	Likely	-	1	1	-	-	-	-
Andrena niveata	Likely	RDB2	1	1	-	-	-	-

Species	Category	Conservation Status	British Flower Visitor		British Pan Trap		Europe Flower Visitor	
			V	S	A	S	V	S
Andrena synadelpha	Likely	-	1	1	-	-	-	-
Andrena tibialis	Likely	Na	-	-	1	1	3	1
Halictus rubicundus	Likely	-	1	1	1	1	-	-
Lasioglossum cupromicans	Likely	-	1	1	-	-	-	-
Lasioglossum leucopus	Likely	-	1	1	-	-	-	-
Lasioglossum zonulum	Likely	-	1	1	-	-	-	-
Andrena semilaevis	Possible	-	-	-	5	1	-	-
Andrena gravida	Possible	RDB1	-	-	-	-	7	3
Andrena minutuloides	Possible	Na	-	-	-	-	1	1

Table 2.3d: List of bee species identified as potential pollinators of strawberry, including flower visitor category (definite, likely or possible), conservation status (if applicable), type of study recorded in (British flower visitor, British pan trap, European flower visitor), number of visits recorded (V) or abundance sampled (A), and number of studies (S) recorded in.

			British Flower Visitor		British Pan Trap		Europe Flower Visitor	
Species	**Category**	**Conservation Status**	**V**	**S**	**A**	**S**	**V**	**S**
Bombus terrestris agg.	Definite	-	2562	4	35	1	315	4
Bombus lapidaries	Definite	-	891	4	57	1	154	4
Bombus pratorum	Definite	-	166	4	6	1	2	2
Bombus pascuorum	Definite	-	97	4	-	-	7	2
Bombus hypnorum	Definite	-	23	2	1	1	2	1
Andrena haemorrhoa	Definite	-	12	1	20	1	10	2
Colletes daviesanus	Definite	-	7	1	-	-	-	-
Andrena chrysosceles	Definite	-	1	1	8	1	19	2
Lasioglossum calceatum	Definite	-	1	1	13	1	4	1
Andrena nigroaenea	Likely	-	-	-	9	1	19	2
Andrena scotica	Likely	-	-	-	13	1	10	1
Halictus rubicundus	Likely	-	-	-	2	1	5	1
Andrena cineraria	Likely	-	-	-	9	1	2	1
Andrena minutula	Likely	-	-	-	4	1	1	1
Andrena bicolor	Likely	-	1	1	1	1	-	-
Bombus hortorum	Possible	-	-	-	13	1	-	-
Bombus jonellus	Possible	-	-	-	3	1	-	-
Hylaeus hyalinatus	Possible	-	-	-	1	1	-	-
Lasioglossum cupromicans	Possible	-	-	-	4	1	-	-
Lasioglossum leucopus	Possible	-	-	-	3	1	-	-

Species	Category	Conservation Status	British Flower Visitor		British Pan Trap		Europe Flower Visitor	
			V	S	A	S	V	S
Lasioglossum villosulum	Possible	-	-	-	1	1	-	-
Osmia bicornis	Possible	-	-	-	-	-	117	5
Andrena subopaca	Possible	-	-	-	-	-	63	3
Andrena helvola	Possible	-	-	-	-	-	28	3
Andrena nitida	Possible	-	-	-	-	-	13	2
Halictus tumulorum	Possible	-	-	-	-	-	13	2
Andrena gravida	Possible	RDB1	-	-	-	-	6	3
Andrena flavipes	Possible	-	-	-	-	-	11	2
Lasioglossum fulvicorne	Possible	-	-	-	-	-	3	2
Andrena varians	Possible	-	-	-	-	-	2	1
Lasioglossum pauxillum	Possible	Na	-	-	-	-	2	1
Andrena fulva	Possible	-	-	-	-	-	1	1
Osmia bicolor	Possible	Nb	-	-	-	-	1	1

2.4.4 Dominant crop flower visitors

Twenty datasets were available to estimate the dominant flower visiting bee species to each crop (Table 2.4). Ten bee species were attributed with 80% of flower visits across the four crops (Figure 2.4). There were differences however in the number and composition of those species making up the 80% of flower visits on a per crop basis. Differences in crop communities were even more distinct when considering the entire suite of bee species included in the characterisation of each crops' total flower visiting community (Figure 2.3; Figure 2.4).

2.4.5 Contribution of wild bees and honey bees to crop flower visitation

Sixteen data sets (Table 2.4) were available to estimate the contribution of wild bees to crop flower visitation relative to honey bees. Wild bees were attributed with an average of between 63% and 83% of crop flower visits compared to honey bees ((Apple: wild bee visits = 68%; Bean: wild bee visits = 83%; Oilseed: wild bee visits = 63%; Strawberry: wild bee = 77%) Figure 2.5).

Table 2.4: Number of datasets per crop used to establish wild bee species attributed with 80% of flower visits (number used to compare the proportion of flower visits attributed to wild bees and honey bees in brackets).

Crop	**Number of Datasets**
Apple	5 (4)
Field Bean	5 (4)
Oilseed Rape	8 (6)
Strawberry	2 (2)

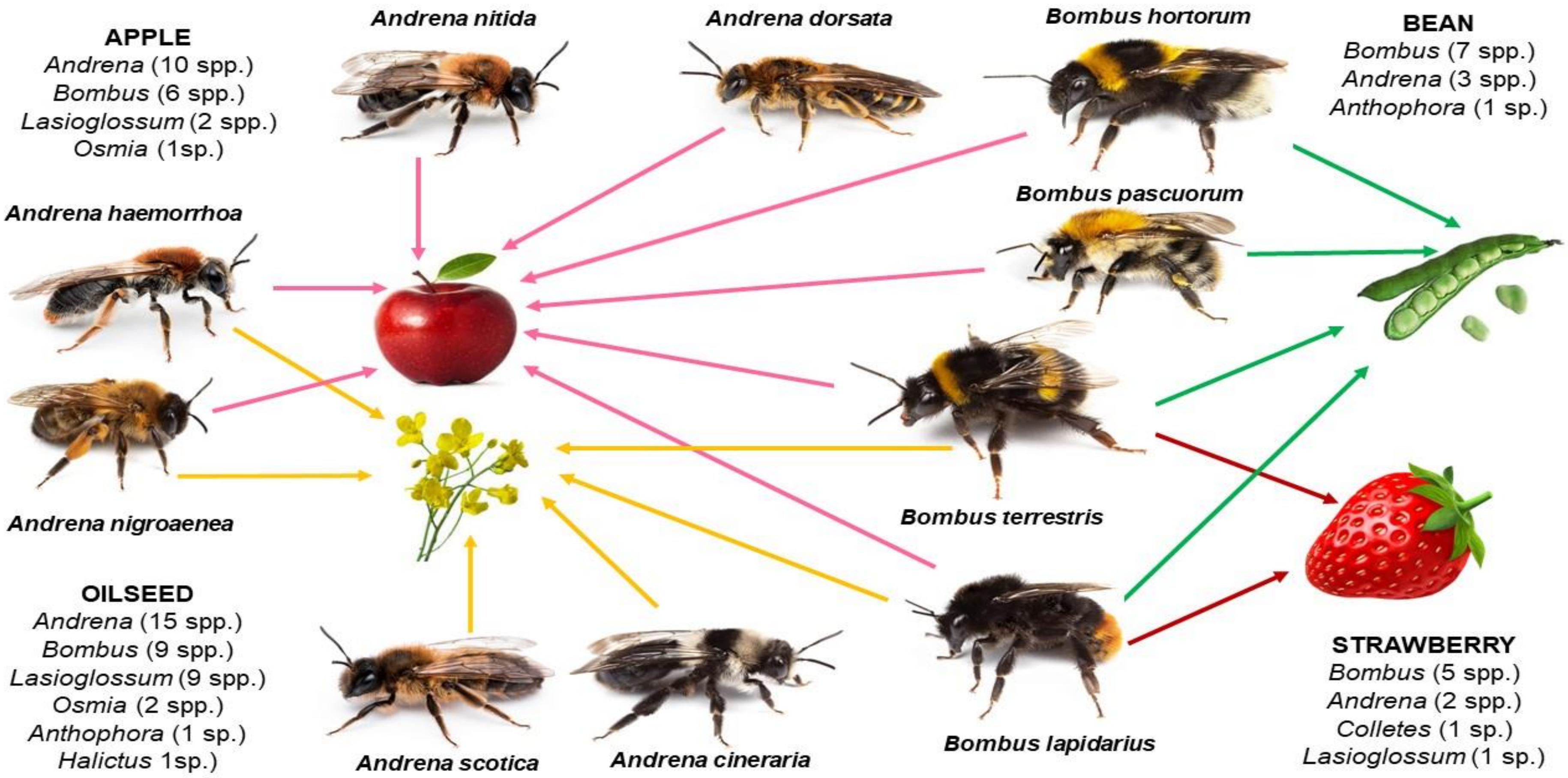


Figure 2.4: Dominant crop visiting bee species (attributed with ~80% of flower visits in field studies per crop) shown as photographs, with number of bee species in each genus that are 'definite' flower visitors for each crop. (Bee photographs courtesy of Nicolas J. Vereecken and Stephane De Greef).

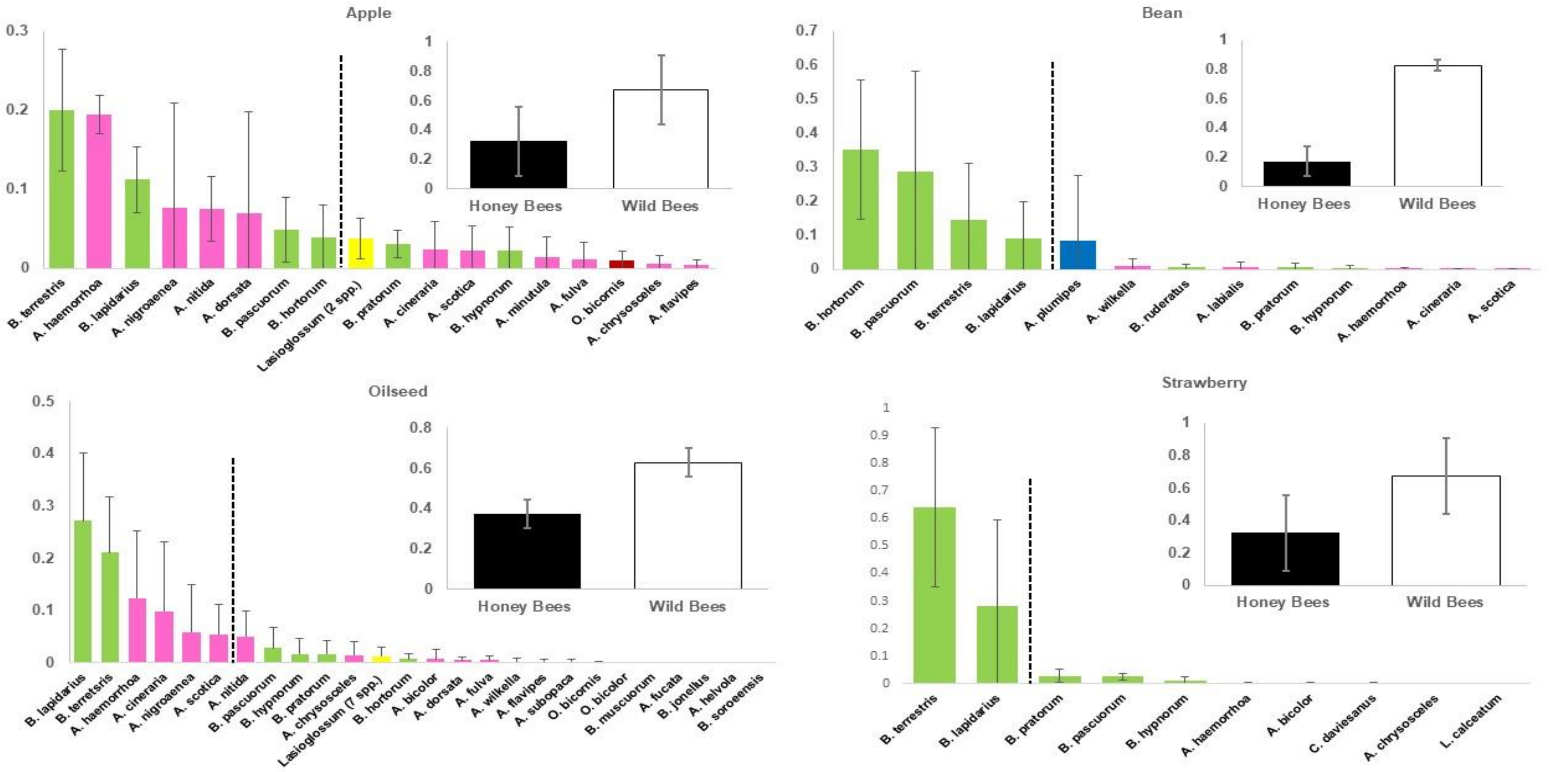


Figure 2.5: Bee species recorded visiting flowers in crop studies and mean proportion of flower visits they were attributed with across all studies. Error bars represent standard deviation. Point at which 80% of recorded flower visits was reached is marked with a dashed line. Inlay shows the mean proportion of crop flower visits attributed to all wild bee species colletively compared to those attributed to honey bees. Bars are coloured to represent different genera (Pink = *Andrena*, Blue = *Anthophora*, Green = *Bombus*, Yellow = *Lasioglossum*, Red = *Osmia*).

2.5 Discussion

2.5.1. Crop pollinator species

This study is the one of the first to evaluate the entire wild bee pollinator community of multiple crops on a national basis and can be used as a model approach for other countries, crops and pollinators. With the identification of bee species important for pollinating crops we build the basis to more sustainably manage pollination services by facilitating crop specific management aimed at both key pollinating taxa (Garratt et al. 2014a) and 'insurance' species (Yachi & Loreau 1999) which can supplement pollination services when dominant species are performing suboptimal (Fijen et al. 2018). Whilst in accordance with other studies (Rader et al. 2012; Kleijn et al. 2015) our results indicated that a small proportion of common, generalist bee species make the majority of crop flower visits, we show that many more species, including rare and specialist ones, also visit crop flowers. Our species list closely correlates with a previous extensive survey of bee species in farmland (Wood, Holland & Goulson 2016a) and together they indicate that at least 25% of the British bee fauna may be potential crop pollinators. As such current agri-environment schemes, which have predominantly been developed and evaluated based upon the ecological needs of bumblebee species, are unlikely to be optimally designed to support species rich bee pollinator communities (Wood, Holland & Goulson 2015), especialy as just 12 bumblebee species (5% of all bee species) were identified as potential crop pollinators in our study.

Management aimed at a small proportion of dominant species (Kleijn et al. 2015) is unlikely to promote stable and resilient pollination services at large temporal or spatial scales (Fijen et al. 2018; Winfree et al. 2018), or in the face of accelerating rates of environmental changes (Oliver et al. 2015a). A substantial surplus of bee species in crop pollinator communities can mitigate against further declines in pollination services due to ongoing climatic and land use changes (Nayak et al. 2015; Oliver et al. 2015b). Furthermore, substantial evidence indicates that biodiverse pollinator communities not only accrue benefits for crop yield and quality, but also for stability of production (Kremen, Williams & Thorp 2002; Hoehn et al. 2008; Garibaldi et al. 2011a; Rader et al. 2012; Senapathi et al. 2021), due to considerable spatio-temporal species turnover at both the field and landscape scale (Martins et al. 2018; Winfree et al. 2018). High inter-annual variations and pollinator limitations in agricultural crops represent significant threats to future food security (Garibaldi et al. 2011b; Holland et al. 2020), but these can be mitigated by practices to conserve and augment wild bee pollinators (Reilly et al. 2020).

Notably our results also support a growing view that the contribution of wild bee species to crop flower visitation may be even greater than previously thought (Ollerton 2017). Contrary to previous estimates that wild bees make a similar overall contribution to honey bees (Kleijn et al. 2015), when considering the entire suite of flower visiting species, our results indicate that wild bees make on average between 63% and 83% of flower visits to our target crops. Historically honey bees have been attributed as the most significant pollinators of most agricultural crops (Morse 1991; Carreck & Williams 1998). However, an increasing body of research has demonstrated that they are not the most effective pollinators of many crops (Klein et al. 2007 and references therein) and that their contribution to crop pollination has previously been overestimated (Aizen & Harder 2009; Breeze et al. 2014a). As such our study further highlights the need for agricultural management aimed at crop pollinators to target a more significant proportion of the wild bee fauna than at present (Wood, Holland & Goulson 2015, 2016a; Gresty et al. 2018).

Establishing a list of currently important, but also potentially important crop pollinators, is necessary to help target monitoring and conservation (Carvell et al. 2017). Our results also support prior evidence of distinct differences in individual crop pollinator communities (Garratt et al. 2014a) and of a link between trait matching of bee species and crop flowers for pollination service (Garibaldi et al. 2015). For example, whilst the majority of field bean and strawberry flower visits were attributed to bumblebees, field bean was almost exclusively visited by two of the longest tongued bumblebee species in Britain, whereas strawberry crops were more commonly visited by two other bumblebee species, with relatively shorter tongues. Furthermore, we found evidence that strawberry flowers may also be visited by a number of short tongue solitary species. This is likely to be directly linked to associated differences in the floral morphology of both crops. Bean has narrow, tubular flowers with deep nectaries that generally only long-tongued species can access (Breeze, Roberts & Potts 2012). Conversely strawberry has shallow, open flowers with high nectar accessibility (Garibaldi et al. 2015) that can be effectively pollinated by a range of short-tongued solitary bee species (Bansch et al. 2021).

Bombus species were also recorded visiting apple and oilseed rape. However, due to their low abundance in early spring during apple flowering (Martins et al. 2015), and lower rate of pollen transfer when visiting oilseed flowers (Woodcock et al. 2013) they are less important pollinators of these crops compared to some solitary species (Joshi et al. 2016). *Andrena* and *Lasioglossum* species were prevalent across both apple and oilseed flower visitor categories. *Andrena* are known to be highly efficient pollinators of both crops (Martins et al. 2015; Woodcock et al. 2013), especially apple (Russo et al. 2017). Most *Lasioglossum*, species however, generally emerge later than many *Andrena* species, and peak during oilseed flowering time, which tends to flower later and longer than apple. *Lasioglossum* are likely to be important pollinators of oilseed rape (Perrot et al. 2018; Catarino et al. 2019). Furthermore, we almost certainly significantly underestimated the diversity and abundance of *Lasioglossum* bees visiting oilseed rape, given that many studies did not include detailed quantitative data on this genus; which reflects the fact that *Halictidae* are rarely considered as a distinct pollinator group in crop pollination studies (Brandtm, Glenitz & Schroder 2017).

Our datasets also indicate that rare and specialist species may visit crop flowers when they are locally abundant or are especially attracted to crop flowers (MacLeod et al. 2020). Several rare species recorded in apple orchards are most common in south-east England, Britain's principal apple growing region, and bee species that are oligolectic on *Brassicaceae* were recorded in oilseed rape studies. Given that biodiversity benefits pollination (Dainese et al. 2019), strategies to support biodiverse crop communities may prove critical to sustain ecosystem service provision. Yet current agri-environment schemes options rarely consider rare species (Senapathi et al. 2015). There is however, a significant overlap in the floral resources used by common and rare crop pollinators (Sutter et al. 2017; MacLeod et al. 2020), and thus there are opportunities to promote both biodiversity and conservation in agricultural landscapes.

Our findings also offer an opportunity to anticipate potentially important future crop pollinators. For example, whilst a number of European crop flower visitors not presently recorded in British crop fields are currently geographically restricted, should they expand their range in the future, they could ameliorate the threat of ecological mismatches between current pollinators and crops due to climate change (Polce et al. 2013, 2014; Settele et al. 2016). Taken further, this information could be used to refine existing models of bee populations used to project pollinator populations at large spatial scales (e.g. Gardner et al. 2020), which can assist in larger scale planning of pollinator management.

Identifying specific bee crop pollinating species, as we have done here, can inform refinements to agri-environment schemes to promote more biodiverse communities in agricultural landscapes. For example, *Andrena* were the most speciose genus of bees identified across flower visitor categories in three of the four crops. Currently European agri-environment measures to boost pollinator populations have focused on the creation of flower-rich habitats, including wildflower buffer strips (Wratten et al. 2012). Yet evidence suggests these are primarily visited by bumblebees, with solitary bees preferring non-sown, wild plants (Wood et al. 2015; Wood, Holland & Goulson 2015). In apple orchards for example, early-flying *Andrena* species have been positively associated with dandelions (Taraxacum agg.) rather than sown species, which often bloom later than apple flowers (Campbell et al. 2017). Reduced mowing regimes in orchards, and other crop areas, particularly in early spring could boost *Andrena* numbers and hence pollination. Such interventions are also likely to benefit early flying *Lasioglossum,* many species of which are known be attracted to yellow flowers in the family *Asteraceae* (BWARS 2020b).

Osmia species have also been demonstrated as efficient pollinators of apple, oilseed and strawberry crops (Abel et al. 2003; Garratt et al. 2016; Horth & Campbell 2018), but as in this study, are frequently recorded in low numbers, likely due to a lack of suitable nesting and floral resources in agricultural landscapes for cavity nesting species (Blitzer et al. 2016; Image et al. 2022). Incorporating hedgerow species such as Dog Rose and Bramble, alongside, areas of old and dead wood, around crop areas would provide both forage and nesting resources (Else & Edwards 2018; Gresty et al. 2018) for these and other cavity nesting bees. Future management to support long-tongued solitary bees could benefit field bean pollination. *Anthophora plumipes*, for example, prefers to nest in vertical soil profiles (BWARS 2020c), which are not currently a common feature in agricultural landscapes.

2.5.2. Data constraints and limitations

There are caveats to using foraging ecology to identify potential bee pollinators, as done here and elsewhere (Ahrenfeldt et al. 2015). Firstly, there is a lack of published data for many bee species and others visit a wider range of flowers than can be realistically documented (Else & Edwards 2018). As such, determining the status of bee species as crop flower visitors requires field survey data for confirmation. Yet comprehensive crop pollinator data is currently lacking as sampling is irregular, and undertaken almost exclusively as part of bespoke research projects rather than systematic monitoring (Breeze et al. 2021). Furthermore, whilst census methods can provide information on floral associations, they require experienced surveyors to comprehensively record species richness (O'Connor et al. 2019). Across all four crops the only bees which were consistently identified to species level were large, conspicuous ones from the genera *Bombus* and *Andrena*. Small and inconspicuous species, particularly from the genus *Lasioglossum*, were often only extensively sampled in the pan trap surveys, and likely frequently missed during crop flower visit studies.

Additionally, whilst the visitation rate of dominant species is strongly correlated to pollination service delivery (Winfree et al. 2015; Fijen et al. 2018), the assumption here and elsewhere that quantitative visitation data alone can be used to infer pollination (Kleijn et al. 2015), neglects to factor in that flower visitation alone is not a perfect proxy for pollination (King et al. 2013; Senapathi et al. 2015; Ollerton 2017). Certain physiological and behavioural traits also influence pollination service delivery (Martins et al. 2015). Further detailed data and research is required before any definitive conclusions can be made about the contributions of individual bee species to crop pollination. Finally, all the species identified here as dominant crop pollinators are larger, relatively easily identifiable species. As such our results may not entirely accurately reflect the contribution of these species, but rather, at least in part, be an aretefact of the fact that they are more likely to be observed visiting flowers compared to smaller species, which are often missed during active survey methods (Berglund et al. 2019).

2.6 Conclusions

Given the importance of wild pollinators, and the detrimental impacts of conventional agriculture on their populations, it is unsurprising that the management of wild and managed pollinating insects is considered a critical step for future food security (Garibaldi et al. 2019; Kleijn et al. 2019; Reilly et al. 2020). Yet information on which species contribute to ecosystem service delivery has long been elusive (Kremen & Chaplin-Kramer 2007) despite its critical importance for both monitoring and conservation measures. Here we combine ecological and field data to provide a uniquely comprehensive overview of the crop pollinating bees of a single region, Great Britain. Whilst we have focused on Great Britain, a similar approach would be applicable across Europe and other crops, and could also be applied to non-bee species that have been identified as important crop pollinators (Rader et al. 2016).

Our research bolsters evidence that many wild bee species, including rare and specialised ones, may contribute to crop pollination (Klein et al. 2003; Sutter et al. 2017; Winfree et al., 2018; MacLeod et al. 2020); thus it can be argued that agri-environment scheme options should not focus solely on dominant crop pollinators. Future climatic changes threaten to further deplete already impoverished bee populations (Soroye et al. 2020) and create spatial mismatches between crops and their pollinators, which could exacerbate existing pollination deficits (Polce et al. 2014). To that end, the species identified as possible crop pollinators could represent an as yet untapped pollinator resource. Whilst some species may not currently visit crops due to ecological or environmental constraints, they could be assisted to expand by dedicated conservation measures in agricultural landscapes, allowing them to compensate for any declines in current crop pollinating species. Many such species are solitary, which presently benefit much less from agri-environment schemes than social species (Wood, Holland & Goulson, 2015, 2016a, 2016b; Gresty et al. 2018). As such land managers may need to re-evaluate existing pollinator management interventions and consider a broader range of species to safeguard the ecosystem service of crop pollination in an uncertain future.

Chapter 3: Inventorying and monitoring crop pollinating bees: Evaluating the effectiveness of common sampling methods

This chapter is a modified version of the following publication:

Hutchinson, L. A., Oliver, T. H., Breeze, T. D., O'Connor, R. S., Potts, S. G., Roberts, S. P. & Garratt, M. P. (2021). Inventorying and monitoring crop pollinating bees: Evaluating the effectiveness of common sampling methods. *Insect Conservation and Diversity*, 15, 299-311. https://doi.org/10.1111/ICAD.12557

Author contributions: Conceptualisation: LH, MG, TB, TO; study design: LH, MG, TB, TO; data curation: LH, MG, SP; formal analysis: LH; writing – original draft preparation: LH; writing – review and editing: all authors.

This chapter is based upon the above publication. The methodology and findings remain unchanged from the published version. However, some alterations have been made to the following version to improve clarity and readability of the thesis:

- Additional information and references have been added to the introduction and discussion sections.
- An additional section 'Data constraints and limitation' has been added at the end of the discussion.
- Some of the supplementary material from the published version has been incorporated into the main text, and has resulted in minor textual changes to the methods and results sections.
- Some small changes have been made throughout the chapter to correct minor textual errors in the published version.

3.1 Abstract

Wild bees provide a critical ecosystem service by pollinating globally important crops. Documented bee declines, notably in agricultural landscapes, therefore threaten future food security. Yet, evaluations of methods to inventory and monitor bees are rarely carried out in different crops or focus specifically upon crop pollinating species. We utilised standardized field datasets to elucidate differences in the capacity of transect walks, observation plots and pan traps to sample wild bee pollinator communities in four contrasting crops. Our results indicate that individual survey methods detect different components of crop pollinator communities, with guild (bumblebee or solitary bee) sampled being an important causal factor behind these differences. Transects detected half or less of the total potential pollinator community in three of our four study crops. Whilst transects were the most efficient method for sampling bumblebees, they often missed solitary species, which were most efficiently sampled by yellow pan traps. Whilst transects alone are sufficient in crops pollinated predominantly by bumblebees, pan traps, and potentially observation plots, may be an important addition in some crops where smaller solitary bee species are potentially important pollinators. Our results indicate that the most efficient methods to sample bee species in agricultural landscapes are dependent upon crop type and pollinator community composition. We use our findings to make a set of recommendations on the inventorying and monitoring of bee pollinator crop communities that can inform regional and national monitoring programmes.

3.2 Introduction

Wild bees provide a critical ecosystem service by pollinating the majority of global food crops that are essential for human health (Potts et al. 2016). Furthermore, agriculture is becoming increasingly pollinator dependent due to a growing, global population driving increased demand for entomophilous crops (Aizen et al. 2008; Science for Environment Policy 2020). Diverse assemblages of wild bee species have been shown to increase yield quantity, quality and stability of insect-pollinated crops (Bartomeus et al. 2014; Garibaldi et al. 2011a). Furthermore, it is now well established that, in many parts of the world, this pollination service cannot be reliably replaced by honeybees (Garibaldi et al. 2013; Breeze et al. 2014a). As such documented declines in wild bees (Biesmeijer et al. 2006; Powney et al. 2019), notably in agricultural landscapes (Potts et al. 2010), and evidence of insufficient pollination limiting crop production (Garratt et al. 2014a; Holland et al. 2020), raise serious concerns about future food security (Reilly et al. 2020). There are now growing calls for the urgent implementation of long-term schemes to systematically inventory and monitor crop pollinator populations (Potts et al. 2021; Woodard et al. 2021).

Despite the protection of pollinators rising as a policy priority (Breeze et al. 2021; Gonzalez et al. 2020), response actions have failed to keep pace with the threats facing the services they provide (Potts et al. 2016). Currently, our understanding of trends in wild pollinator populations is limited, being primarily based upon ad-hoc records (Powney et al. 2019). These records are rarely collected in intensively cultivated agricultural landscapes (Garratt et al. 2019), meaning the status of pollinating insects in crop areas is a particular evidence gap (Scherber et al. 2019). Additionally, emerging monitoring schemes in agricultural landscapes are currently focused upon the entire species community (Carvell et al. 2017; O'Connor et al. 2019), rather than specifically upon crop pollinators. Growing evidence suggests that individual crops have different pollinator communities (Hutchinson et al. 2021; Kleijn et al. 2015). The identification and monitoring of crop flower visitors in agricultural settings is essential to inform management that can improve and sustain crop production (Garratt et al. 2016; Hutchinson et al. 2021).

Whilst progress has been made in identifying the specific bee pollinators of individual crops (Hutchinson et al. 2021), the focus has been primarily upon common and dominant flower visitors (Kleijn et al. 2015), which also tend to be the main beneficiaries of agri-environment measures (Senapathi et al. 2015). Yet diverse communities, which can include rare species, are important for sustainable crop pollination service, due to species turnover (Winfree et al. 2018). Furthermore, supporting biodiverse crop pollinator communities is imperative to maintain ecosystem service resilience in the face of substantial predicted environmental changes (Oliver et al. 2015a). A significant obstacle for establishing schemes to survey and monitor pollinating insects has been concern over the cost of such an endeavour (Science for Environment Policy 2020; Senapathi et al. 2015). Recent evidence, however, demonstrates that even the most expensive professional-run monitoring schemes are cost-effective when compared to the economic consequences of further pollinator losses (Breeze et al. 2021), and that farmers, agronomists and citizen scientists are able and willing to implement pollinator surveys (Garratt et al. 2019).

Two broad categories of methods exist to sample pollinators; active (observation plots, transect walks) and passive (e.g., pan traps, trap nests) (Westphal et al. 2008). Active methods can assess flower visitors and visitation rates (Garibaldi et al. 2019), but results are contingent upon recorder skill (Krahner et al. 2021). Passive methods do not provide information on floral associations (Westphal et al. 2008), but do not require much training to conduct in the field; although considerable expertise is needed to identify specimens in the laboratory. Whilst many studies have evaluated different sampling techniques, results can be conflicting, and may be contingent upon the study system being tested. For example, pollinator size and trap colour may influence the efficacy of different sampling methods (Krahner et al. 2021). Furthermore, assessments of sampling techniques are predominantly carried out in non-crop areas (McCravy 2018), or do not focus specifically on crop habitats, nor account for the impacts of crop type on results. Identifying the most appropriate survey methods for wild bees in agricultural settings is essential to ensure a representative sample of crop pollinator communities (Templ et al. 2019), support long-term monitoring of crop pollinators (Breeze et al. 2021) and to allow for localised assessments of pollination service to inform farm management (Garratt et al. 2019).

We evaluate the most commonly employed sampling methods (transects, observation plots, pan traps) to assess wild bees in European crops, focusing on four insect-pollinated crops that exhibit differences in morphology, growing conditions and pollinator community: apple – *Malus domestica*, field bean – *Vicia faba*, oilseed rape – *Brassica napus* and strawberry – *Fragaria x ananassa*.

We had four aims:

(i) Investigate the frequency with which passive and active methods are used to survey crop pollinators in the wider literature;

(ii) Using an established list of bee pollinators for each crop (Hutchinson et al. 2021), compare the abundance, richness and proportion of bee species detected by these sampling methods;

(iii) Compare the similarity of crop pollinator species communities sampled by active and passive methods, and evaluate to what degree body size and trap colour influences detection rates, and

(iv) Consider how this information could be used to inform protocols to effectively sample and monitor the bee communities of crops.

3.3 Methods

Analysis

All analyses were performed using RStudio version 3.4.2 (RStudio Team 2020). For generalised linear mixed models (glmer) and generalised linear models (glm) the relevant datasets were tested for overdispersion by generating qqplots, and either by running a DHARMa non-parametric dispersion test (Hartig 2020) or a generalised function overdispersion test from the AER package (Kleiber & Zeileis 2008). These identified overdispersion within all datasets, and so subsequently, all generalised linear mixed models and generalised linear models were run with a negative binomial error distribution using the ‘glmer.nb’ function from the ‘lme4’, v1.1–25 package (Bates et al. 2020) or the ‘glm.nb’ function from the ‘MASS’ package (Venables & Ripley 2002), respectively.

3.3.1 Crop bee community studies

We conducted a literature search to compile all available peer reviewed European studies, which were published between 2010 and 2019, and in which the wild bee community of one or more of our four focal crops was sampled. We confined our search to European countries only, as previous studies suggest all four crops are visited by a similar suite of species (Hutchinson et al. 2021), whereas elsewhere these crops are visited by different species (Kleijn et al. 2015). Additionally, wild bees are known to make an important contribution relative to honey bees in this region (Breeze et al. 2014a; Garibaldi et al. 2013; Hutchinson et al. 2021).

We limited our search to the last 10 full years of publications, to focus on the methods used to make recent assessments of bee crop communities. We performed four separate searches on Google Scholar and Web of Science using the key words ‘wild’, ‘bee’, ‘bees’, ‘pollination’, ‘pollinator’ and ‘pollinators’, without the use of operators, and preceded in turn by both the common and scientific names of our target crops; ‘apple’, ‘*Malus domestica’*, ‘bean’, ‘*Vicia faba’*, ‘oilseed’, ‘*Brassica napus’*, ‘strawberry’, ‘F*ragaria x ananassa’*. Studies using small numbers of ‘bait’ or phytometer plants were excluded from analysis, as we wanted to focus upon sampling protocols in real world crop field conditions.

Sampling methods were categorised according to the main types identified by Westphal et al. (2008) – observation plots (a fixed plot of flowers observed for a set time, and bees either visually identified and/or caught for laboratory identification), pan traps (coloured bowls filled with water, and placed at ground-level, or mounted at surrounding crop flower height, in order to trap bees for subsequent laboratory identifications), or transect walks (a fixed or variable corridor of flowering plants walked for a set distance and/or time, and bees either identified through visual observations, caught for laboratory identification, or a mixture of both approaches). Trap nests were excluded from analyses as they are restricted to sampling a small number of cavity nesting species and generally have low species coverage (Prendergast et al. 2020; Westphal et al. 2008).

3.3.2 Field data and crop pollinators

To evaluate and compare the most commonly used methods to sample bee communities of our focal crops we focused upon Great Britain, where wild bees have been demonstrated to make a significant contribution to crop pollination (Breeze et al. 2011; Hutchinson et al. 2021). We used datasets held by the University of Reading, UK. The first collection of datasets was from sites of all four focal crops and collated as part of the UK Insect Pollinators Initiative (IPI) (University of Reading 2018). Surveys were carried out by teams of researchers from the University of Reading and University of Leeds. All team members received training in catching insects and identifying broad taxonomic groups of pollinators to ensure all surveyors were well matched in terms of expertise and experience (Table 3.1: datasets 1.1a – 1.1d).

The second collection of datasets was from sites of bean and oilseed and collated as part of the European Union's Sixth Framework Integrated Project ALARM (Settele et al. 2005). Surveys were carried out by a hymenopterist and two field assistants from the University of Reading (Table 3.1: datasets 1.2a – 1.2d).

All bees were caught, where possible, during transect walks, for subsequent identification to species level, alongside pan trap specimens. In the IPI observation plots, only bumblebees and easily identifiable Andrenids were identified to species level. For the Alarm observation plots, species that could not be identified in the field were caught for identification. We chose our focal crops and datasets as a case study for investigating the relationships between methods, and their potential biases, as they were all conducted in crop fields, and so applicable in a real world agricultural context. They also allowed us to control for other influential factors such as floral diversity and recorder expertise, and their methodology reflected how these approaches are typically executed in the field.

Table 3.1: University of Reading crop studies used in analysis, including details on the dataset number, crop(s), project, sampling technique(s) carried out and methodology, number of days surveys were carried out for, and how specimens were identified and stored.

Dataset Number	Crop(s)	Project	Sampling Technique	Methodology	Identifications
1.1a	Apple, Bean, Oilseed, Strawberry	IPI	Observation Plots	Six defined plots of 50 x 50cm were observed for 10 - 15 minutes at 8 sites per crop. At each site 2 (apple) or 3 (bean, oilseed and strawberry) rounds of 6 observation plots were carried out.	Bees were identified on the wing. Only a select number of readily identifiable *Andrena* and *Bombus* were identified to species level. All other bees were identified to genus or guild (Bombus or solitary bee).
1.1b	Apple, Bean, Oilseed and Strawberry	IPI	Pan Traps	Six triplets of pan traps were left out either early in the morning and collected in the evening of the same day or for 24 hours at 8 sites per crop. Pan traps, were sprayed blue, white or yellow with UV fluorescent paint, filled with 100ml of water and detergent, and Each fixed to stake at the average height of crop flowers. At each site 2 (apple) or 3 (bean, oilseed and strawberry) rounds of pan traps were carried out.	All bees were identified to species level by Hymettus http://www.hymettus.org.uk/ Specimens are stored at the University of Reading.

Dataset Number	Crop(s)	Project	Sampling Technique	Methodology	Identifications
1.1c	Apple, Bean, Oilseed and Strawberry	IPI	Transect Walks	Six fixed 50m transect corridors were walked for 10 minutes at 8 sites per crop. At each site 2 (apple) or 3 (bean, oilseed and strawberry) rounds of 6 transect walks were carried out.	As above.
1.1d	Apple and Oilseed	IPI	Transect Walks	Six fixed 50m transect corridors were walked for 10 minutes at 8 (oilseed and 15 (apple) sites per crop. At each site 1 (apple) or 4 (oilseed) rounds of 3 transect walks were carried out.	As above
1.2a	Bean	ALARM	Transect Walks	Six fixed 150m x 4m transect were walked for 30 minutes at 10 sites. At each site 4 rounds of transect walks were carried out.	Specimens identified by surveyor – Stuart P.M. Roberts. Specimens are stored at the University of Reading.

Dataset Number	Crop(s)	Project	Sampling Technique	Methodology	Identifications
1.2b	Oilseed	ALARM	Observation Plots	Ten quadrats of 1 x 2 m were observed for 6 minutes at 4 sites. At each site 1 round of observation plots were carried out.	As above
1.2c	Bean	ALARM	Pan Traps	Two sets of three of pan traps were left out for 6 hours at 10 sites. Pan traps, were sprayed blue, white or yellow with UV-reflecting paint, and filled with 400ml of water plus a drop of detergent. Each triplet was fixed to stake and set at the average height of crop flowers. At each site 1 round of pan traps were carried out.	As above
1.2d	Oilseed	ALARM	Pan Traps	Five triplets of pan traps were left out for 48 hours at 4 sites. Pan traps, were sprayed blue, white or yellow with UV-reflecting paint, and filled with 400ml of water plus a drop of detergent. Each triplet was fixed to stake and set at the average height of crop flowers. At each site 1 round of pan traps were carried out.	As above

As we were specifically interested in the capacity of these three sampling methods to detect the bee pollinators of these crops, we used an existing list of bee species known to definitely, or likely visit (recorded in British pan traps and recorded visiting these crops elsewhere in Europe), each of the four crops in the United Kingdom. This is referred to hereon as our 'reference list' of crop pollinators (Hutchinson et al. 2021). Only species which met these criteria were included in analyses. All other species which were recorded in our datasets were considered non-pollinators, and excluded from analyses.

For subsequent analyses, bees were split into two guilds – bumblebees and solitary bees. We use the term 'solitary' to refer to all non-*Bombus* species of bee, however, it should be noted that many species commonly included in such categorisation are in fact primitively eusocial (Holzschuh et al. 2016).

3.3.3 Abundance of bumblebees and solitary bees detected by different sampling methods

To establish if the three sampling methods detected similar numbers of the two main guilds of wild bee pollinators – bumblebees and solitary bees – in crop areas, we used datasets for three crops where observation plots, transect walks and pan traps were carried out simultaneously (datasets 1.1a–1.1c). Bean was excluded, from this analysis, however, due to it being almost exclusively pollinated by *Bombus* spp. (Hutchinson et al. 2021). To prepare the data for analysis, we calculated the abundance of each guild sampled per site (n = 8) and per round of sampling (apple: n = 2; oilseed and strawberry: n = 3) for each of the three sampling methods. We fitted generalised linear mixed models with a negative binomial error distribution (glmer.nb function) and analysed the effect of both sampling method and guild, and their interaction, on the abundance of bees detected in each crop. Site and sampling round were included as random effects. The 'multcomp' package (v1.4–17, Hothorn et al. 2012) was then used to conduct multiple comparisons with Tukey tests.

3.3.4 Abundance and species richness of bee genera detected by different sampling methods

To establish if the three main sampling methods detected similar numbers of individual bee genera, we first used the data described above (datasets 1.1a–1.1c), but this time included the data for bean. We calculated the mean abundance and richness of crop pollinating bee species per site (n = 8) for the five most common crop pollinator genera as identified by Hutchinson et al. (2021); *Andrena*, *Bombus*, *Halictus*, *Lasioglossum* and *Osmia*, and abundance of unidentified solitary bee for transect walks. For observation plots, we only calculated mean abundance as a limited selection of bees were identified to species.

Furthermore, we also estimated the mean abundance and species richness of bees that would be sampled by pan traps (dataset 1.1b) if they were carried out for an equivalent time period to that of transect walks. This was done to account for the fact that pan traps are commonly left out at sites for a full day, whilst total transect walk time per site in most crop studies is generally much less than this. Therefore, pan traps may sample more individuals of different bee genera simply due to their much greater sampling time, and not necessarily because they are a more comprehensive sampling method. To do this we repeated the analyses described above, but this time divided all of the pan trap raw data by eight before calculating the mean to approximate the number of bees caught in a two-to-three-hour time period, which was equivalent to total transect walk time at each crop site.

Additionally, to further consider how crop type and pollinator community may influence sampling detectability during active and passive methods we used two additional datasets (datasets 1.2a–1.2d) carried out by a hymenopterist on the two crops with the most contrasting pollinator communities – bean, which is almost exclusively bumblebee pollinated, and oilseed which is pollinated by a wide variety of bumblebee and solitary bee species (Hutchinson et al. 2021). Again, we calculated the mean abundance and richness of crop pollinating bee species per site (bean: n = 10; oilseed: n = 4) for the most common crop pollinator genera as identified by Hutchinson et al. (2021). We then compared the mean abundance and species richness of bee genera sampled by active methods (bean – transect walks; oilseed – observation plots) with that sampled by pan traps in the same crop sites.

For all the above datasets (datasets 1.1a–1.1c & 1.2a–1.2d), we also calculated the total number of every bee species sampled by each survey method to provide an overview of whether or not detectability differed amongst individual species within each genus.

3.3.5 *Proportion of the pollinator species pool sampled by pan traps and transect walks.*

To assess the proportion of the total crop pollinator community sampled by different methods we first used the IPI datasets (datasets 1.1a–1.1c), but excluded the observation plot data due to the lack of species-level identifications. We calculated the total number of bee species identified as pollinators that were sampled across eight sites per crop for both methods (transect walks and pan traps). We then calculated the total number of those species sampled by each method individually.

Additionally, we calculated the percentage of the two main guilds of pollinators – bumblebees and solitary bees – that were identified to species levels on transect walks (pan traps were not considered as they provided species level identification for all but eight specimens of solitary bee in apple surveys). For apple and oilseed, there was an additional year of sampling for comparison (dataset 1.1d) in which a further 15 (apple) and eight (oilseed) sites were sampled.

Finally, we carried out all analyses described above for datasets 1.2a–1.2d for the additional bean sites (n = 10) and oilseed sites (n = 4). In this case, we compared the proportion of the pollinator community sampled by transects walks (bean) and observation plots (oilseed) to that of pan traps, and calculated the percentage of both bee guilds identified to species level.

3.3.6 Pollinator community comparisons between pan traps and transect walks

We assessed the degree of dissimilarity between the bee pollinator communities sampled by passive (pan trap) and active methods (transect walks) in datasets 1.1b–1.1c using permutational multivariate analysis of variance (PERMANOVA) (R: vegan: adonis v2.5–6, Oksanen et al. 2015) against random permutations (=999 for each crop dataset) of the original dataset as per the methodology described in O'Connor et al. (2019). PERMANOVA is a non-parametric statistical method that compares groups of objects and tests the null hypothesis that there are no differences in a set of variables among objects from different groups (Anderson 2014; CSCU n.d.) i.e., in this case the richness and abundances of different bee species sampled by transects walks and pan traps. We did not use datasets 1.1a and 1.1d for this analysis due to the lack of species level data in the observation plots, and because no simultaneous pan trapping was carried out for the second year of transect walks. We also excluded datasets 1.2a–1.2d due to the relatively few oilseed sites (n = 4) and because the bean dataset largely comprised of bumblebee pollinators only. Results were visualised using multidimensional scaling (NMDS) based on Bray–Curtis dissimilarity (R: vegan: MetaMDS; Oksanen et al., 2015). The similarity of the pollinator communities sampled by pan traps and transect walks was then compared using a visual assessment of the NMDS plots.

Additionally, SIMPER analyses were used to determine which species contributed most to the observed differences in the pollinator communities sampled by pan traps and transect walks in each crop. The SIMPER function provides the contribution of individual species to the overall Bray-Curtis dissimilarity by performing pairwise comparisons of groups of sampling units, and providing the average percentage contribution of each species to the average overall Bray-Curtis dissimilarity (Rdrr.io 2019).

3.3.7 Body size and abundance of bee species sampled by active and passive methods

To explore whether the dissimilarity in the pollinator communities sampled by pan traps and transect walks was related to bee body size we again use datasets 1.1b and 1.1c. A generalised linear model with a negative binomial distribution was used to explore the relationship between the abundance of bees sampled (response variable) and crop type (all crops), survey type (transect walks and pan traps) and bee body size, based upon intertegular distance (ITD; mm) measurements (obtained as per the methodology described in Greenleaf et al. 2007) in a traits database (compiled by Stuart Roberts for the EU-FP6 ALARM-project). All three explanatory variables and their two- and three-way interactions were included in the model. We use overall AIC as our criterion for model selection. For *Bombus*, we used the measurements for workers, rather than queens. It should be noted, however, that some *Bombus* records in our datasets will likely represent queens and thus our results for the relationship between body size and abundance of bees sampled will be a conservative estimate.

3.3.8 Effects of trap colour on bee guilds and species sampled by pan traps

To compare the catch rates of different colour pan traps when sampling bee crop pollinators, we first used dataset 1.1b. To establish if the three pan colours caught similar numbers of the two main guilds of wild bee pollinators – bumblebees and solitary bees – across crop sites, we fitted generalised linear mixed models with a negative binomial error distribution and conducted multiple comparisons with Tukey tests as per the methodology described above in the section on the number of bee pollinator guilds detected by different sampling methods, but only calculating the mean abundance of bees, not species richness this time. Finally, to compare the attractiveness of different pan colours to individual bee species, we calculated the total number of each bee species caught in each pan colour per crop study. We also compared the additional ALARM pan traps samples (datasets 1.2b and 1.2d) in the same manner.

3.4 Results

3.4.1 Crop bee community studies

A total of 42 studies were found which sampled bee communities in our focal crops (Appendix 6). Of those, 27 used transect walks, 13 used observation plots and 12 used pan traps (Figure 3.1).

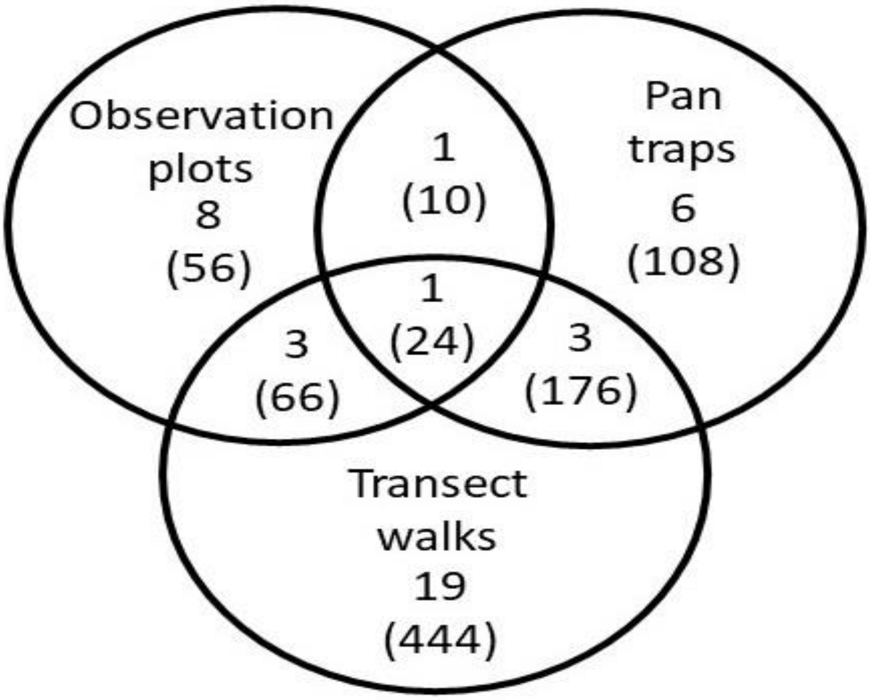


Figure 3.1: Number of studies that used Observation Plots, Pan Traps, Transect Walks, or a combination of methods to sample bee communities in crops. Total number of studies = 42 (total number of sites in brackets).

Eleven of the twelve studies employing pan traps identified all bees to species level, and all studies mounted pan traps at the approximate height of the surrounding crop flowers. Six studies used blue, white and yellow bowls, three studies only used yellow bowls, two studies used only white bowls and one study used both white and yellow bowls. Most studies employing pan traps used between two and fifteen pan traps per site and left them out for between one and four days.

All but two studies employing transect walks used a fixed transect protocol, in which a set corridor was walked to observe bees. Most studies (seventeen) employing transect walks recorded all bees to species level, but five only recorded *Bombus* to species, with solitary bees recorded to genera or guild. Studies employing transect walks generally used a corridor of between 50 and 150 m long and between 1 and 4 m wide, and carried out between one and fifteen transects per site. Eight studies employing transect walks identified bees through visual observation only, ten by netting all bees for later laboratory identification, and nine using a mixture of both approaches.

Studies employing observation plots typically sampled an area between 0.9 and 4 m^2 in size for 5–15 min and conducted between three and twenty-four observation plots per site. Only three studies employing observation plots identified all bees to species, using a combination of visual identifications and netting for subsequent identification. A further three studies only identified *Bombus* to species, all through visual observations in the field. The remaining seven studies were primarily focused on recording the visitation rates of individual guilds and only recorded bees as bumblebees or solitary bee. Four of those studies, however, did record species level data also, three using transect walks and one using pan traps.

3.4.2 Field data and crop pollinators

Eight datasets were used to evaluate the most commonly used methods to sample bee crop communities (Table 3.1: datasets 1.1a – 1.2d) and fifty-three bee species from seven genera were identified as potential pollinators of one or more of our four focal crops in Great Britain (Hutchinson et al. 2021). Of those a total of thirty-seven species from five genera were sampled in one or more of our eight datasets. The following number of species were sampled per crop: apple - 31; bean - 8; oilseed - 22; strawberry – 14 (Table 3.2).

Table 3.2: List of bee species identified as pollinators per crop (Apple – A, Bean – B, Oilseed – O, Strawberry – S) and datasets(s) in which they were recorded – IPI^1 (Table 3.1: datasets 1.1 a – 1.1d) and Alarm^2 (Table 3.1: datasets 1.2a – 1.2d).

Species (taxon authority)	**Crop(s)**
Andrena bicolor (Fabricius, 1775)	A^1, O^{1,2}, S^1
Andrena chrysosceles (Kirby, 1802)	A^1, O^{1,2}, S^1
Andrena cineraria (Linnaeus, 1758)	A^1, O^{1,2}, S^1
Andrena dorsata (Kirby, 1802)	A^1,
Andrena flavipes (Panzer, 1799)	A^1, O^2
Andrena fulva (Müller, 1766)	A, O^{1,2}
Andrena gravida (Imhoff, 1832)	A^1
Andrena haemorrhoa (Fabricius, 1781)	A^1, O^{1,2}, S^1
Andrena helvola (Linnaeus, 1758)	A^1,
Andrena labiata (Fabricius, 1781)	A^1,
Andrena minutula (Kirby,1802)	A^1, S^1
Andrena nigroaenea (Kirby,1802)	A^1, O^{1,2}, S^1
Andrena nitida (Müller,1776)	A^1, O^2
Andrena scotica Perkins, 1916	A^1, O^2, S^1
Andrena subopaca (Nylander,1848)	A^1,
Andrena tibialis (Kirby,1802)	O^1
Andrena trimmerana (Kirby,1802)	A^1
Andrena wilkella (Kirby,1802)	B^{1,2}, O^2
Bombus hortorum (Linnaeus,1761)	A^1, B^{1,2}, O^{1,2}
Bombus hypnorum (Linnaeus, 1758)	A^1, B^1, O^1, S
Bombus lapidarius (Linnaeus,1758)	A^1, B^{1,2}, O^{1,2}, S^1
Bombus pascuorum (Scopoli,1763)	A^1, B^{1,2}, O^{1,2}, S^1
Bombus pratorum (Linnaeus,1761)	A^1, B^{1,2}, O^{1,2}, S^1
Bombus ruderatus (Fabricius,1775)	B^1
Bombus terrestris (Linnaeus,1758)	A^1, B^{1,2}, O^{1,2}, S^1
Halictus rubicundus (Christ,1791)	O^{1,2}, S^1
Halictus tumulorum (Linnaeus,1758)	A^1,
Lasioglossum calceatum (Scopoli,1763)	A^1, O^{1,2}, S^1
Lasioglossum fulvicorne (Kirby,1802)	A^1, O^2
Lasioglossum leucopus (Kirby,1802)	A^1,
Lasioglossum malachurum (Kirby, 1802)	A^1, O^2
Lasioglossum morio (Fabricius,1793)	A^1,
Lasioglossum parvulum (Schenck,1853)	A^1,
Lasioglossum pauxillum (Schenck,1853)	A^1,
Lasioglossum punctatissimum (Schenck,1853)	A^1
Lasioglossum xanthopus (Kirby, 1801)	O^2
Osmia bicornis (Linnaeus,1758)	A^1

3.4.3 Abundance of bumblebees and solitary bees detected by different sampling methods

Guild and sampling method both had a significant effect on the abundance of bees detected in all three crops [apple ($F_{2,84} = 13.062$, $p \leq 0.001$); oilseed ($F_{2,144} = 8.3404$, $p \leq 0.001$); strawberry ($F_{2,144} = 51.288$, $p \leq 0.001$). In particular, there were significantly more ($p \leq 0.001$) solitary bees detected by pan traps than observation plots or transect walks in all crops (Figure 3.2; Appendix 7).

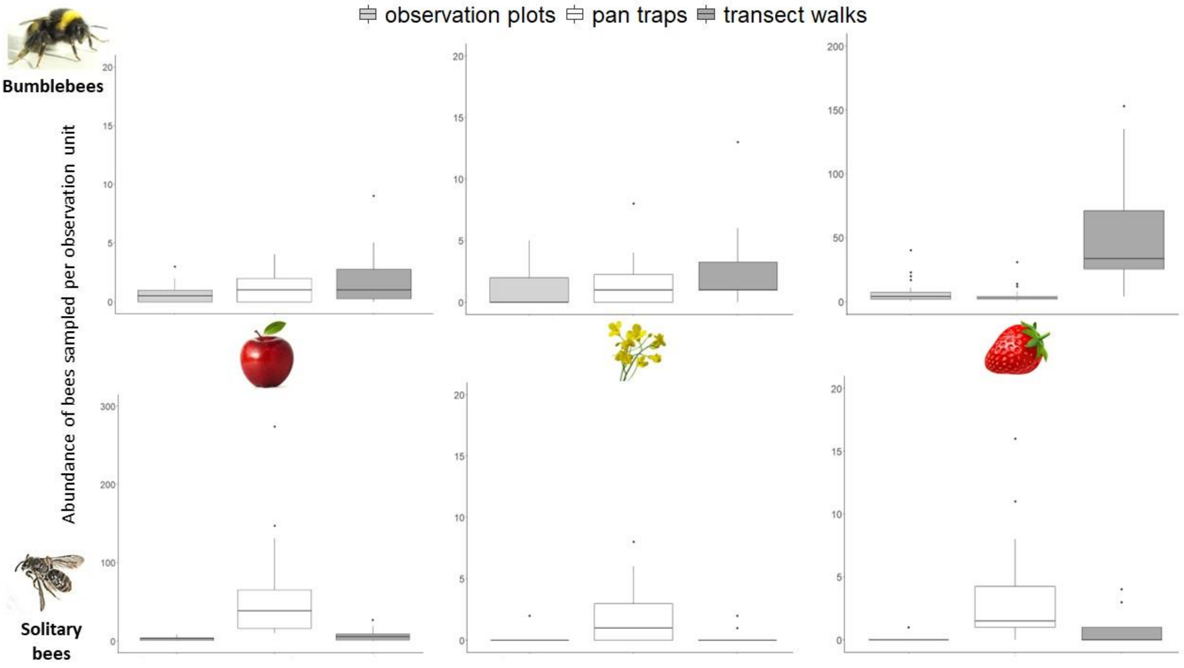


Figure 3.2: Abundance of bumblebees (top row) and solitary bees (bottom row) detected by observation plots (light grey/left), pan traps (white/middle) and transect walks (dark grey/right) per sampling unit for each crop (apple: n = 16; oilseed and strawberry: n = 24).

3.4.4 Abundance and species richness of bee genera detected by different sampling methods

The method which sampled the greatest mean abundance and species richness of bees differed according to genera (Figure 3.3; Appendix 8.1 & 8.2). A greater mean abundance of *Bombus* was sampled by transect walks in all four crops, including the additional bean surveys by a hymenopterist, as was species richness in all crops, except oilseed. Conversely, a greater mean abundance and species richness of *Andrena*, *Halictus* and *Lasioglossum* were sampled by pan traps in apple, oilseed and strawberry in all datasets, including the additional oilseed surveys by a hymenopterist. *Osmia* species were only present in apple and oilseed, where they were sampled most abundantly by pan traps and observation plots respectively. The remaining unidentified solitary bees that were recorded in crop sites (datasets 1.1a–1.1.c) were sampled in a greater abundance by transects in apple and strawberry, and by observation plots in bean and oilseed.

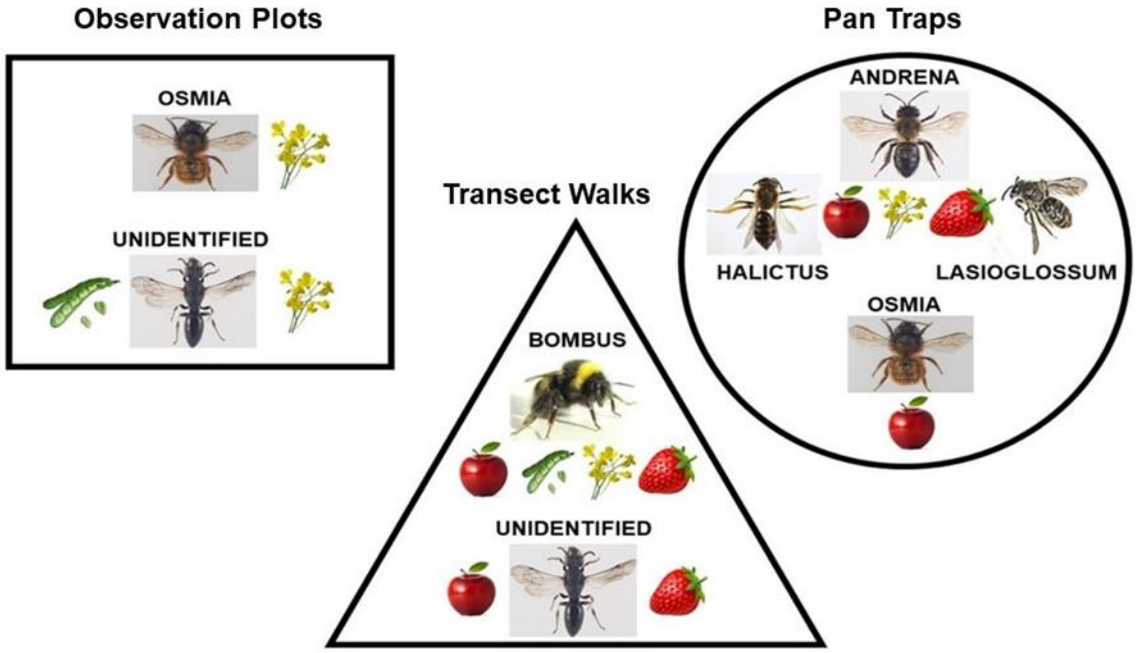


Figure 3.3: Genera of bee species sampled in apple, field bean, oilseed rape and strawberry crops sites and which sampling method – observation plots (square), pan traps (circle), transect walks (triangle) – generally detected the greater abundance and species richness of that bee genus/group.

For the dataset in which the pan trap sample data were standardised to estimate, and compare, the mean abundance and species richness of each bee genera sampled if pan traps and transect walks were carried out for equal amounts of time, the patterns followed those above, except for a couple of notable exceptions. When the pan trap data sample time was standardised for a direct comparison with transect walks, it was estimated that a lower mean abundance of *Andrena* species would be sampled by pan traps, compared to transect walks, in apple and strawberry sites, and that a lower mean species richness of *Andrena* would be sampled compared to transect walks in oilseed sites (Appendix 8.1)

For the crop surveys where both observation plots and transect walks were carried out simultaneously (datasets 1.1a and 1.1c), whilst a similar average proportion of bumblebee and solitary bee visits were recorded in apple by both methods, on average 10 and 86 times more bumblebee visits were recorded in oilseed and strawberry sites respectively by transect walks compared to just 4 and 5 times more visits recorded during observation plots.

All but one *Bombus* species were consistently sampled by both active methods and passive methods in each crop dataset (Appendix 8.3), whereas only two-thirds of *Andrena* species were detected by both active and passive methods, and all were sampled more abundantly by pan traps. These *Andrena* mostly comprised of relatively larger and easily recognisable species that can be identified on the wing such as *A. bicolor*, *A. cineraria*, *A. fulva* and *A. haemorrhoa*. The remaining *Andrena* species were sampled by pan traps only. Only two of the eleven *Halictid* species sampled across all crop datasets were detected by active methods, with the remainder sampled by pan traps only.

3.4.5 Proportion of the pollinator species pool sampled by pan traps and transect walks

Pan traps sampled a greater proportion of the total bee pollinators in all crop sites, except bean, where more species were sampled by transect walks (Table 3.3). In apple, oilseed and strawberry crop sites transect walks sampled approximately half or less of the total known pollinator community, whereas pan traps sampled 90 – 100% of species. Most species were also sampled by pan traps only in all crop sites, except bean.

Table 3.3: Total number of bee species identified as pollinators by Hutchinson *et al.* (2021) that were sampled in apple, field bean, oilseed rape and strawberry sites (n=8) for datasets 1.1b & 1.c (top row) and field bean and oilseed sites (bean: n=10; oilseed: n=4) for datasets 1.2a – 1.2d (bottom row), and number of those detected by pan traps and transect walks (including in brackets the number of species that were sampled by that method only).

Crop	**Number of species sampled by each survey method (Number of species sampled by that survey method only)**		
	Total number of species sampled	**Pan traps**	**Transect walks/ Observation Plots**
Apple	31	31 (19)	12 (0)
Field Bean	8	6 (0)	8 (3)
	7	6 (0)	7 (1)
Oilseed Rape	14	13 (8)	7 (2)
	20	20 (13)	7(0)
Strawberry	14	13 (6)	8 (1)

During transect walks for datasets 1.1c–1.1d, the majority of bumblebees observed were identified to species level in apple (89%), oilseed (78%) and strawberry (87%) crops. Conversely, in most cases, the majority of solitary bees observed visiting apple (66%), oilseed (75%) and strawberry (79%) were not identified to species. The mean percentage of bumblebees and solitary bees that were identified per site are provided in Table 3.4.

Table 3.4: Mean percentage (and standard error) of bumblebees and solitary bees observed during transect walks that were identified to species level in sites of apple (n = 23), oilseed (n = 16) and strawberry (n = 8) crops.

Crop	**Bombus**	**Solitary**
Apple	92 ± 3	55 ± 8
Oilseed	70 ± 6	33 ± 11
Strawberry	84 ± 4	15 ± 9

For datasets 1.2a–1.2b, where transect walks were carried out in bean sites, and observation plots in oilseed by a hymenopterist, 100% of all bees visiting bean were identified to species, as were 100% of bumblebees during observation plots in oilseed. During the oilseed observation plots carried out by a hymenopterist 90% of observed solitary bees were identified to species level.

3.4.6 Pollinator community comparisons between pan traps and transect walks

There was significant dissimilarity between the pollinator communities sampled by pan traps and transect walks (Figure 3.4) in all crop types (apples ($R_2 = 0.310$, $F_{1,14} = 6.281$, $p = 0.001$); field beans ($R_2 = 0.279$, $F_{1,14} = 5.411$, $p = 0.004$); oilseed rape ($R_2 = 0.143$, $F_{1,14} = 2.341$, $p = 0.014$); strawberries ($R_2 = 0.391$, $F_{1,14} = 8.972$, $p = 0.001$).

The SIMPER analysis indicated that across the four crops, ten species collectively contributed to more than 50% of the dissimilarity between the pollinator communities sampled by pan traps and transect walks in one or more crops (Table 3.5): *Bombus lapidarius* and *Bombus terrestris,* which were sampled more abundantly by transect walks in all crops, and *Andrena flavipes*, *Andrena haemorrhoa*, *Andrena minutula*, *Andrena nigroanea*, *Lasioglossum calceatum*, *Lasioglossum malachurum*, *Lasioglossum morio* and *Lasioglossum pauxillum* which were all sampled exclusively, or more abundantly, by pan traps in all crop sites in which they were present.

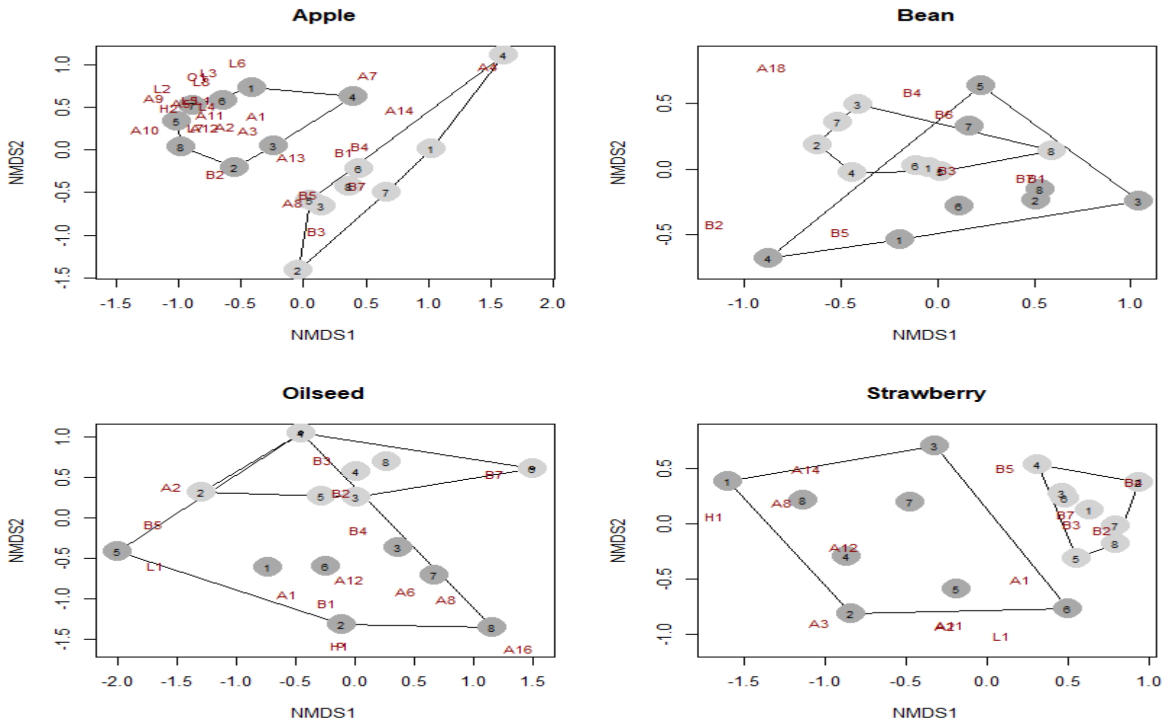


Figure 3.4: Non-metric multi-dimensional scaling (NDMS) plots of pan traps (dark grey circles) and transects (light grey circles) for all potential pollinating bee species detected in apple (stress =0.1141659), field bean (stress = 0.1069335), oilseed rape (stress = 0.1167524) and strawberry (stress = 0.1068908) crop sites. Number is circles represent the site number and the polygons connecting sites indicate the overlap between samples. Codes A1 to O1 indicate individual bee species (A=*Andrena*, B=*Bombus*, H=*Halictus*, L=*Lasioglossum*, O=*Osmia*; full codes found in Table 3.5).

Table 3.5: List of bee species identified as pollinators per crop (Apple – A, Bean – B, Oilseed – O, Strawberry – S) based upon Hutchinson et al. (2021) with species codes and percentage contribution to dissimilarity between pollinator communities sampled by pan traps and transect walks as identified by SIMPER analyses.

Species	**Code**	**A**	**B**	**O**	**S**
Andrena bicolor	A1	0.5%		6%	0.5%
Andrena chrysosceles	A2	6%		1%	
Andrena cineraria	A3	1%		1%	1%
Andrena dorsata	A4	4%			
Andrena flavipes	A5	17%			
Andrena fulva	A6			5%	
Andrena gravida	A7	0.2%			
Andrena haemorrhoa	A8	10%		14%	3%
Andrena helvola	A9	0.5%			
Andrena labiate	A10	0.3%			
Andrena minutula	A11	6%			1%
Andrena nigroaenea	A12	7%		12%	1%
Andrena nitida	A13	5%			
Andrena scotica	A14	1%			2%
Andrena subopaca	A15	0.1%			
Andrena tibialis	A16			2%	
Andrena trimmerana	A17	0.05%			
Andrena wilkella	A18		1%		
Bombus hortorum	B1	1%	18%	2%	
Bombus hypnorum	B2	0.3%	2%	1%	2%
Bombus lapidarius	B3	1%	22%	18%	44%
Bombus pascuorum	B4	0.4%	4%	3%	1%
Bombus pratorum	B5	1%	2%	6%	1%
Bombus ruderatus	B6		1%		
Bombus terrestris	B7	2%	50%	19%	40%
Halictus rubicundus	H1			1%	0.5%
Halictus tumulorum	H2	4%			
Lasioglossum calceatum	L1	1%		9%	2%
Lasioglossum fulvicorne	L2	0.1%			
Lasioglossum leucopus	L3	0.3%			
Lasioglossum malachurum	L4	13%			
Lasioglossum morio	L5	8%			
Lasioglossum parvulum	L6	0.2%			
Lasioglossum pauxillum	L7	9%			
Lasioglossum punctatissimum	L8	0.05%			
Osmia bicornis	O1	1%			

3.4.7 Body size and abundance of bee species sampled by active and passive methods

The GLM indicated that there were significant two-way interactions between body size and crop type, and body size and survey type ($p = < 0.05$) on the abundance of bees sampled, suggesting that there is a relationship between body size and the abundance of bees, but that this relationship is dependent upon sampling method and crop type. Apple was the only crop in which there appeared to be a clear negative and positive relationship respectively between body size and abundance of bees sampled by pan traps and transect walks (Figure 3.5).

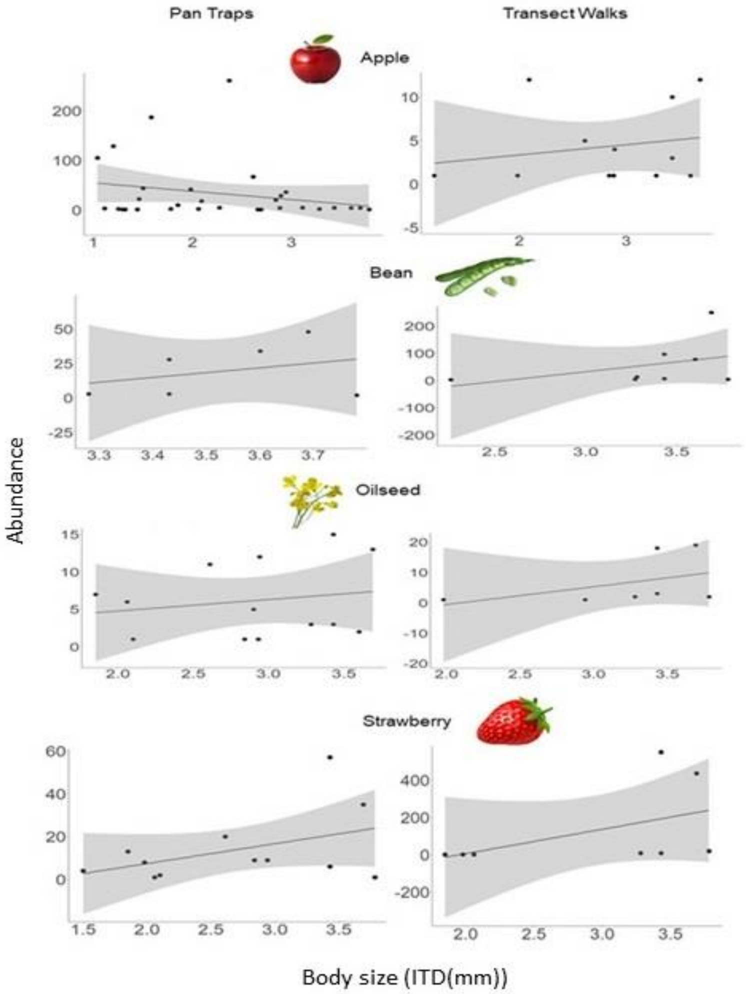


Figure 3.5: Relationship between body size (ITD) and abundance of bees sampled by pan traps and transect walks in apple, bean, oilseed and strawberry crop sites

3.4.8 Effects of trap colour on bee guilds and species sampled by pan traps

A greater overall mean abundance of bees were caught in yellow pan traps in all crops, except bean, where a greater mean abundance were caught in blue traps (Table 3.6). Guild and colour had a significant effect on the number of bees caught by pan traps in apple (P = >0.001). In particular, there was a highly significant difference (p ≤ 0.001) in the number of solitary bees caught by different pan colours, with significantly more solitary bees caught in yellow pan traps than in blue or white ones, and significantly more solitary bees caught in white pan traps than blue ones (Figure 3.6). Whilst neither guild nor colour had a significant effect on the number of bees caught by pan traps in oilseed or strawberry, the same pattern was observed in both crops as in apple, with more solitary bees caught in yellow pan traps than blue or white ones. Conversely, more bumblebees were caught in blue and white pan traps than yellow ones in apple, bean and oilseed (Appendix 9.1)

Across all crop and datasets combined 27 of the 30 solitary bee species included in analyses were caught in yellow pan traps, the remaining three were all sampled solely in white pan traps (Appendix 9.2 and 9.3). Ten solitary bee species were not caught at all in blue pan traps. Conversely, all seven *Bombus* species were sampled by blue pan traps in all four crops.

Table 3.6: Mean abundance ±SE bees caught by blue, white and yellow pan traps in eight sites of apple, bean, oilseed and strawberry crops (with the colour that caught the greatest abundance of bees in that crop highlighted in blue or yellow accordingly).

	Pan Trap Colour		
Crop	**Blue**	**White**	**Yellow**
Apple	12.4 ± 10.2	32.3 ± 26.5	79.3 ± 68.4
Field Bean	7.3 ± 3.0	2.9 ± 1.1	4.6 ± 1.7
Oilseed Rape	4.2 ± 1.1	5.5 ± 1.1	7.3 ± 2.6
Strawberry	2.8 ± 0.6	6.1 ± 2.0	13.1 ± 4.2

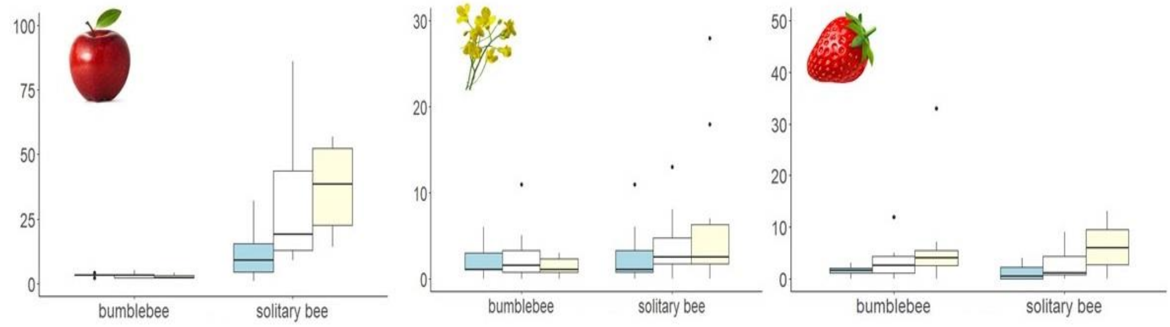


Figure 3.6: Number of bumblebees and solitary bees caught in blue, white and yellow pan traps in sites of apple, oilseed and strawberry crops.

3.5 Discussion

3.5.1 Inventorying and monitoring crop pollinating bee species

Declines in wild bee populations pose a significant threat to future food security (Reilly et al. 2020). There is an urgent need to inventory and monitor pollinator populations in order to develop effective conservation and management strategies (LeBuhn et al. 2013; Breeze et al. 2021). Yet, the identification of crop pollinating species and status of pollinator trends in agricultural settings is currently especially meagre. Whilst monitoring schemes for pollinator communities are emerging (Carvell et al. 2017; Potts et al. 2021), a specific emphasis on crop pollinators in agricultural settings is vital to safeguard crop production (Garibaldi et al. 2020). Whilst several studies have compared wild bee sampling methods, they are rarely carried out in crop areas, or consider multiple different crops (Krahner et al. 2021 and references therein). Furthermore, where studies have been carried out in crop habitats (O'Connor et al. 2019; Westphal et al. 2008) they have included the entire bee species community, and thus likely many non-crop pollinating bee species.

We used a comprehensive list of crop pollinating bee species in Great Britain (Hutchinson et al. 2021) to evaluate the effectiveness of the most commonly employed survey techniques to sample bee pollinator communities in different crop types. As reflected in recent global assessments (Dainese et al. 2019; Kleijn et al. 2015), we found that observational methods are the principal methods by which to identify crop pollinating bee species. However, we further substantiate the results of previous work showing that individual survey methods are biased towards different components of pollinator communities (O'Connor et al., 2019; Westphal et al. 2008), with the relative effectiveness of survey methods differing according to taxon (Prendergast et al. 2020). Our results concur with the results of a recent assessment of the performance of different methods to sample wild bees in a single and different crop (vineyards) habitat (Krahner et al. 2021). As in our study, there was evidence of a potential effect of bee guild on the capacity of survey methods to sample bee pollinators. Netting along transects was found to disproportionately sample bumblebees, compared to pan trapping, which, as in our study, sampled both the highest number of individuals and species. Pan trap colour was also found to differ in its attractiveness to different guilds, with, in line with our findings, yellow traps being more attractive to solitary bees, and blue pan traps generally being more attractive to bumblebees in crops where they are prominent pollinators.

Our findings support prior evidence that observational methods are less effective at distinguishing finer taxonomic levels (Westphal et al. 2008; Prendergast et al. 2020), with pan traps being a more effective means to inventory the abundance and species richness of some crop pollinator communities. Additionally, as well as reinforcing evidence that pan trap bowl colours vary in their attractiveness to different bee guilds (Krahner et al. 2021), we demonstrate that the optimal colour to sample pollinators is based upon bee guild. Notably, we provide some of the first evidence that differences in the capacity of survey methods to sample pollinating bee species in crop habitats are likely driven by the species composition of the pollinator community being sampled, and that the most efficient method to sample pollinator communities is contingent upon crop type.

Whilst observational methods are currently the principal means by which to identify insect species that are delivering crop pollination services (Kleijn et al. 2015; O'Connor et al. 2019), many field studies only identify larger bees such as *Bombus* to genus or species, with other bees grouped together into one guild (e.g., see Appendix 6). Pan traps have been associated with low captures of pollinating species compared to netting techniques (e.g. Cane, Minckley & Kervin 2000). But, in our study, transect walks generally detected a relatively smaller proportion of the overall crop pollinator bee community, while pan traps sampled almost the entire suite of pollinating species present in three of the four crops, with the exception of bean, which is almost exclusively visited by bumblebees, that are often sampled more comprehensively during active methods (Krahner et al. 2021). Our results build upon an established body of research indicating that solitary bees are more comprehensively sampled by pan traps (McCravy 2018; Roulston et al. 2007; Westphal et al. 2008). This was especially prevalent in our results for apple, which had the greatest proportion of solitary bees in its pollinator community in our field datasets, and was the one crop which indicated a negative association between bee body size and abundance sampled by pan traps.

Furthermore, we excluded species from pan trap samples that, whilst known to forage on the target crop plant family (Hutchinson et al. 2021), lacked visitation data to substantiate their status as potential pollinators, but may be crop flower visitors. Most of the species we excluded as such were particularly small solitary bees. Given this, and the fact that we used

ITD measurements for Bombus workers, rather than queens, which are significantly larger, it is therefore likely our results are a conservative estimate of the impacts of body size on detection rates. Additionally, the oilseed dataset which we used to analyse the relationship between pan trap abundance and body size contained very few solitary species, even though this crop is known to be frequently visited by many such species from multiple genera (Hutchinson et al. 2021). This could reflect the high density of nectar rich yellow flowers in oilseed fields (Thompson, Stefan & Knight 2021), which could draw bees away from pan traps and may account for why the trends observed in apple were not apparent in oilseed. Additionally, the oilseed observational methods which were carried out by trained researchers, rather than an expert entomologist, also sampled low numbers of solitary bees, which may relect the difficulty of recording certain species in dense crops with reduced visibility (Garratt et al. 2019).

Pan traps, however, do not provide information on floral associations, and their effectiveness may vary depending on the density of floral resources in the surrounding environment (O'Connor et al. 2019). As such observational methods play an integral role in inventorying those species visiting crop flowers. Whilst trained citizen scientists could record most bumblebees on the wing (excluding cryptic species, e.g., the *Bombus lucorum* complex [see Bossert, 2014]), taxonomic experts, who can produce species data commensurate with pan traps, are indispensable for identifying solitary species visiting flowers (O'Connor et al. 2019). We found that whilst our surveys were conducted by trained researchers, high proportions of solitary bee pollinators present in fields were not observed, nor identified to species when they were, during transect walks. This was especially pronounced in oilseed rape fields, potentially due to it being grown in dense masses in fields, whereas the other crops are primarily grown in spaced out rows, making it easier to capture insects for identification purposes. It is possible in such densely grown crops that the movement of surveyors during transect walks may disturb small solitary bees, which are subsequently not detected and/or identified. Further research into the capacity of different survey methods to sample bee species in oilseed, and other densely grown crops that may be frequently visited by small solitary species, would be a useful focus of further research.

Efforts to inventory crop pollinators would also benefit from cross-national collaborative efforts. Observational data from other countries with a similar bee fauna can supplement national surveys and inform protocols using pan trap samples, by allowing the differentiation of pollinators from non-pollinators (Hutchinson et al. 2021). Additionally, it can also be used to identify 'insurance' species which could deliver this service in the future, should current pollinators undergo declines. Some species may currently be present in low numbers in agricultural areas in certain countries due to climatic or ecological constraints, but could undergo climate-induced range shifts or be promoted via agri-environment measures. It is important to note, however, that our results solely reflect the capacity of these sampling methods to identify those species potentially contributing to pollination service. There is a clear distinction between establishing the presence and abundance of insects in crop fields, and measuring their actual contribution to pollination service. In that respect, observation plots have been evidenced elsewhere as the most reliable means by which to measure visitation rates (Garibaldi et al. 2020).

Once the suite of pollinating species for individual crops has been established, the critical task of monitoring them using taxonomically robust, standardised protocols (O'Connor et al. 2019) can be implemented. Given that a lack of skilled taxonomists remains a major bottleneck in monitoring pollinators (Science for Environment et al. 2020), the verified capacity of trained volunteers to implement pollinator surveys (Garratt et al. 2019) will prove integral to monitoring programmes. To facilitate this, however, protocols may benefit from being as simple as possible, particularly where resources are a limiting factor, focusing on the quality, rather than quantity of data. Bumblebee species are relatively easy to catch, due to a combination of their large size and slow flight speed (Prendergast et al. 2020). As such transect walks alone are likely sufficient to sample them in crops, such as field beans, which is almost exclusively pollinated by them (Hutchinson et al. 2021).

In crops where small solitary bees are a key provider of pollination service delivery, such as apple and oilseed (Hutchinson et al. 2021), pan traps may be an important source of complementary data. One approach is to use bowl colours that match the colour of the target crop flower (Ahrenfeldt et al. 2019; Marini et al. 2012), but more detailed pilot studies to determine the efficacy of such an approach are required. Our results support existing evidence that the driving influence behind pan trap colour efficiency is the guild (eusocial, e.g., Bombus or non-eusocial (solitary) bees) being targeted (Campbell & Hanula 2007; McCravy 2018; McCravy et al. 2019). As also indicated in our study, eusocial bees may be more attracted to blue and white pan traps, whereas non-eusocial bees may be more attracted to yellow (Sircom, Jothi & Pinksen 2018). Using colour to target specific groups may help reduce pan trap by-catch of non-pollinators, if the time to process specimens and a lack of taxonomic experts remains a major bottleneck in pollinator sampling (Science for Environment Policy 2020). Regardless of resources a more targeted approach, and reduced by-catch, also has potential ethical benefits as it could reduce the number of insects killed.

Given increasing evidence, here and elsewhere (O'Connor et al. 2019; Templ et al. 2019), of the propensity of observational methods, notably transect walks, to under-sample small solitary bees, monitoring programmes could benefit from employing separate searches for bumblebees (and potentially larger, conspicuous *Andrena* species, which our results indicate could potentially be sampled by transect walks), and small solitary bees. This may be particularly beneficial in densely grown field crops, such as oilseed, where reduced visibility may present a constraint on the accurate recording of small species (Garratt et al. 2019). In our study, a far higher proportion of bumblebee visits were recorded relative to solitary bee visits in oilseed and strawberry during transect walks compared to observation plots. Transect walks may overestimate the relative abundance of bumblebees on crop flowers relative to solitary bees, possibly due to solitary bees being more visible, and less likely to fly away, if the surveyor is relatively stationary, as in observation plots.

Observation plots, by trained surveyors where solitary bees are recorded to at least genus, may provide more accurate information on the relative abundance of solitary bees compared to bumblebees. Equally, employing designated transect walks for solitary bees alone, could help increase recordings of small inconspicuous species, which findings here, and elsewhere (Prendergast et al. 2020), indicate are otherwise underrepresented. Whilst some especially small species may still be overlooked, it is likely such an approach will still cover relatively larger species, which often make the greatest contribution to pollination service delivery (Földesi et al. 2021).

A final point of note is the similar under-representation of non-bee pollinators during observational surveys (Földesi et al. 2021), which may also be mirrored in pan trap samples (Hall & Reboud 2019). Given the important contribution to crop pollination of such insects (Rader et al. 2016), more work evaluating the best means to inventory, and monitor, non-bee crop pollinators should be considered an urgent next step. Additionally, the anthropocentric view of protecting ecosystem service providers should not be the sole basis for biodiversity conservation (Prendergast 2020) and monitoring programmes should consider the whole spectrum of species in agricultural landscapes, and not just those bee species that contribute to crop pollination.

3.5.2 Data constraints and limitations

It should be noted that our assessments are based upon both a limited number of datasets and time periods, with surveys carried out across small number of sites and over a period of just one to two years. Previous studies suggest that crop pollinator communities can vary considerably across sites and years (Kremen, Williams & Thorp 2002; Adamson et al. 2012; Fijen & Kleijn 2017). The oilseed datasets also sampled less than half of all known definite and likely pollinators of this crop (Hutchinson et al. 2022) and as such an assessment of sampling methodologies for surveying most of its pollinating species was not possible. Further evaluations of sampling methods based upon larger site numbers and time periods are therefore needed before more definitive conclusions can be drawn. Our results may also not be applicable to all crop types and additional studies in further crop sites would be beneficial. Finally, our field surveys for each crop were carried out in different months and years. Weather during surveys, including precipitation, temperature and wind can affect bee activity (Brittain, Kremen & Klein 2013; Papanikolaou 2017), with not all bee species responding the same to daily environmental changes (Rogers, Tarpy & Burrack 2014). Furthermore, whilst all personnel received training prior to surveys, recorder experience can have a significant impact on the diversity of bees sampled in crop fields (O'Connor et al. 2019). These factors were not accounted for in our analyses, or incorporated into our models, and could have had some impact upon our results that are not considered in our conclusions.

3.6 Conclusions

Threats to food security are no longer a theoretical future concern (Aizen et al. 2008). Empirical evidence now demonstrates the capacity of wild pollinator limitations to translate into reduced crops yield and productivity (Reilly et al. 2020). Whilst national-level monitoring of all species is critical for conserving wider biodiversity, a specific focus upon crop pollinators in agricultural landscapes is essential for resilient crop pollination service delivery (Carvell et al. 2017). Given the established benefits of diverse assemblages for resilient crop productivity (Potts et al. 2016), inventories of crop pollinators should aim to sample the whole suite of species delivering the service (Winfree et al. 2018). The elucidation of the roles of different pollinator taxa is a critical first step as optimal management strategies will differ amongst species (Woodcock et al. 2013).

Applying the most effective method(s) to ensure a representative sampling of crop pollinator community species richness by trained volunteers will help optimise the sampling of target bee species or groups (Garratt et al. 2019; Templ et al. 2019). Future work should also focus on how to apply survey methods that more accurately reflect relative abundance of individual species, particularly small solitary ones. Inventorying bee species that visit crop flowers will allow for targeted management to conserve and promote their persistence at both the national and farm level. Monitoring thereafter is essential to verify whether policies are having the desired effect (Science for Environment Policy 2020). Our findings can inform the design of optimal and comprehensive sampling protocols for crop pollinating species. Key to their success will be collaboration and standardisation to ensure national and international policies can protect crop pollinators and the integral ecosystem service they provide for human well-being.

Chapter 4: Bee occupancy dynamics: The influence of pollinator community composition and species richness on crop pollinator occurrence.

This chapter is a modified version of the following publication:

Hutchinson, L., Oliver, T. H., Breeze, T., Greenwell, M.P., Powney, G. & Garratt, M. (2022). Bee occupancy dynamics: The influence of pollinator community composition and species richness on crop pollinator occurrence. *Frontiers in Sustainable Food Systems*, 313. https://doi.org/10.3389/fsufs.2022.943309

Author contributions: Conceptualisation: LH, MG, TB, TO; study design: LH, MG, TB, TO; data curation: LH, GP; formal analysis: LH, MPG; writing – original draft preparation: LH; writing – review and editing: all authors.

This chapter is based upon the above publication. The methodology and findings remain unchanged from the published version. However, some alterations have been made to the following version for completeness and to improve clarity and readability of the thesis:

- Additional information and references, and minor edits, have been added to the introduction and discussion sections.

4.1 Abstract

Bees provide a vital ecosystem service to agriculture by contributing to the pollination of many leading global crops. Human well-being depends not only on the quantity of agricultural yields, but also on the stability and resilience of crop production. Yet a broad understanding of how the diversity and composition of pollinator communities may influence crop pollination service has previously been hindered by a scarcity of standardized data. We used outputs from Bayesian occupancy detection models to examine patterns in the inter-annual occupancy dynamics of the bee pollinator communities of four contrasting crops (apples, field bean, oilseed and strawberries) in Great Britain between 1985 and 2015. We compared how the composition and species richness of different crop pollinator communities may affect the stability of crop pollinator occurrence. Across the four crops, we found that the inter-annual occupancy dynamics of the associated pollinator communities tended to be more similar in smaller communities with closely related pollinator species. Our results also indicate that crop pollinator communities composed of a small number of closely related bee species show greater variance in mean occupancy compared to crops with more diverse pollinator communities. Lower variance in the occurrence of crop pollinating bee species may lead to more stable crop pollination services. Finally, whilst our results initially indicated some redundancy within most crop pollinator communities, with no, or little, increase in the variance of overall mean occupancy when species were initially removed, this was followed by a rapid acceleration in the variance of crop pollinator occurrence as each crop's bee pollinator community was increasingly depreciated. High inter-annual variations in pollination services have negative implications for crop production and food security. High bee diversity could ensure more stable and resilient crop pollination services, yet current agri-environment schemes predominantly benefit a limited suite of common species. Management may

therefore benefit from targeting a wider diversity of solitary species in order to safeguard crop pollination service in the face of increasing environmental change.

4.2 Introduction

Insect pollinators provide vital ecosystem services to agriculture, including most notably pollination of crop plants (Zhang et al. 2007). The majority of leading global crops benefit to some degree from biotic pollination (Klein et al. 2007). Insect pollination increases crop yields, quality and market value (Bommarco, Marini & Vaissière 2012; Klatt et al. 2014; Garratt et al. 2014a). Animal-pollinated crops are also disproportionately more important from an economic and nutritional perspective than pollinator-independent staple crops (Vanbergen et al. 2014; Ollerton 2017). Demand for major insect-pollinated crops has continued to rise in recent decades, leading to global agriculture becoming increasingly dependent upon insect pollinators (Aizen et al. 2019). Documented declines in wild bees (Potts et al. 2010; Powney et al. 2019; Zattara & Aizen, 2021), which provide important pollination services to many crops (Klein et al. 2007), and evidence of pollinator limitation in agricultural crops, have therefore raised concerns about future food security (Reilly et al. 2020).

There is an urgent need to explore the relationship between biodiversity and ecosystem function (Oliver et al. 2015a; Suárez-Castro et al. 2022). Prior evidence indicates that many ecosystem functions are predominantly maintained by a small number of species (Schwartz et al. 2000; Cardinale et al. 2006). This may, however, reflect the small spatio-temporal scales at which most experiments are conducted (Winfree 2013). For example, Kleijn et al. (2015) conducted a global review of field studies, which reported that 80% of crop flower visits were attributable to just 2% of bee species. However, more recently, Winfree et al. (2018) found that the number of bee species required to provide adequate crop pollination services on a landscape scale is at least one order of magnitude higher than in field experiments, due to species turnover. Calls for cost-effective management to focus on those species that make the greatest contribution to pollination (Kleijn et al. 2015) may not protect crop pollination services due to a failure to encompass species that supplement service provision during times of suboptimal pollination by dominant species (Fijen et al. 2018).

Human well-being depends not only on the amount, but also the stability, of agricultural crop production (Garibaldi et al. 2011a). Wild bee populations exhibit significant temporal fluctuations (Roubik 2001; Williams, Minckley & Silveria 2001), and around half of yield instability in pollinator-dependent crops has been attributed to inter-annual variation in pollination service (Garibaldi et al. 2011a). Species-rich pollinator communities have been shown to positively influence the spatial and temporal stability of crop pollination service delivery (Senapathi et al. 2021). Bee crop pollinators can exhibit marked community variation across crop fields and years (Kremen, Williams & Thorp 2002; Klein 2009; Adamson et al. 2012). Species rich pollinator communities, and lower variability in bee richness, can increase the spatio-temporal stability of crop yields (Martins et al. 2018; Winfree et al. 2018; Hünicken et al. 2021), because less abundant, non-dominant pollinators can potentially replace dominant pollinators if the latter undergo transient declines (Fijen et al. 2018; Winfree et al. 2018).

Pollinator management also needs to consider the resilience of crop pollination services (Senapathi et al. 2015), due to accelerating rates of anthropogenic induced environmental change (Oliver et al. 2015a; Oliver et al. 2015b). Bees with different functional traits have been demonstrated to vary in their sensitivity to climate and land use change (Kammerer et al. 2021), and high bee diversity has been shown to buffer crop pollination delivery from changes in weather conditions (Brittain, Kremen and Klein 2013; Rogers, Tarpy & Burrack 2014) and landscape disturbance (Winfree & Kremen 2008). This is in line with what has been termed the 'insurance hypothesis', whereby biodiversity insures against fluctuations in ecosystem service function, because some species continue to contribute at times when others do not (Yachi & Loreau 1999). Biodiverse pollinator communities could ensure that crop pollination service is sustained under a range of environmental conditions (Science for Environment Policy 2020), yet current agri-environment schemes predominantly benefit a limited suite of common species (Vasiliev & Greenwood 2020).

Whilst species diversity can increase the stability of agricultural production, differences in the traits of both bee species and crop flowers mean that bee species vary in their effectiveness as pollinators of different crops (Garibaldi et al. 2015). Many crops have distinct pollinator communities (Garratt et al. 2014b; Hutchinson et al. 2021). Therefore, the degree to which species richness and functional diversity can stabilise pollination service may vary among crops. However, a broad understanding of how crop pollinator community composition could affect crop pollination service has previously been limited by a dearth of standardized data. Biological records represent a burgeoning tool to address such questions (Powney & Isaac 2015), with a suite of statistical techniques being developed to overcome the challenges presented by such unstandardized data (Isaac et al. 2014). Employing Hierarchical Bayesian Occupancy Models, distribution records of bee species have been used to develop a pollinator indicator for the UK Biodiversity Indicators that is similar to the abundance data used for other indicator species (Outhwaite & Isaac 2015).

The aim of this study was to explore how the inter-annual occupancy dynamics of different wild bee crop pollinator communities differed, and the potential implications of this for the resilience of crop pollination service. Temporal variability in crop pollinator abundances is directly linked to crop pollination service stability (Senapathi et al. 2021), and given the link between year-to-year changes in the distribution and abundance of pollinating insects (Mason et al. 2018), crop pollination service delivery is also likely to be underpinned by stability of crop pollinator occurrence. Great Britain was used as a case study due to the availability of data on its bee populations (Powney et al. 2019). Four economically important insect-pollinated crops - apple (*Malus domestica*), field bean (*Vicia faba*), oilseed rape (*Brassica napus*) and strawberry (*Fragaria x ananassa*) – were chosen as focal crops. These crops represent the main orchard, protein, arable, and soft fruit crops, respectively, in Great Britain (Breeze et al. 2021). Previous work has demonstrated that these crops exhibit differences in their bee pollinator community composition. Field bean and strawberry are predominantly visited by bumblebees, whereas apple, and particularly oilseed, can also be visited by a wide diversity of solitary bees (Hutchinson et al. 2021).

Here we combine lists of crop-pollinating bee species for our focal crops (Hutchinson et al. 2021), alongside outputs from occupancy models based upon biological records collected by the Bees, Wasps and Ants Recording Society (BWARS 2020a). Occupancy models are designed to account for variations in the detectability of species, as well as incomplete and biased sampling. The output consists of a mean estimate for the proportion of 1 km grid squares in Great Britain occupied by a given bee species in a particular year, and has previously been used to determine long-term population trends amongst wild bee species (Powney et al. 2019). Long-term temporal trends in such occupancy models are closely related to long term abundance trends (Oliver et al. 2015a), and year-to-year changes in citizen-collected distribution records, have been demonstrated to act as a reasonable surrogate for inter-annual changes in abundance (Mason et al. 2018). We examined patterns in the inter-annual occupancy dynamics of the bee pollinators of these crops to address three main aims:

(i) Identify groups of crop-pollinating bee species with similar and contrasting inter-annual occupancy dynamics;

(ii) Compare the stability of the occupancy dynamics of different crop pollinator communities, and

(iii) Investigate to what extent pollinator species richness affects the stability of crop pollinator occurrence.

4.3 Methods

Analysis

All analyses were performed using RStudio version 3.4.3 (RStudio Team, 2020).

4.3.1 Crop Flower Visitors

For each crop a list of bee species was compiled based upon a previous study that used a literature review of crop field surveys, combined with bee ecological trait data, to determine the potential pollinators of each crop in Great Britain (Hutchinson et al. 2021). In this study a total of 229 bee species were initially considered, of which 32% (73) were deemed to be potential pollinators of one or more of our four focal crops. To reflect the fact that not all species make an equal contribution to crop pollination, bee species in this study were grouped into three nested categories as follows:

1. Primary Flower Visitors – species identified as ‘dominant’ pollinators (attributed with a combined total of 80% of flower visits in British crop field studies) in Hutchinson et al. (2021).
2. Core Flower Visitors – Primary flower visitors and all other species classed as ‘definite’ flowers visitors (species recorded visiting crop flowers in British field studies) in Hutchinson et al. (2021).
3. All flower visitors – all above species, and all other species classified as ‘likely’ flower visitors (species recorded in pan traps with crop flower visitation data from other European studies to validate their status as crop flower visitors) in Hutchinson et al. (2021).

4.3.2 Inter-annual changes in occupancy

Outputs from Bayesian occupancy detection models held by the UK Centre for Ecology and Hydrology (UK CEH) were utilized in all analyses. The occupancy models use occurrence records of bees extracted from the Bees, Wasps and Ants Recording Society (BWARS 2020a) in 1 km grid cells across Great Britain. These observations represent presence-only data, so non-detections from records are inferred from other species within the taxonomic group on the same grid cell and date. The output is derived from two hierarchically coupled sub-models that simultaneously estimate and account for variation in the detectability of different species, while estimating species presence for a given site (1 km grid cell) and year combination. Detectability was included as a covariate in the detection model to account for variation in recorder effort. Further details of the occupancy models used can be found in Outhwaite et al. 2018. Gary Powney from UK CEH ran the Bayesian occupancy models and produced the occupancy estimates for each bee species and year; all subsequent analyses below were carried out by the lead author, Louise Hutchinson.

To identify groups of crop-pollinating bee species with similar and contrasting occupancy dynamics the mean annual occupancy estimates for each bee species that met the ‘core flower visitor’ criteria described were initially used, as these species represent the main known flower visitors of our crops (Hutchinson et al. 2021). Inter-annual changes in occupancy from 1985 to 2015 were calculated for all forty bee species categorized as core flower visitors of one or more of the four crops. Inter-annual changes were calculated by subtracting the occupancy estimate for each year from the year preceding it to establish relative change from one year to the next.

Inter-annual changes in species occupancy were then used to characterise groups of species with comparable occupancy dynamics (i.e., similar directional annual change in the mean proportion of occupied 1km squares). Using Pearson’s correlation coefficient, an occupancy dynamics correlation matrix was created to compare the inter-annual changes in occupancy between each pair of species. The occupancy dynamics matrix was transformed into a distance matrix using the base function ‘dist’ in R (R Core Team 2020). All values were multiplied by -1 so that pairs of species with the most asynchronous occupancy dynamics had positive values. One was then added to all values because the following analysis cannot include negative values. This resulted in pairs of species with the most asynchronous occupancy dynamics having the highest scores, and species with the most synchronous occupancy dynamics having the lowest scores.

Hierarchical cluster analysis, using Euclidean distances, was then performed with the base function ‘hclust’ in R (R Core Team 2020), following the methodology described in Greenwell et al. (2019) to identify groups of species with the most similar inter-annual occupancy dynamics. The ‘hclust’ function assigns each species to its own cluster, then proceeds iteratively, joining the two most similar clusters at each stage, until there is just a single cluster. The results were visualised as a dendrogram. To prune the output and identify clusters of species with similar occupancy dynamics, we applied the Kelley–Gardner–Sutcliffe (KGS) penalty function (Kelley, Gardner & Sutcliffe 1996) in the ‘maptree’ package (White & Gramacy 2012). The KGS penalty function uses the species pairwise distance matrix to maximise differences between clusters and similarity within clusters (Carvalho et al. 2011; Soultan, Wikelski & Safi 2020). The minimum output value of the KGS function corresponds to the optimal number of clusters.

4.3.3 Inter-annual occupancy variation

To compare the stability of the occupancy dynamics of different crop pollinator communities over time we created a dataset per crop containing the inter-annual changes in occupancy from 1985 to 2015 was created following the methodology described above, for all bee species identified as flower visitors. For field bean, bees were only split into primary and core flower visitors, as no additional likely pollinators were identified for this crop (Hutchinson et al. 2021).

The arithmetic means of occupancy per year for all bee species for each group of flower visitors per crop, as well as the standard deviation, were then calculated. Using standard deviation to assess variance, as used elsewhere (e.g., Karp et al. 2011; Morin et al. 2014; Hautier et al. 2015), rather than the coefficient of variation, was appropriate here because our time series were already centred around a mean of zero. We do not use standard error, which adjusts variance estimates by sample size, because we are interested in absolute deviations in crop pollinator occurrence, which have implications for potential deficits in crop pollination service and crop yields.

4.3.4 Impact of removing bee species on stability of crop pollinator occurrence

To investigate to what extent species richness affects the stability of crop pollinator occurrence the potential impact of a progressive loss of bee species from crop areas on the stability of crop pollinator occurrence for each of the four focal crops was explored. First the mean occupancy of all fifty bee species identified as crop flower visitors between 2013 and 2015 was calculated. This was done in order to rank species based upon their overall occupancy across Great Britain. The last three years of data were chosen to ensure that recent estimates of occupancy were utilised, but also to account for the fact that a single year of data alone may not reflect the true occupancy of each species, given that bee species exhibit significant inter-annual population fluctuations (Roubik 2001; Williams, Minckley & Silveira 2001). The standard deviation of mean occupancy was then calculated as described above, but this time one bee species at a time was successively removed, to calculate the standard deviation (SD) if one species, then two, then three, and so forth, was removed. Species were removed based upon their mean occupancy between 2013 and 2015, with the species calculated as having the lowest mean occupancy figure removed first, and so on, until only one species, that with the highest mean occupancy, remained.

The above methodology was chosen because those species with the lowest mean occupancy figures will almost certainly correspond to those bee pollinators that are the least likely to occur within each crop's pollinator community. Geographically restricted species are likely to be species that exhibit a greater degree of ecological specialisation compared to more geographically widespread species, and in turn are likely to be less abundant in farmland (Wood, Holland & Goulson 2016a), as well as at greater risk of population declines (Goulson et al. 2005; Williams 2005). As such these species are likely to be amongst the first to disappear from crop areas. This hypothesis is supported by increasing evidence that agri-environment schemes developed to increase bee farmland populations predominantly benefit a limited suite of common and generalist bee species (Wood et al. 2015; Wood, Holland & Goulson 2017).

4.3.5 Occupancy uncertainty confidence limits.

There is a degree of uncertainty associated with the mean occupancy estimates of all modelled species and this is represented by 95% confidence intervals (Powney et al 2019). As such all analyses described above were also run using the lower 2.5 and upper 97.5 confidence limit occupancy estimates to check that patterns in occupancy dynamics at the minimum and maximum confidence limits of the occupancy estimates matched those of the mean occupancy estimates.

4.4 Results

4.4.1 Crop flower visitors.

A total of fifty bee species were identified as flower visitors of one or more of the four crops (Appendix 10). Forty species were identified as core flower visitors, ten of which were also identified as primary flower visitors of one or more of the four crops. The primary pollinators comprised six species of *Andrena* and four species of *Bombus* (*Andrena cineraria*, *Andrena dorsata*, *Andrena haemorrhoa*, *Andrena nigroaenea*, *Andrena nitida*, *Andrena scotica*, *Bombus hortorum*, *Bombus lapidarius*, *Bombus pascuorum* and *Bombus terrestris*).

4.4.2 Inter-annual changes in occupancy

The hierarchical clustering analysis using the mean occupancy estimates for the core flower visitors produced a dendrogram that was split into five clusters based upon the KGS penalty function (Figure 4.1; Appendix 11). Flower visitors for each crop were distributed across the dendrogram, with both apple and oilseed rape visitors occurring in five clusters, field bean visitors in four, and strawberry visitors occurring in three clusters.

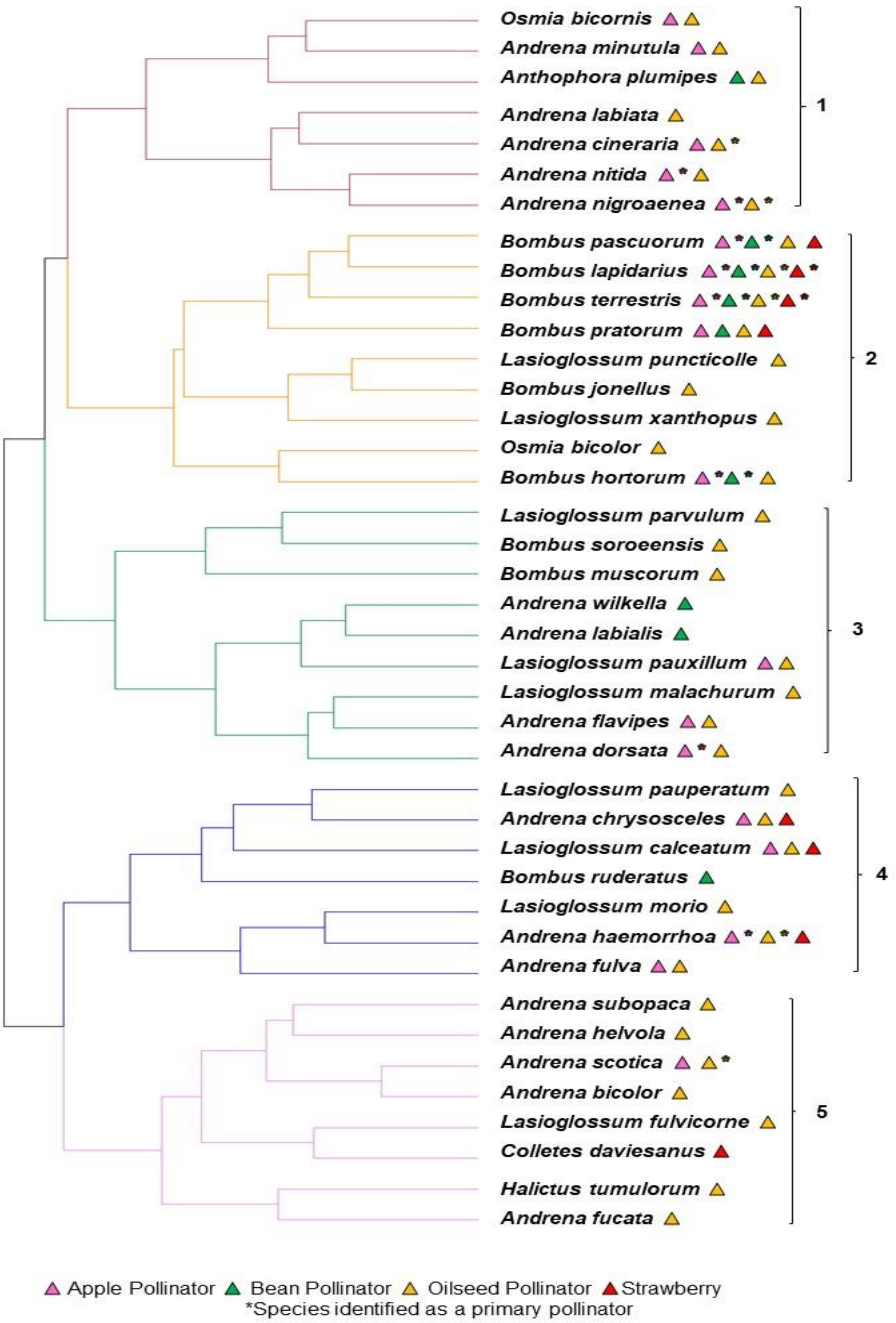


Figure 4.1: Dendrogram showing the hierarchical relationships amongst five clusters of bee crop pollinators for apple (18 spp.), bean (9 spp.), oilseed (36 spp.) and strawberry (8 spp.) Individual clusters are coloured for clarity. Species with more correlated occupancy dynamics join further to the right-hand side of the dendrogram. Triangles with an asterisk to the right-hand side denotes species identified as primary pollinators of that crop.

Amongst the ten species identified as primary pollinators, species from the same genus generally had more synchronous inter-annual occupancy dynamics than species from different genera (Table 4.1). All species pairs of *Andrena* (i.e., all possible combinations of two species) were positively correlated (nine of fifteen of which were significant (P≤0.05) correlations), as were all species pairs of *Bombus (*five of six of which were significant (P≤0.05) correlations). Of the 24 mixed genus species pairs (i.e., one species of *Andrena* and one species of *Bombus*) seventeen were negatively correlated (4 of which were significant (P≤0.05 correlations) and seven were positively correlated (1 of which was significant (P≤0.05). The four *Bombus* species identified as the sole primary flower visitors of bean, two of which are also the sole primary flower visitors of strawberry (Figure 4.1), were all placed in one cluster. Of those four species the pairs with the most synchronous occupancy dynamics were *B. lapidarius* and *B. pascuorum*, and *B. lapidarius* and *B. terrestris* (Figure 4.2a). The same *Bombus* species were also identified as primary pollinators of apple and oilseed, alongside six species of *Andrena* (Figure 4.1). The primary flower visitors of apple and oilseed rape were split across four clusters. Amongst the shared primary flower visitors to apple and oilseed rape several species pairs had asynchronous occupancy dynamics, including most notably *A. nigroaenea* and *B. terrestris* and *A. haemorrhoa* and *B. terrestris* (Figure 4.2b).

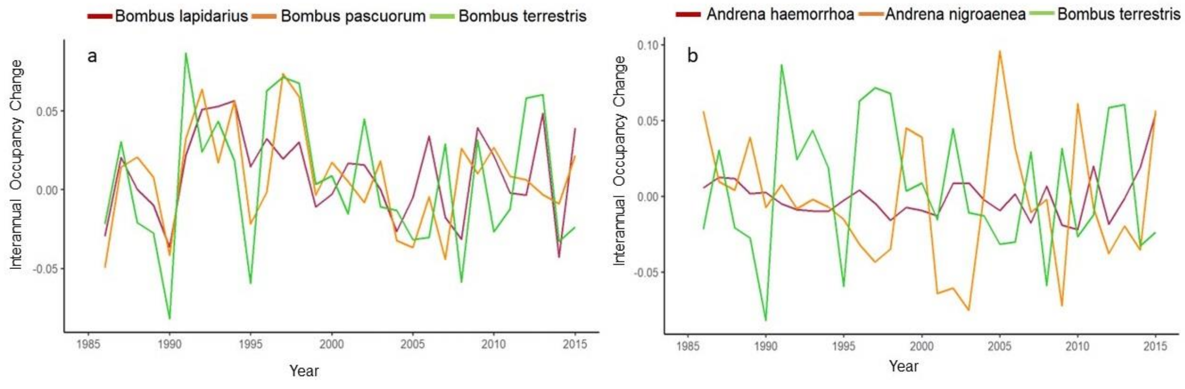


Figure 4.2: Three Bombus species (a) have positively correlated occupancy dynamics. Two Andrena species have positively correlated occupancy dynamics, but have negatively correlated occupancy dynamics with Bombus terrestris (see table Table 4.1 for r scores).

Table 4.1: Pearson’s r correlation scores of inter-annual occupancy estimates for bee species pairs identified as primary pollinators of apple (A), field beans (B), oilseed rape (O) and strawberry (S) crops (positive scores highlighted in blue and negative scores highlighted in red, *indicates a significant (P≤0.05) correlation).

	Andena cineraria (O)	*Andrena dorsata* (A)	*Andrena haemorrhoa* (A,O)	*Andrena nigroaenea* (A,O)	*Andrena nitida* (A)	*Andrena scotica* (O)	*Bombus hortorum* (A,B)	*Bombus lapidarius* (A, B,O,S)	*Bombus pascuorum* (A,B)	*Bombus terrestris* (A,B,O,S)
Andrena cineraria	**1**	**0.20**	**0.03**	**0.31***	**0.42***	**0.23**	**-0.07**	**-0.33***	**-0.05**	**-0.09**
Andrena dorsata		**1**	**0.09**	**0.25***	**0.51***	**0.33***	**0.14**	**-0.05**	**0.01**	**-0.14**
Andrena haemorrhoa			**1**	**0.14**	**0.25**	**0.57***	**-0.02**	**-0.13**	**-0.07**	**-0.31***
Andrena nigroaenea				**1**	**0.57***	**0.47***	**0.01**	**-0.15**	**-0.23**	**-0.36***
Andrena nitida					**1**	**0.59***	**0.33***	**-0.08**	**0.11**	**-0.18**
Andrena scotica						**1**	**0.14**	**-0.13**	**0.03**	**-0.35***
Bombus hortorum							**1**	**0.41***	**0.37***	**0.20**
Bombus lapidarius								**1**	**0.57***	**0.53***
Bombus pascuorum									**1**	**0.44***
Bombus terrestris										**1**

4.4.3 Inter-annual occupancy variation

Across all crops, when considering only the primary flower visitors, a greater variation in mean occupancy was found compared to when the core flower visitors or all flower visitors combined were considered. For all crops as the number of species increased across flower visitor categories there was a corresponding decrease in variation in mean occupancy. When only primary pollinators were included, standard deviation ranged between 0.015 and 0.032. The inclusion of all core flower visitors reduced the standard deviation by between 25% and 60%, compared to the primary flower visitors alone. The inclusion of all flower visitors combined reduced the standard deviation by between 40% and 70% compared to the primary flower visitors alone (Table 4.2; Figure 4.3a-4.3d).

For the primary and core flower visitor groups, strawberry, which had the fewest bee species in these categories, had the greatest standard deviation. When including all flower visitors, bean, which had the fewest flower visitors overall, had a standard deviation of 0.014, the highest of the four crops. Conversely, when considering all flower-visiting bee species, oilseed, which has the highest number of overall flower visitors, had a standard deviation of 0.007, which was the lowest of all four crops.

Table 4.2. Standard deviation of mean occupancy for primary, core and all flower visitors per crop (number of species in brackets).

Crop	Primary Flower Visitors*	Core Flower Visitors**	All Flower Visitors***
Apple	0.015 (n=8)	0.011 (n=18)	0.009 (n=30)
Bean	0.025 (n=4)	0.014 (n=9)	
Oilseed	0.015 (n=6)	0.008 (n=36)	0.007 (n=44)
Strawberry	0.032 (n=2)	0.013 (n=8)	0.009 (n=14)

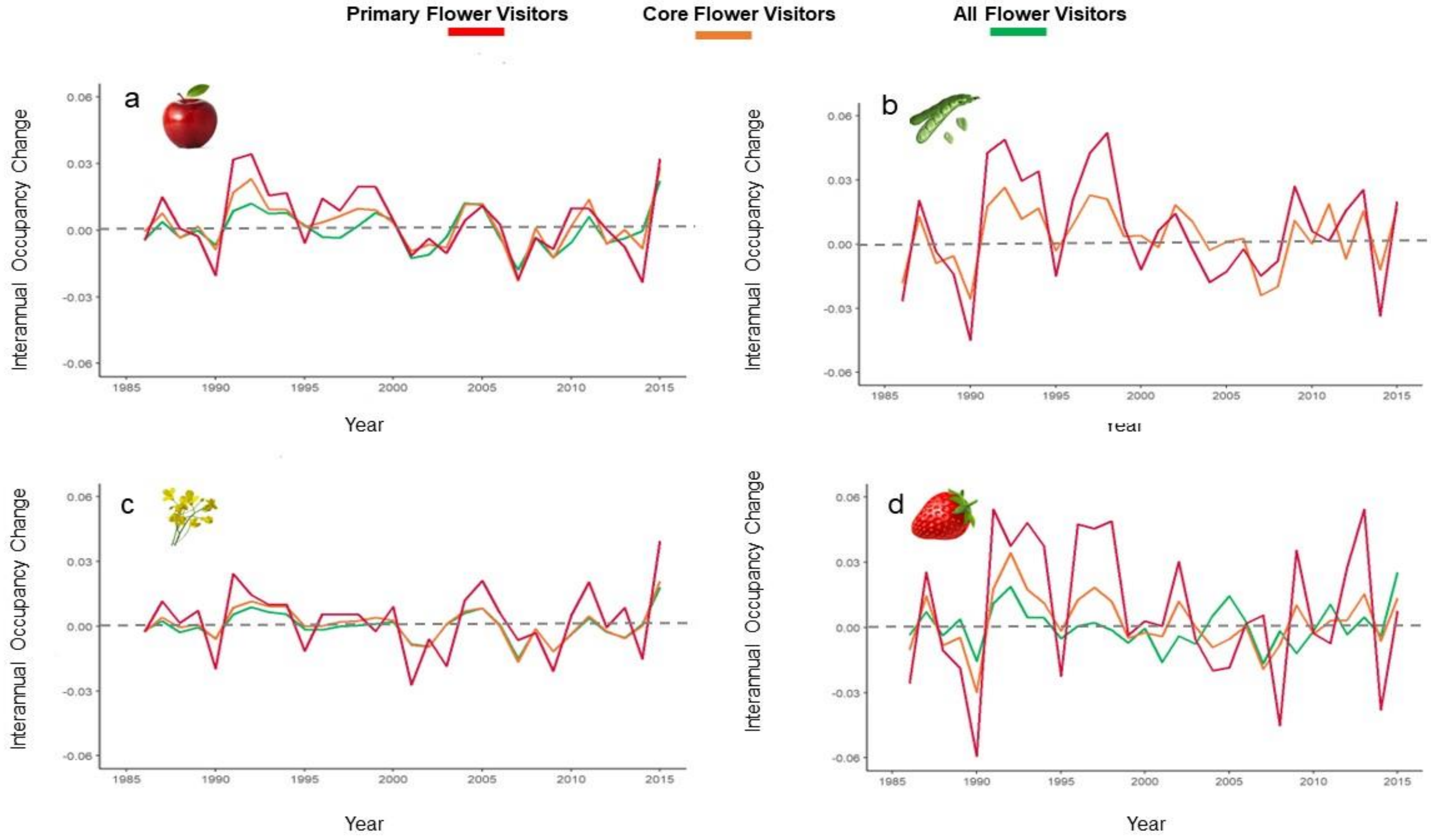


Figure 4.3. Mean inter-annual occupancy change of primary, core and all visitors for (a) apple, (b) bean (primary and core only), (c) oilseed and (d) strawberry crops. Dashed grey line denotes a mean inter-annual occupancy change of zero.

4.4.4 Impact of removing bee species on stability of crop pollinator occurrence

As species were removed from each crop's pollinator community, based upon their overall mean occupancy, from low to high, the variation in mean occupancy initially showed no or little increase across all four crops, before beginning to show a marked increase. When approximately a third of each crop's bee pollinators were removed from the dataset set, standard deviation increased by around 25%, which extended to a 50%, 100% and 200% increase when approximately half, two thirds and three quarters of each crop's bee pollinators were removed (Figure 4.4; Appendix 12).

4.4.5 Occupancy uncertainty confidence limits.

When using the lower 2.5 and upper 97.5 confidence limit occupancy estimates for each species, the same analyses described above generated slightly different numerical results, but followed almost identical patterns to that of the mean occupancy estimates. For both sets of confidence limit occupancy estimates the hierarchical clustering analysis produced a dendrogram that was split into five clusters based upon the KGS penalty function. The number of clusters to which each crop's flower visitors were assigned was identical to the mean occupancy estimate, except for the upper 97.5 strawberry data, where crop flower visitors were split across four, rather than three, clusters. Whilst some species were placed into slightly different clusters, the same broad patterns remained (Appendix 13). The lower 2.5 and upper 97.5 confidence limit occupancy estimate data again indicated that amongst the ten primary pollinators, species from the same genus generally had more synchronous occupancy dynamics than species from different genera (Appendix 14).

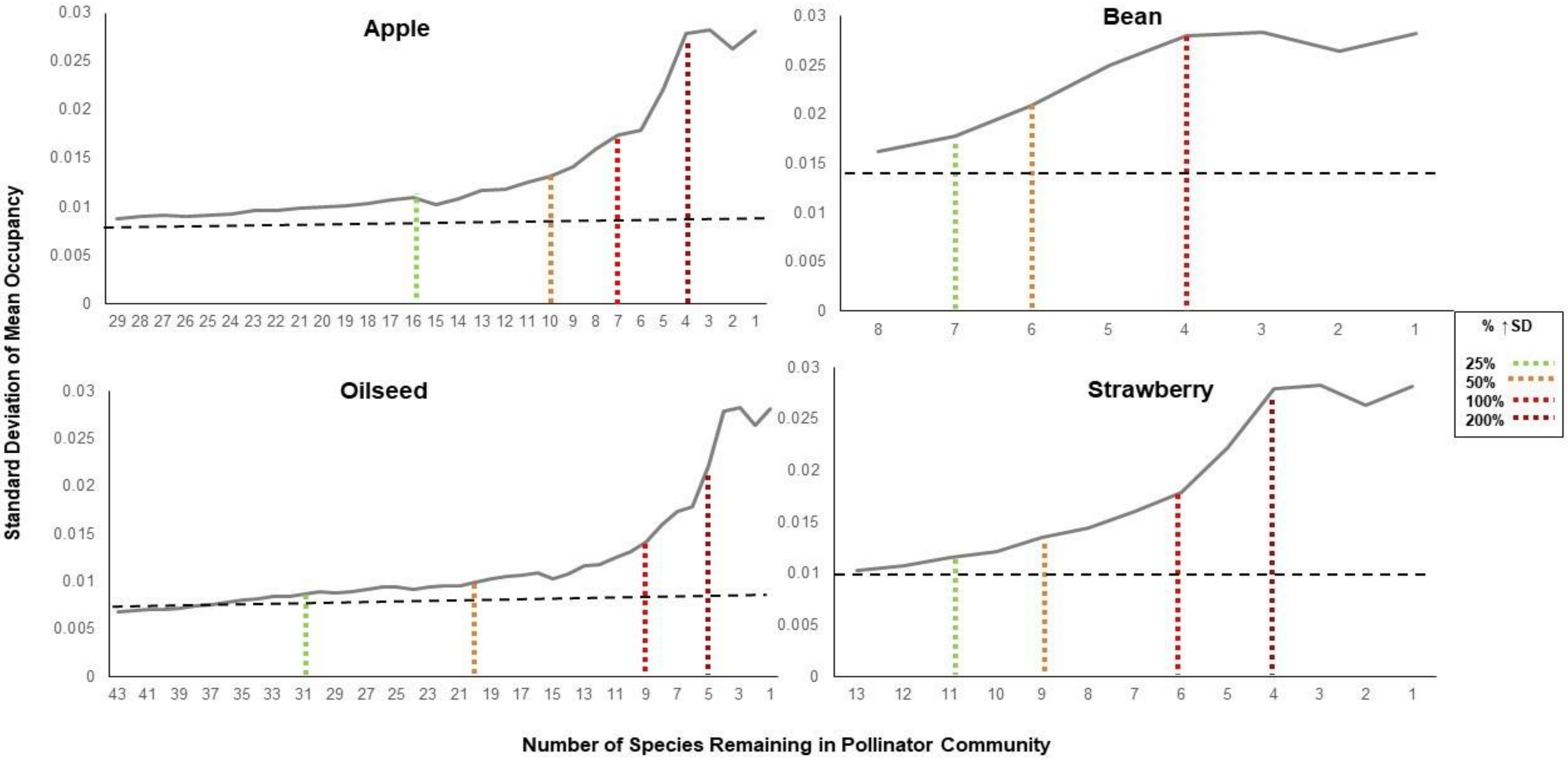


Figure 4.4: Standard deviation of mean occupancy for bee crop pollinator communities as successive species are removed for apple, bean, oilseed and strawberry crops. Grey dashed line denotes standard deviation of mean occupancy for bee crop pollinator community if all species are present.

For the data considering the stability of pollinator occurrence both the lower 2.5 and upper 97.5 confidence limit occupancy estimates, whilst generating slightly different SD numbers, followed an identical pattern to that of the mean occupancy estimate data (Appendix 15). Additionally, as species were gradually removed the same patterns emerged, with an initial gradual increase in standard deviation as species were removed, followed by marked increase as each crop's pollinator community was reduced (Appendix 16).

4.5 Discussion

4.5.1 Overview

This study is one of the first to explicitly test how bee crop pollinator community composition and species richness might affect the stability of crop pollinator occurrence, and consider the implications of this for pollination services. We found that bee crop pollinator communities composed of a small number of closely related species are likely to exhibit more synchronised inter-annual occupancy dynamics, and show a greater variation in mean occupancy, compared to crop pollinator communities comprised of a more diverse set of bee species. Our results indicate that more species-rich crop pollinator communities comprised of bees from different genera encompass species with asynchronous occupancy dynamics. Asynchrony between species populations is an important mechanism of diversity-stability relationships, and asynchronous fluctuations in pollinator communities could increase the inter-annual stability of the crop pollination services they provide (Senapathi et al. 2021). Our findings support this by showing that crops composed of diverse, species rich pollinator communities are likely to show lower variation in mean occupancy, compared to less species-rich communities. Whilst we focused specifically on crop pollinator occurrence, in the form of inter-annual changes in occupancy, based upon citizen science collected biological records, inter-annual changes in citizen science-based distribution records have been demonstrated to act as proxy for year-to-year changes in species abundances in another group of pollinating insects - butterflies (Mason et al. 2018). It is therefore reasonable to expect that the general patterns we found in bee species occupancy will be reflected in bee species abundances.

4.5.2 Inter-annual changes in occupancy

The first of our analyses indicate that different bee species show variable occupancy dynamics, which may reflect differences in the corresponding life history traits of bee species (Williams et al. 2010), such as body size, nesting type, phenology and reproductive strategy (Michener 2000). For example, the bee pollinators included in our analyses encompass both cavity and ground-nesting species, as well as a range of dietary breadths, flight periods and sizes. Additionally, these results indicate that crops with dominant pollinators from different genera are more likely to include species with asynchronous occupancy dynamics compared to crops whose dominant pollinators are all from the same genera. For example, relatively synchronous occupancy dynamics were observed within the dominant crop pollinating *Andrena* species and *Bombus* species, respectively, which were in contrast to the relatively asynchronous occupancy dynamics observed between the two genera. Previous work in other insects (*Lepidoptera*) has shown that synchrony in population dynamics is linked to phylogeny (Greenwell et al. 2019) and that traits that mediate response to environmental conditions (cf. ‘response traits’) have a phylogenetic signal (Melero et al. 2022).

The four *Bombus* species identified as dominant pollinators of the four crops all have relatively similar life histories. They are large species, found throughout Great Britain, nesting in colonies below, or occasionally above, ground in old bird and mammal nests, and fly from March until around October (Else & Edwards 2018). In contrast the six *Andrena* species identified as dominant pollinators are relatively less widespread, medium-sized species, found predominantly in the southern half of Great Britain, with single females laying eggs in self-excavated burrows in scattered, or occasionally dense, aggregations in sparsely vegetated soil. In most cases they are spring-flying species, active between March and June (Else & Edwards 2018). The asynchronous occupancy dynamics exhibited between the two genera indicate that crops pollinated by both *Andrena* and *Bombus* species may have pollinator communities with, overall, more stable occupancy dynamics, which could translate to more stable and resilient pollination services. Future work, investigating the phylogenetic relationships, and traits, of bee species could help to explain why particular species exhibit similar, or contrasting, inter-annual changes in occupancy, and inform management to promote more stable occurrence dynamics.

4.5.3 Inter-annual occupancy variation

Our findings support evidence that high bee diversity may stabilize crop pollination service (Klein, 2009; Senapathi et al. 2021) and that a species-rich community of pollinators could help ensure that pollination service is sustained under a range of conditions (Fijen et al. 2018; Science for Environment Policy, 2020). High inter-annual variations in crop pollination service have negative implications for food security and farmer livelihoods (Garibaldi et al. 2011a). Thus, whilst crop pollination is often predominantly delivered by a small number of species (Fijen et al. 2018), our results indicate that pollinator management to increase crop yield stability may need to target a more diverse set of bee species than at present. Currently agri-environment schemes primarily benefit common bumblebee species (Wood et al., 2015). However, solitary bee species are more important pollinators of some crops (Hutchinson et al. 2021), and based upon our findings show different occupancy dynamics to bumblebee species, likely driven by differences in ecology that underpin functional trait diversity (Forrest et al. 2015).

Based upon our results the degree to which species richness can reduce variation in mean occupancy, and potentially bee species abundances, may vary, however, among crop types in Britain. Field bean has long tubular flowers, which generally only long-tongued bees, such as *Bombus* species, can legitimately pollinate (Cook et al. 2003). This crop may be especially susceptible to inter-annual variation in pollination service delivery due to the relatively synchronous occupancy dynamics of its primary pollinator community. Field bean had the lowest total number of bee species identified as flower visitors across the four crops, some of which are short-tongued *Andrena* species that are unlikely to make a significant contribution to bean pollination (Hutchinson et al. 2021). Long-tongued bees, including bumblebees, are amongst the most severely declining species in the UK, and across Europe (Goulson, Lye, & Darvill, 2008). As such, management to ensure sustainable pollination service delivery to field bean may be reliant upon encouraging more stable populations of a relatively small core group of bumblebee species. For example, hedgerows have been demonstrated to stabilise bumblebee populations in agricultural fields (Gardner et al. 2021). Additionally, at least one species of long-tongued solitary bee - *Anthophora plumipes* - has been evidenced as an effective pollinator of field bean (Bond & Kirby 1999), and based upon our results has less synchronous occupancy dynamics with beans' four primary flower visitors than between them. However, *A. plumipes* prefers to nest in vertical soil profiles (BWARS 2021), which are currently not a common feature of agricultural landscapes.

Strawberry, which whilst primarily visited by bumblebees, has flowers with high nectar accessibility (Garibaldi et al. 2015) and can be effectively pollinated by a range of short-tongued solitary species (Bansch et al. 2021). The lack of current diversity in its known pollinators could reflect the fact that strawberry production is often achieved through the use of plastic-protected tunnel environments (Allen et al. 2015), which may inhibit access by smaller solitary species (Chagnon, Gingras & DeOliveira 1993). Intensive production of crops under plastic may benefit from making flowers more attractive to different pollinators by opening the sides during crop flowering and providing appropriate floral and nesting resources to support short-tongued solitary species.

Oilseed rape and apple had the greatest number of bee species across all three categories of flower visitors and the lowest standard deviation of mean occupancy amongst our four focal crops. Even amongst their primary pollinators, composed of a core group of *Andrena* and *Bombus* species, there was evidence of relatively asynchronous occupancy dynamics, possibly related to differences in their solitary versus social ecology (Michener, 2000). Additionally, both crops are known to be visited by a range of other solitary bee genera (Hutchinson et al. 2021), which our results indicate have variable occupancy dynamics. Stability of pollinator occurrence, and potentially crop pollination service delivery, for both crops could therefore be further promoted through management targeted at a wide diversity of solitary species. For example, current agri-environment measures are heavily biased towards ground-nesting bee species (Image et al. 2022) and rarely incorporate suitable nesting and floral resources for cavity-nesting species (Gresty et al. 2018), which can be important pollinators of both apple and oilseed crops (Hutchinson et al. 2021).

4.5.4 Impact of removing bee species on stability of crop pollinator occurrence

Whilst we found that there within was no, or little, increase in the variation of overall mean occupancy as species were initially removed from each crop's pollinator community, this was followed by a rapid acceleration as each crop's pollinator community was increasingly depreciated. Whilst rarer crop pollinators may not contribute significantly to increased stability of pollinator occurrence, management recommendations aimed at supporting a limited subset of dominant pollinating species (Kleijn et al. 2015) could fail to protect crop pollination services under all circumstances (Fijen et al. 2018; Winfree et al. 2018). A diversity of non-dominant crop pollinating species could supplement service provision when dominant ones are performing sub-optimally; for example, after periods of disturbance (Senapathi et al. 2015), such as extreme weather events (Oliver et al. 2015b). Current crop pollinating species that are not dominant now may also ultimately replace dominant species should future environmental conditions force current pollinators outside their climatic niches (Oliver et al. 2015b). Bee species have been demonstrated to show differential responses to a range of factors, including daily weather (Brittain, Kremen & Klein, 2013; Rogers, Tarpy & Burrack 2014) and long-term climate warming (Bartomeus et al. 2013). Conservation measures aimed at promoting greater species richness amongst crop pollinator communities may therefore be vital to protect service provision in light of accelerating rates of anthropogenic-induced environmental changes (Oliver et al. 2015a).

4.5.5 Study limitations

There are a number of caveats to consider when interpretating our results related to the stability of pollinator occurrence across our focal crops. Firstly, whilst the occupancy model estimates utilised in this study have been demonstrated to perform well at dealing with many of the biases associated with using unstructured biological records (Issac et al. 2014), there is some degree of uncertainty inherent within the output, which varies among bee species and years (Powney et al. 2019). Additionally, the low sample sizes of some of the categories, i.e., the primary pollinators, could also have resulted in slightly less accurate estimates of variance compared to the other two larger categories of pollinators, in the analyses related to the stability of pollinator occurrence. However, whilst we treated all bee species, years and categories equally, we were largely investigating relative change in mean occupancy estimates, and not making any predictions based upon absolute values. The patterns and observations reported should reflect the true differences among each crop's stability of pollinator occurrence.

Furthermore, whilst there is known to be a positive relationship between species occupancy and abundance (Holt, Gaston and He, 2002), this may not be the case for all species and all contexts, and may also depend on the scale at which occupancy is considered. We also looked specifically at bee species occupancy, but ecosystem service function depends not only on species occurrence, but also their local abundance (Waldock et al. 2021). We make the assumption here that pollinator occurrence and abundance are closely related, based upon prior evidence that inter-annual changes in citizen science collected distribution records are a reasonable proxy for inter-annual changes in abundance (Mason et al. 2018). However, further work exploring this relationship is urgently required. The positive relationship observed between occupancy and abundance can be noisy and non-linear for some taxa (Schulz, Vanhatalo & Saastamoinen 2020). This inconsistent relationship between abundance and occupancy is likely driven by different life histories amongst species, and more research is needed to further understand the relationship between the two measures (Steenweg et al. 2018). Nonetheless given the difficulties in identifying many species, true abundance data to investigate bee trends would be difficult to obtain and our results currently represent the best alternative in its absence.

The differing geographical coverage of individual crops may also play an influential role and should also be considered in future research. For example, whilst field bean and oilseed are grown across much of lowland Britain, apple and strawberry production is more concentrated around areas of south-east and western England, where agri-environment participation is generally lower (Image et al. 2022). Consequently, these landscape differences may impact upon the occupancy dynamics of bee species. Finally, whilst bees are the primary pollinators of insect-pollinated crops (Potts et al. 2010), many other insect groups are important pollinators of many crops (Rader et al. 2016). For example, *Diptera*, notably hoverflies, are known to be abundant and effective pollinators of a wide range of crop types (Rader et al. 2020). A comprehensive review of the impacts of inter-annual occupancy dynamics and community diversity on crop pollination service would also need to consider these, and other, insect groups.

4.6 Conclusions

Bee pollinators provide a critical ecosystem service to agriculture by pollinating the majority of leading global crops (Klein et al. 2007). As well as improving the quantity and quality of crop yields (Bommarco, Marini and Vaissière 2012; Klatt et al. 2014; Garratt et al. 2014a), increasing evidence indicates that insect pollinators can positively influence pollination service stability (Klein, 2009; Garibaldi et al., 2011a). Our study indicates that species rich and diverse bee crop pollinator communities exhibit more diverse inter-annual occupancy dynamics and show less variance in mean occupancy than communities composed of small numbers of closely related species. High inter-annual variations in pollinator populations pose risks to both average crop yields and yield stability, and threaten food security (Senapathi et al. 2021). Given evidence of a positive link between species diversity and the stability of crop pollination services (Garibaldi et al. 2015; Senapathi et al. 2021), agri-environment schemes aimed at conserving ecosystem-providing organisms (Batary et al. 2015) may benefit from a greater consideration of solitary bee resource provision. Solitary species are highly speciose (Wood, Holland and Goulson, 2016) and are important pollinators of many crops (Martins et al. 2015, Russo et al. 2017; Woodcock et al. 2013; Perrot et al. 2018). Given differences in pollinator community composition, crop-specific management, aimed at specific pollinator taxa, should also help improve future crop pollinator service provision (Garratt et al. 2014b).

5 General Discussion

5.1 Summary

5.1.1 Overview

The benefits of diverse pollinator communities on the scale, quality and stability of crop pollination service delivery are well established (Vasiliev & Greenwood 2020). Declines in wild bee species (IPBES 2016), the principal pollinators of many agricultural crops (Klein et al. 2007; Potts et al. 2010) therefore represent a significant threat to human food systems (Marshman, Blay-Palmer & Landman 2019), due to increased risks of pollination deficits, yield instability and loss of crop system resilience (Dicks et al. 2021). Whilst agri-environment schemes aimed at protecting biodiversity and ecosystem services are well-established (Batary et al. 2015), their effectiveness has been highly variable (Scheper et al. 2013; Cole et al. 2020), with most measures benefitting a limited suite of common bee species (Senapathi et al. 2015; Wood, Holland & Goulson 2015). There is an urgent need to develop more targetted conservation measures to protect and restore pollinator biodiversity in agricultural landscapes (Vasiliev & Greenwood 2020). However, this hinges on understanding the role of different bee species and how assemblages vary with crop type, in order to develop appropriate measures to protect crop pollinators and the services they provide (Isaac et al. 2017). Identifying economically important crop pollinating species, monitoring their status and trends in agricultural areas, and understanding how these crop pollinator communities vary across time and space were identified by the European Commission as key objectives to "facilitate more targeted management" of pollinators and protect future food security (Potts et al. 2021).

5.1.2 Chapter findings

Chapter 2 produced national lists of bee pollinators of four economically important crops in Great Britain, and identified bee species which likely represent the dominant pollinators of each crop. Understanding which species provide pollination services to crops can help facilitate targeted management aimed at improving agricultural production (Garratt et al. 2014a) and guide national schemes aimed at monitoring crop pollinator populations in agricultural landscapes (Carvell et al. 2020). Chapter 2 fills a major research gap by outlining a methodology by which comprehensive, crop-specific lists of pollinators can be identified (Potts et al. 2021). The results demonstrated that whilst a small suite of *Andrena* and *Bombus* species may make a disproportionate contribution to crop flower visitation, a wide diversity of solitary species, from across eight different genera, are potential pollinators of our focal crops.

Chapter 3 evaluated the capacity of the most commonly employed survey methods to sample crop pollinating bee species in our four contrasting focal crops. Systematic monitoring of crop pollinator abundance and diversity in agricultural landscapes is essential to assess and refine management measures aimed at protecting pollinator populations, pollination services and community resilience (Breeze et al. 2021; Cole et al. 2020). Chapter 2 fills a research gap by being the first assessment of sampling methodologies to cover multiple crops and focus on known crop pollinating species. The results supported existing evidence that transect walks and pan traps sample distinct components of pollinator communities (Westphal et al. 2008; O'Connor et al. 2019; Pei et al. 2022). Transect walks were a more efficient means to sample bumblebee diversity. Pan traps, particularly yellow ones, however, sampled both a higher abundance and richness of crop pollinating solitary bees. The results indicate that transect walks are appropriate to sample the bee crop pollinator communities of primarily bumblebee pollinated crops, such as field bean, and potentially dominant crop pollinating species, provided surveyors are trained at catching and/or identifying target *Andrena* species (Birtle 2020). However, for crops such as oilseed where smaller solitary species (e.g. *Lasioglossum* sp.) are abundant and important pollinators, pan traps represent an essential complementary sampling method. Furthermore, to measure visitation rates of different guilds observation plots are likely to be a vital addition, given the potential propensity of transect walks to overestimate the contribution of bumblebee crop flower visits relative to solitary bees.

Pollinator management needs to consider both current circumstances and future environmental conditions (Senapathi et al. 2015) in order to support resilient communities. Chapter 4 examined patterns in the inter-annual occupancy dynamics of our focal crops' pollinator communities. It is the first piece of research to investigate to what extent pollinator community composition and species richness may affect the stability of crop pollinator occurrence. This can inform our understanding about the resilience of pollination services in the face of increasing rates of anthropogenic induced environmental change (Oliver et al. 2015a, 2015b). The results indicated that crop pollinator communities composed of a small number of closely related bee species show more synchronous occupancy dynamics and exhibit greater variance in mean occupancy compared to crops with more diverse pollinator communities. The results indicate that crops with a diversity of pollinating bee genera may experience less variable inter-annual fluctuations in the availability of pollinators, which could increase both the inter-annual stability and long term resilience of crop pollination services.

5.2 Synthesis of key findings in the wider context

5.2.1 Agri-environment schemes

The results of chapter 2 indicate that current AES are not optimally designed for many crop pollinator communities, as they do not support diverse communities of solitary species (Wood, Holland & Goulson 2015). A favoured AES option for increasing pollinator numbers in farmland is sowing wildflower seed mixes along field margins (Nichols, Holland & Goulson 2019) to provide floral resources that are attractive to insect pollinators (Gresty et al. 2018). In England this includes a 'nectar flower' mix (AB1) and a 'bumblebird' mix (AB16) that are rich in *Fabaceae* plants (DEFRA 2018a). Whilst such mixes are beneficial for bumblebee populations (Wood et al. 2015), they are rarely utilised by solitary species, which predominantly rely on non-sown species in the wider environment (Wood, Holland & Goulson 2016a; Gretsy et al. 2018). Even the more diverse flower-rich mix (AB8) recommended, fails to encompass many of the wildflowers which are most commonly visited by the solitary bee species (Gretsy et al. 2018; Nichols, Goulson & Holland 2019) that we identified as potential pollinators of apple, oilseed and strawberry.

Recent evidence that AES participation in England is not translating into improved visitation by solitary bees to our focal crops (Image et al. 2022), further highlights the need for management to support a broader range of solitary species (Wood, Holland & Goulson 2016a; Gretsy et al. 2018). This is particularly imperative in light of evidence that crop pollinator communities can vary considerably across fields and years (Kremen, Williams & Thorp 2002; Adamson et al. 2012; Winfree et al. 2018). In chapter 2 half or less of the species identified as dominant crop pollinators were recorded in all field studies. Additionally a surplus of pollinators can protect pollination services from ongoing climatic and land use changes (Nayak et al. 2015; Oliver et al. 2015b).

Current AES are especially poor at providing early-season floral resources (Nichols, Holland & Goulson 2022a), which are critical for spring-flying *Andrena* species (Wood, Holland & Goulson 2016a) that are important apple pollinators (Campbell et al. 2017). The low diversity and abundance of *Hylaeus* and *Osmia* species in the crop flower visitor lists generated for chapter 2 likely reflects the lack of AES provision for cavity nesting species (Image et al. 2022). Hedgerows provide nesting opportunities for cavity-nesting species (Gresty et al. 2018), and early and late floral resources for bees (Image et al, 2022), when wildflowers are not in bloom (Nichols, Holland & Goulson 2022a). However, reductions in the presence, length and quality of hedgerows in farmland within Britain have reduced their potential to support pollinator populations (Garratt et al. 2017; Wood & Roberts 2017). The overall lack of diverse resource provision by AES (Image et al. 2022) is particularly critical for oilseed pollination, which relies upon a diverse range of pollinators that require appropriate nesting sites and floral resources outside of its flowering time (Woodcock et al. 2013).

A recent meta-analysis of apple, oilseed and field bean field studies evidenced that insect pollination can increase crop yield stability (Bishop, Garratt & Nakagawa 2022). Chapter 4 highlighted the potential importance of diverse bee communities for the stability and resilience of crop pollination services due to the asynchronous occupancy dynamics of different bee species. Mass-flowering crops such as oilseed and field bean, are often grown in rotations with cereal crops, which do not provide floral resources for pollinators (Hass et al. 2019). This variability in resources is likely to compound natural fluctuations in bee populations (Roubik 2001; Williams, Minckley & Silveria 2001), and may be particularly critical for field bean pollination due to the synchronous occupancy dynamics of its small suite of bumblebee pollinators. Evidence suggests that field boundaries (wide agri-environment margins and hedgerows), in agricultural landscapes can stabilise bumblebee populations, which may be particularly critical in the future to buffer populations against weather extremes and increasing average temperatures due to climate change (Gardner et al. 2021), which are predicted to adversely affect bumblebee populations (Uthoff & Ruxton 2022).

5.2.2 Pollinator monitoring

Effective sampling protocols are vital to assess the effectiveness of management measures and identify where refinements may be necessary (Cole et al. 2020). Additionally, long-term monitoring data could be used to refine the assessments of the dymanic trends of pollinators as investigated in chapter 4. The development of standardised sampling and monitoring frameworks that provide information on both population trends and activity within crop fields are critical to protect crop pollinator populations and the services they provide (Garratt et al. 2019; Breeze et al. 2021; Potts et al. 2021). Monitoring key pollinating taxa in agricultural areas is an emerging aim of both international (Potts et al. 2021) and national (Carvell et al. 2020) schemes. Targeting crop pollinating species would allow for indirect assessments of the availability of pollinators and changes in pollination service (Potts et al. 2021). Chapter 2 demonstrated that *Andrena* and/or *Bombus* species represent the key crop pollinating genera of our focal crops. Additionally, *Lasioglossum* species were identified as potentially important pollinators, particularly of oilseed rape, for which they can be both abundant and effective flower visitors (Perrot et al. 2018). These three genera also represent the major flower visitors of most economically important insect pollinated crops in Europe (Kleijn et al. 2015). Given the considerable cost of specific pollination service monitoring

(Breeze et al. 2021), protocols for crop pollinating species and/or pollination services could focus on gathering data for species within these genera. However, given the established benefits of an entire species pool of crop pollinators for achieving high thresholds of pollination service (Winfree et al. 2018) monitoring schemes may wish to broaden the suite of species targeted in agricultural landscapes.

The results of chapter two are being used as part of the UK pollinator monitoring scheme by highlighting the key crop pollinating species that could be the focus of monitoring protocols in crops (Carvell et al. 2020). Monitoring schemes may also wish to consider *Osmia* species in surveys of key crop pollinators, particularly if agri-environment schemes are better adapted to cater for their ecological needs in the future (Gretsy et al. 2018), both to measure their trends and assess the impact of targeted interventions. Several species, including notably *O. bicornis*, were identified as potential crop pollinators in chapter 2. *O.bicornis* is documented as a key pollinator of apple, oilseed and strawberry crops (Kleijn et al. 2015). It is readily identifiable, and offer opportunities to enhance the functional diversity of pollinator communities, which can benefit crop yields (Woodcock et al. 2019).

Chapter 3 supports existing evidence that observational methods are biased towards slower-flying, visually conspicuous bees (Prendergast et al. 2020). We found that even when carried out by trained researchers, transect walks predominantly sample bumblebees, which tallies with another crop study which found that, compared to pan traps, transect walks sampled a higher diversity of bumblebees (Krahner et al. 2021). As in other studies (Gibbs et al. 2017; Templ et al. 2018; Boyer et al. 2020; Krahner et al. 2021) we also found that some larger, more conspicuous *Andrena* species where also observed during transect walks, although in our study this was predominantly in low numbers in apple. Transects may be suitable for surveying bumblebees, and potentially some large and conspicuous solitary bees, such as some *Andrena* and *Osmia* species, which tend to characterise the dominant pollinator communities of most crops (Kleijn et al. 2015). However, our results corroborate existing findings that the ease with which certain taxa can be identified may be contigent upon crop type (Garratt et al. 2019). Chapter 2 showed that oilseed is visted by a wide range of *Andrena*, but relatively few were seen and/or identified on transect walks in the surveys analysed for chapter 3. This may reflect the fact that, compared to apple and strawberry, which are grown in spaced out rows, oilseed is grown in dense fields which may obscure visibility and reduce capture rates (Garratt et al. 2019).

A recent assessment of transect walks for monitoring bees in meadow habitats found that they only sampled around half of species present (Viliani et al. 2022); a result that was mirrored in our surveys of cropped habitats. In particular, transect walks often do not work well for sampling small and more mobile species (Berglund et al. 2019). We found that many *Andrena*, and most *Lasioglossum* species, were more comprehensively, or exclusively, sampled by pan traps. Similar findings have been documented elsewhere (Grundel et al. 2011; Templ et al. 2018; Franceschinelli et al. 2019; Krahner et al. 2021; Pei et al. 2022). These findings indicate that studies to identify crop pollinating taxa which rely on observational methods alone (e.g., Kleijn et al. 2015) may underestimate the diversity and contribution of smaller solitary species, which are often difficult to see and catch (Kranher et al. 2021). Some studies have used pan traps to help identify crop pollinating species. In this approach pan traps matching the colour of the target crop (e.g., Marini et al. 2012; Ahrenfeldt et al. 2019) have been utilised on the premise that they will preferentially catch insects that are attracted to crop flowers of that colour. However, based upon our results this approach may not be effective, given that the pan trap colour matching that of the target crop only caught the most crop pollinating species in oilseed. From a monitoring perspective our results further support the implementation of pan traps, even in the case of professionally run monitoring schemes carried out by trained researchers (Breeze et al. 2021), to capture trend information and assess the impacts of targeted conservation and management on smaller and inconspicuous species (Gill & O'Neal 2015; Carvell et al. 2016; Potts et al. 2020).

Yellow pan traps were the most efficient colour to sample *Andrena* and *Halictidae* bees in our crops; a finding that is also documented across a range of habitats (Abrahamczyk, Steudel, & Kessler 2010; Gollan et al. 2011; Heneberg & Bogusch 2014; Sircom, Jothi & Pinksen 2018; Krahner et al. 2021). Whilst we found that using three colours is the most common protocol, previous studies indicate that blue and white pan traps more commonly catch social bees such as honeybees and bumblebees (Leong & Thorp 1999; Joshi et al. 2015; Glaum et al. 2017; Sircom et al. 2018; Krahner et al. 2021). As such, the sole use of yellow traps could provide a means to carry out targeted sampling and lower the considerable cost of processing pan trap samples (Breeze et al. 2021); although further work is needed to confirm this.

The application of pan traps may not be equally efficient in all crops, however. Despite chapter 2 evidencing that oilseed rape is visited by a wide diversity of *Andrena* and *Lasioglossum* species, a small number and diversity of solitary bees were sampled in our oilseed pan trap datasets. These results mirror monitoring protocol trials in oilseed rape fields for the UK Pollinator Monitoring scheme (Carvell et al. 2020), which due to the low number of crop pollinator visitors sampled by pan traps concluded that they are "not likely to be representative … of which pollinators are visiting a coincident or nearby crop". Growing evidence indicates that pan trap catches are inversely affected by the density of flowers in the surrounding area (O'Connor et al. 2019; Kuhlman et al. 2021; Pei et al. 2022). Additionally, many *Andrena* and *Lasioglossum* bees preferentially forage on open yellow flowers (Lazaro, Hegland & Totland 2008), and thus oilseed with its abundant yellow and nectar rich blooms (Thompson, Stefan & Knight 2021), may draw bees away from pan traps.

5.3 Recommendations

5.3.1 Agri-environment schemes.

Existing policy and grower management strategies generally do not consider the resource needs of solitary bees, despite the important crop pollination services that they provide (Kline & Joshi 2020). Agri-environment measures aimed at enhancing solitary bee pollination services should consider providing new or improved seed mixtures that include suitable and diverse plant species (McHugh et al. 2022). There is now a wealth of studies identifying beneficial floral resources for solitary bee species in farmland and surrounding semi-natural habitats (Wood, Holland & Goulson 2016a; Gretsy et al. 2018; Nichols, Holland & Goulson 2019; Cole et al. 2017; Phillips et al. 2019). Combined with the results of chapter 2, these studies can be used to guide AES and broader landscape policies aimed at promoting diverse crop pollinator populations (Figure 5.1).

Based upon the solitary bee species we identified as potential pollinators of one or more of our focal crops, at least twenty plant species emerge as important sources of forage (Table 5.1). Several of these are also visited by various specialist species (Wood, Holland & Goulson 2016b) and offer opportunities to simultaneously conserve broader biodiversity (Sutter et al. 2017). Such plant species can be promoted via reduced herbicide application around field crops such as bean and oilseed (Crochard et al. 2022) and relaxed mowing regimes in alleyways around orchards and soft-fruit farms (Campbell et al. 2017). Several, however, are considered weeds and communicating their value to land-managers and policy makers represents a significant challenge (Balfour & Ratnieks 2022). Nonetheless, encouraging tolerance of at least some beneficial weeds, within, for example, ‘cultivated margins for arable plants’ (DEFRA 2022a), represents an opportunity to provide diverse floral resources for solitary bees within farmlands (McHugh et al. 2022). Weeds, including around pollinator-independent crop fields, can provide important foraging resources for crop pollinating bee species (Crochard et al. 2022). Furthermore, open patches between plants in such margins provide bare areas of soil (DEFRA 2022a) provide valuable nesting sites for ground-nesting solitary bees (McHugh et al. 2022), including *Andrena* and *Lasioglossum* species, who’s nesting requirements are currently not incorporated into any AES options (Nichols, Holland & Goulson 2022a).

Legiminous rich wildflower mixes currently recommended as part of agro-environment measures, such as Countryside Stewardship (DEFRA 2018b), e.g., mixes AB1 and AB8, are likely to be sufficent for land-owners and farmers growing crops such as field bean, which are almost exclusively visited by a small number of dominant bumblebee pollinators. Those growing crops such as apples, strawberries, and notably oilseed, whose pollination can be enhanced by diverse communities of solitary species, however, should consider also incorporating novel seed mixes, that contain plants from the families *Apiaceae*, *Asteraceae*, *Brassicaceae*, *Geraniacea*e and *Ranunculaceae* (Nichols, Holland and Goulson 2022a). Such mixes have been shown to support higher abundances and richness of solitary bees, and other insect pollinators, compared to standard mixes (Nichols, Holland and Goulson 2022b). Growers cultivating crops that are visited by diverse communtitie of bees, such as oilseed, should additionally consider incorporating AES options that focus on uncropped cultivated margins around fields (DEFRA 2022a). Within these they should allow at least some ‘weeds’ that emerge from the soil seedback to persist, as many such unsown plant species are the most valuable source of forage for diverse groups of solitary bees (Nichols, Holland & Goulson 2022).

A number of plant species in table 5.1 are good candidates for inclusion in AES sown wildflower seed mixes, and represent an opportunity to diversify and extend the flowering period of current mixes (Nichols, Holland & Goulson 2022a). A further four of these plant species are hedgerow plants which provide forage for spring-flying bees (Wood, Holland & Goulson 2016a). Greater incentivisation of AES that protect and promote high quality hedgerow habitats could benefit crop pollination services by providing richer and earlier sources of nectar and pollen (Gyan & Woodell, 1987; Baude et al. 2016) compared to current wildflower mixes (Nichols, Holland & Goulson 2022a), while also ensuring more nesting opportunities for cavity-nesting solitary species (Morandin & Kremen, 2013; Pufal et al. 2017).

Field boundary features can also have a stabilising effect on populations of bumblebees, which is likely to be particularly beneficial for crops such as field bean, which are almost exclusively pollinated by bumblebees. A recent modelling study demonstrated more stable inter-annual bumblebee visitation rates to field bean, as well as oilseed rape, when flower-rich field margins and hedgerows are present; likely related to these features promoting larger, more stable bumblebee populations through the provision of continuous floral resources and nesting sites (Gardener et al. 2021). Farmers growing bumblebee pollinated crops, such as field bean could therefore especially benefit from incorporating hedgerow AES options, such as ‘BE3: Management of hedgerows’ (DEFRA 2022b), alongside standard mixes, to provide earlier and later floral resources, and nesting opportunities for bumblebees.

Table 5.1: Plant species evidenced as important sources of forage for solitary bee species identified as potential pollinators in chapter 2 and the bee genera known to visit them (Wood, Holland & Goulson 2016a; Gretsy et al. 2018; Nichols, Holland & Goulson et al. 2019).

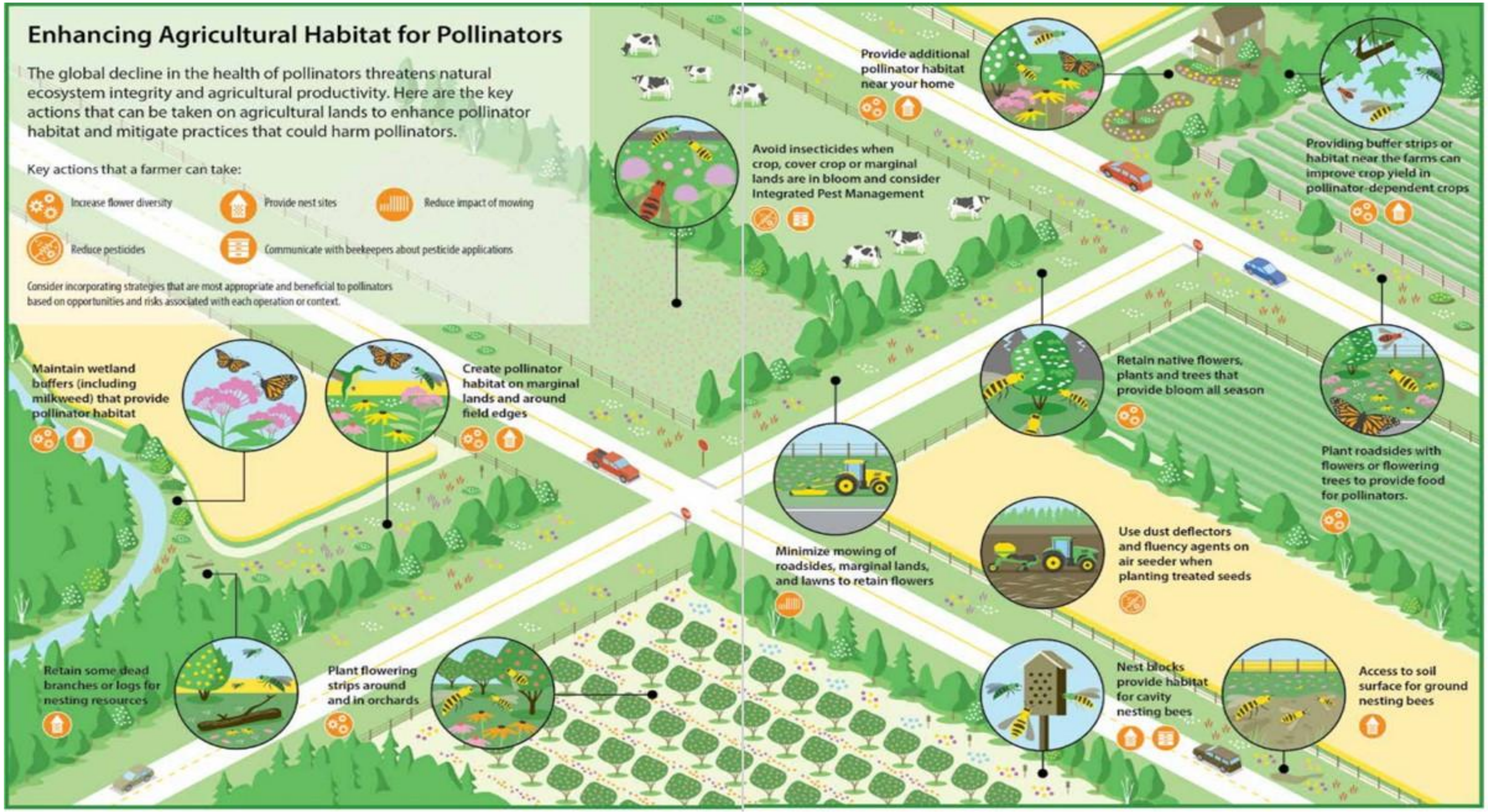
Plant Species	**Bee Genera**
Anthriscus sylvestris (Apiaceae)	*Andrena, Hylaeus, Lasioglossum, Osmia*
Brassica rapa (Brassicaceae)	*Andrena, Halictus*
Chaerophyllum temulum[a] *(Apiaceae)*	*Andrena, Hylaeus, Lasioglossum*
Crataegus monogyna[c] *(Rosaceae)*	*Andrena, Halictus, Lasioglossum*
Convolvulus arvensis[a,b]*(Convolvulaceae)*	*Andrena, Halictis, Lasioglossum*
Crepis capillaris[b] *(Asteraceae)*	*Andrena, Halictus, Hylaeus, Lasioglossum, Osmia*
Geranium pyrenaicum[a] *(Geraniaceae)*	*Andrena, Lasioglossum*
Heracleum sphondylium[a] *(Apiaceae)*	*Andrena, Halictus, Hylaeus, Lasioglossum, Osmia*
Hypochaeris radicata[b] *(Asteraceae)*	*Andrena, Halictus, Lasioglossum*
Lamium album (Lamiaceae)	*Andrena, Anthophora, Halictus, Osmia*
Prunus spinosa[c] *(Rosaceae)*	*Andrena, Osmia*
Pulicaria dysenterica[a] *(Asteraceae)*	*Andrena, Halictus, Lasioglossum*
Ranunculus repens[b] *(Ranunculaceae)*	*Andrena, Halictus, Lasioglossum, Osmia*
Reseda lutea (Resedaceae)	*Andrena, Halictus, Lasioglossum*
Rosa canina[c] *(Rosaceae)*	*Osmia*
Rubus fruticosus agg.[c] *(Rosaceae)*	*Andrena, Halictus, Hylaeus, Lasioglossum*
Senecio jacobea[b] *(Asteraceae)*	*Andrena, Halictus, Lasioglossum*
Sinapsis arvensis[a,b] *(Brassicaceae)*	*Andrena, Lasioglossum*
Taraxacum agg.[a,b] *(Asteraceae)*	*Andrena, Halictus, Lasioglossum, Osmia*
Tripleurospermum inodorum[a,b] *(Asteraceae)*	*Andrena, Halictus, Hylaeus, Lasioglossum, Osmia*

[a] Species identified as potential candidates for inclusion in agri-environment wildflower seed mixes.
[b] Species typically considered as ‘weeds’ (Hicks et al. 2016; Nichols, Holland & Goulson 2019).
[c] Species associated with hedgerows.

Based upon chapter four the dominant pollinating bumblebee species of field bean show relatively synchronous occupancy dynamics, which may also be reflected in the abundance of their populations at the landscape and local scale. The stabilising effects of field margins on their populations could reduce year-to-year fluctuations in their occupancy, and potentially abundances, ensuring more stable levels of visitation to field bean, and in turn result in more consisitent year-to-year crop yields. AES options would also benefit from promoting the creation of hedgerows that provides floral resources before and after field margin flowering to account for the long flight season of bumblebee colonies (Image et al. 2022). For example, the inclusion of species such as Ivy (*Hedera helix*) can provide floral resources for pollinators in the autumn after sown species have ceased flowering (Précigout & Robert 2022). Additionally, for rotational crops such as field bean, hedgerow management would benefit from cutting that is timed to ensure maximum blooming prior to crops flowering, and only half cut in years when the crop is absent (Gardner et al. 2021) as high floral resource availability prior to bean flowering has been linked to enhanced crop seed set (Eckerter et al. 2022).

Recent reviews of measures to protect pollinators and crop pollination services have highlighted the importance of wider landscape scale management to provide floral and nesting resources within a network of well-connected semi-natural habitats (Kovács-Hostyánszki et al. 2017; Krimmer et al. 2019; Cole et al. 2020). Riparian buffer strips, road verges and their associated hedgerows are rich sources of the plant species listed in table 5.1 within agricultural landscapes (Cole et al. 2017; Phillips et al. 2019). The presence of floristically diverse road verges in intensive agricultural landscapes, for example, can result in increased visitation to crops in neighbouring fields (Monasterolo et al. 2022). Additionally, such semi-natural habitats provide nesting and overwintering sites that are often scarce in agricultural landscapes, and act as ecological corridors (Phillips et al. 2020). Appropriate management of semi-natural habitats could aid pollinator conservation in intensive agricultural landscapes, as well as providing benefits for wider biodiversity (Cole et al. 2015; Phillips et al. 2019). The most significant obstacle here will be securing co-operation from multiple stakeholders and policy makers (Cole et al. 2015). This could, however, be achieved through communicating the potential benefits of these habitats for other ecosystem services (Gemmill-Herren et al. 2021), such as pest regulation, enhanced soil nutrient cycling and water purification (Wratten et al. 2012; Figure 5.2).

Additionally, agri-environment scheme would benefit from encouraging the use of artificial nest boxes, or leaving areas of dead wood in hedgerows, for cavity-nesting species (Gretsy et al. 2018; Morandin & Kremen 2013). Alongside a lack of appropriate floral resources for species, including *Hylaeus* and *Osmia*, in current options (Gretsy et al. 2018), such species are often also limited by the availability of nesting sites (Dainese et al. 2018). Based upon the European field data used in chapter 2, both genera represent potential pollinators of apples, oilseed and strawberries. In Great Britain enhanced uptake and sophistication of options that provide nesting resources should particularly focus on orchard- and strawberry-growing regions, where participation is currently especially low (Image et al. 2022). Examples of agri-environment measures to conserve pollinators and promote crop pollination services are shown in Figure 5.1.



Enhancing Agricultural Habitat for Pollinators

The global decline in the health of pollinators threatens natural ecosystem integrity and agricultural productivity. Here are the key actions that can be taken on agricultural lands to enhance pollinator habitat and mitigate practices that could harm pollinators.

Key actions that a farmer can take:

Figure 5.1: Examples of measures to increase pollinator diversity and crop pollination services, including sowing and retaining native plants, maintaining riparian buffer strips, retaining dead wood and bare ground, and minimizing mowing regimes (Pollinator Partnership Canada, n.d.).

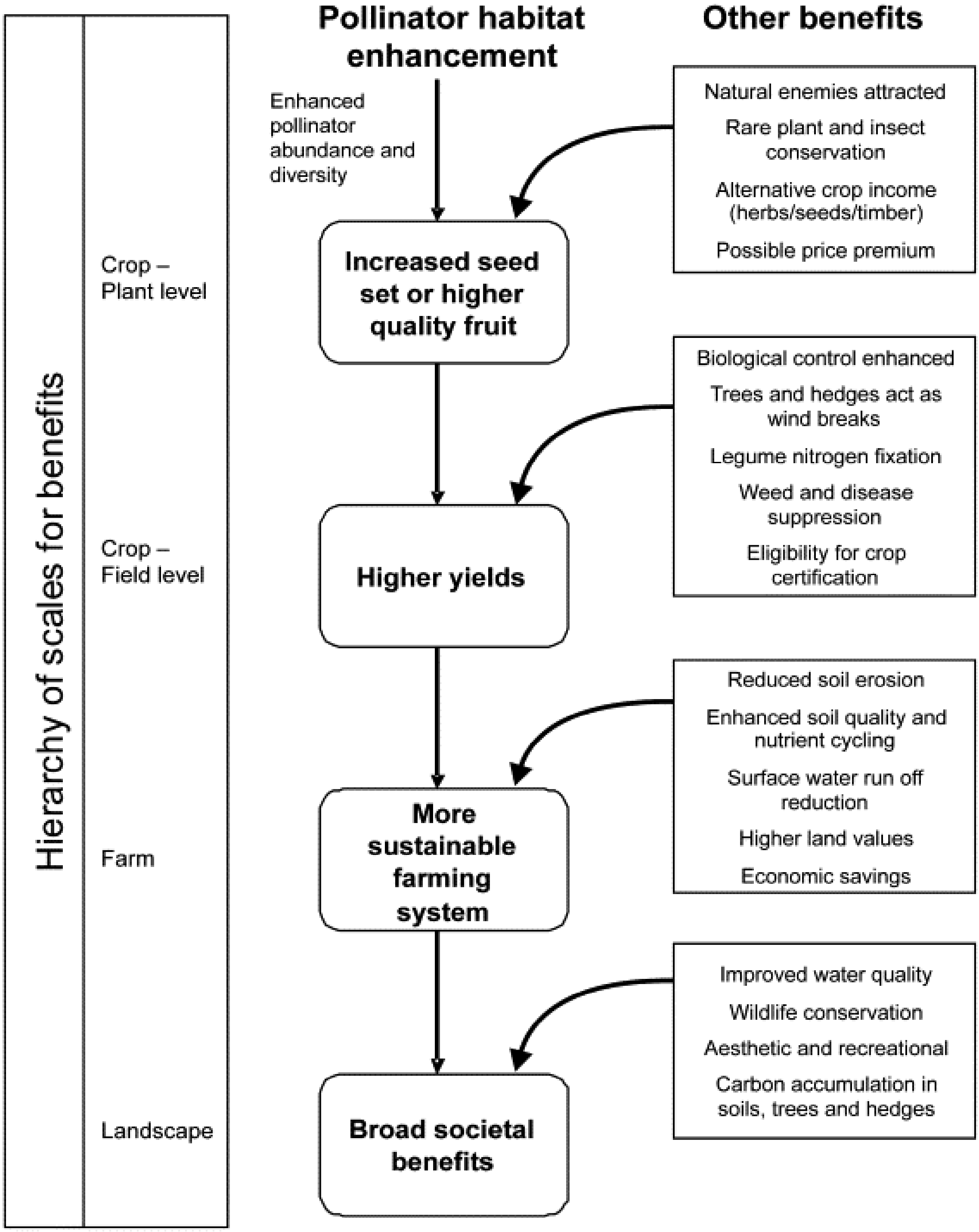


Figure 5.2: Potential benefits of pollinator habitat enhancement for other ecosystem services (Wratten et al. 2012).

5.3.2 Pollinator monitoring.

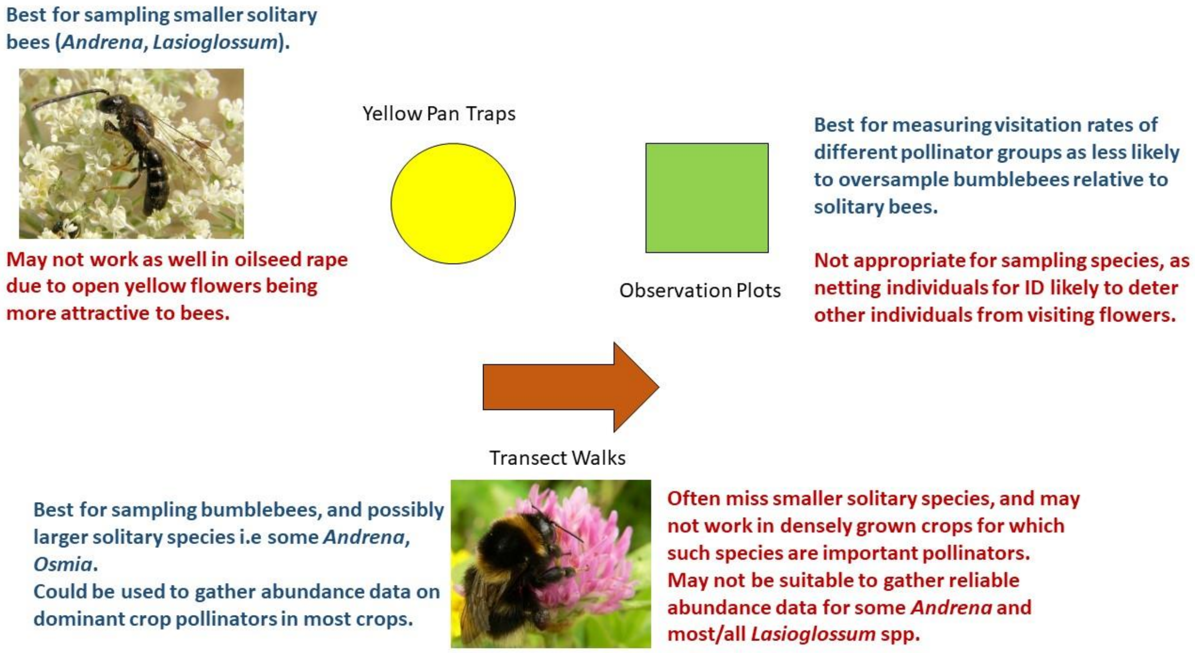
Monitoring schemes for pollinators are essential to guide the protection of the services they provide. However, even well-designed monitoring programmes cannot generate reliable trend data for all species (Carvell et al. 2016). As such a focus of many emerging international (Potts et al. 2021) and national (Carvell et al. 2016) monitoring schemes are capturing trends in key crop pollinating species. Whilst progress has been made in identifying which pollinators provide crop pollination services in Europe (Potts et al. 2021), these assessments have been made based upon a limited number of field studies for many crops (Kleijn et al. 2015). Chapter 2 and chapter 3 both evidenced that many existing crop flower surveys may not comprehensively sample smaller solitary bees. As such countries wishing to produce national lists of bee crop pollinators to guide monitoring schemes could benefit from employing an approach similar to chapter 2. There are already frameworks in place to establish a Europe Union wide pollinator monitoring scheme (Potts et al. 2021), potentially providing opportunities to share data between countries with similar bee communities and economically important crops.

Chapter 3 and other studies indicate that transect walks can adequately sample *Bombus*, and potentially some *Andrena*, species, in crop areas (Gibbs et al. 2017; Templ et al. 2018; Boyer et al. 2020; Krahner et al. 2021). Monitoring of broad functional diversity and abundance of pollinators can act as a proxy for pollination services (Garratt et al. 2019; Potts et al. 2019). As such this could be deployed through the use of transect walks, given that these genera represent the dominant pollinators of most crops (Klein et al. 2019). However, species level data will be a prerequisite for schemes aimed at monitoring trends in the abundance of specific species. Whilst the willingness and capacity of agronomists to identify bumblebees to species during transect walks has been tested (Garratt et al. 2019), the situation for *Andrena* species is unknown, and monitoring schemes would likely need to incorporate comprehensive training on their identification. Additional training could also be focused at certain crops, like oilseed, where, in the absence of expert entomologists, capturing and identifying bee species can be difficult (Garratt et al. 2019), and orchard crops, such as apple, where *Andrena* are often the most abundant and effective pollinating species (Nooten, Odanaka & Rehan 2020). *Osmia bicornis* was also sampled in low numbers during the observational surveys utilised in chapter 3, and alongside other potential key crop pollinating *Andrena* species, can be relatively easily identified by eye. As such *Osmia bicornis* could also be a focus of training aimed at sampling certain species.

Ensuring resilient crop pollination service delivery into the future will be contingent, however, upon protecting a broad diversity of species (Vasiliev & Greenwood 2020). Obtaining species level data beyond dominant pollinator species in agricultural landscapes will be critical to assess the impacts of agri-environment measures and protect crop pollination services. Growing evidence from the UK indicates that declines in bee abundance and richness are more accentuated in agricultural landscapes compared to urban environments (Baldock et al. 2015; Sirohi et al. 2015; Wenzel et al. 2020). As such monitoring data to understand bee trends in farmed environments should be considered an urgent policy priority (Breeze et al. 2021). Gathering additional yearly trend data on non-dominant crop pollinators could also be used to expand upon the work in chapter 4, by providing abundance data at the field level, and further our knowledge of how bee diversity influences pollination service stability and resilience.

Chapter 3 demonstrated many potential crop pollinating species are often not sampled during transect walks. Given that even professionally run monitoring schemes will rely, at least in part, upon citizen scientists and scientific researchers (Breeeze et al. 2021), rather than solely on expert entomologists, pan traps likely represent the best method for sampling most solitary bees (O'Connor et al. 2019). Using only yellow traps in crop fields to monitor crop pollinating species could provide a means to target certain groups (Gollan, Ashcroft & Batley 2010), such as smaller *Andrena* and *Halicitdae* species, which are often otherwise missed during observational methods. The validity of using pan traps to estimate species abundances, and ultimately population trends, has been challenged (Briggs et al. 2022), due to uncertainties around the relationship between catches and floral cover (Portman, Bruninga-Socolar & Cariveau 2020). However, recent evidence suggests that standardized passive sampling can effectively measure relative changes across years (Turley et al. 2022). As such, provided monitoring protocols account for local floral resources (O'Connor et al. 2019), pan traps could represent a comprehensive means to sample most bee species.

Pan traps, however, do not provide information on crop flower vistation rates (Westphal et al. 2008). An emerging area of research interest is the self-assessment of crop pollination service delivery at the field/farm level by land managers (Garratt et al. 2019). At present land managers rarely make direct measures of pollinator activity (Gemmill-Herren et al. 2021). Yet this information is critical to allow farmers to identify circumstances where they may need to alter management practises, or bring in honeybee hives, in order to maximise crop pollination service levels (Isaacs et al. 2017). Both transect walks and observation plots are commonly used to measure pollinator activity. However, chapter 3 indicated that transect walks potentially overestimate the visitation rate of bumblebees relative to solitary bees. As such whilst transect walks, which are generally the easier and quicker method to employ, may be most suitable in bumblebee pollinated crops, in solitary bee pollinated crops observation plots may be more appropriate; especially if farmers wish to gain more refined estimates of pollination service delivery information based upon relative species group richness and/or guide targetted management (Garibaldi et al. 2020) aimed at maximising the benefits accrued by increased pollinator diversity (Gemmill-Herren et al. 2021). An overview of the potential applications and disadvantages of different survey techniques for sampling bee pollinators is provided in Figure 5.3.



Best for sampling smaller solitary bees (*Andrena*, *Lasioglossum*).

May not work as well in oilseed rape due to open yellow flowers being more attractive to bees.

Best for measuring visitation rates of different pollinator groups as less likely to oversample bumblebees relative to solitary bees.

Not appropriate for sampling species, as netting individuals for ID likely to deter other individuals from visiting flowers.

**Best for sampling bumblebees, and possibly larger solitary species i.e some *Andrena*, *Osmia*.
Could be used to gather abundance data on dominant crop pollinators in most crops.**

**Often miss smaller solitary species, and may not work in densely grown crops for which such species are important pollinators.
May not be suitable to gather reliable abundance data for some *Andrena* and most/all *Lasioglossum* spp.**

Figure 5.3: Potential applications (blue) and barriers (red) of different survey techniques for sampling bee crop pollinators in agriculutural landscapes.
Bee pictures taken from Carvell et al. 2016.

5.4 Future research

The focus of this thesis has been upon the wild bee pollinators of apple, field bean, oilseed rape and strawberry crops. However, different crops have distinct pollinator communities (Potts et al. 2021) and many crops are pollinated by a wide diversity of other insect species (Rader et al. 2016; Rader et al. 2020; Garibaldi et al. 2022). The methodology outlined in chapter 2 could be applied to other crops, countries, and insect groups. Identifying key non-bee crop pollinators could help overcome critical evidence gaps in how to develop habitat management to support other insects (Howlett et al. 2021). Additionally, whilst a number of recommendations have been made in this thesis regarding the management, as well as monitoring, of bee pollinators, future research into relevant actors, including farmers and policy makers, will be necessary to determine their capacity and willingness to implement these recommendations. Current evidence suggests farmers view pollinator services as a low priority compared to other issues such as soil quality, and communicating the vital importance of insect pollinators for crop yields will be critical to convincing farmers to measure, promote and protect pollination services (Breeze et al. 2019).

Chapter 3 relied upon a limited number of datasets and further evaluations of sampling methods, including in different crop types, represents a potential area for future research. The bee populations visiting the same crop can vary significantly across small spatial and temporal scales (Adamson et al. 2012; Kremen, Williams & Thorp, 2002) and so future evaluations of survey methods to sample bees should consider datasets over larger scales. Additionally, more research is needed on the relationship between floral chatacteristics and pan trap catches (Portman et al. 2020). Evidence is beginning to emerge of a negative association between floral abundance and pan trap catches (O’Connor et al. 2019; Kuhlman et al. 2021). The degree to which other factors, such as floral colour, may influence pan trap catches is currently untested however. If pan traps utilsed as part of monitoring programmes are to gather reliable abundance data on individual species (Potts et al. 2021) then a greater understanding of both the relationship between catches and the actual abundance of species, and the influence of surrounding floral resources, are urgently needed (Portman 2020). Mark and recapture techniques potentially offer a means to more accurately assess bee species abundance, but more research on this, and the circumstances under which pan traps can provide reliable estimates of bee abundance represent key areas of future research (Briggs et al. 2022).

Chapter 4 looked at how the species richness and composition of crop pollinator communities affected the stability of crop pollinator occurrence. However, ecosystem service function depends not only on species occurrence, but also their local abundance (Waldock et al. 2021). Abundance data from monitoring schemes collected in crop fields could be used in the future to understand how species richness and community composition directly affect the stability and resilience of crop pollination service delivery, or more accurately investigate the relationship between occupancy and population abundances. Further research could also be targeted at evaluating which bee traits most significantly drive synchronous, and conversely asynchronous, population variability amongst bee species. All of the afore mentioned work could also be expanded to include other pollinating insects, and help to inform our understanding of how other groups can influence crop pollination service stability and resilience. Hoverflies represent an ideal candidate species, given that occupancy model data also exists for most species in Great Britain (Powney ey al. 2019) and they also form a key target group of the UK Pollinator Monitoring Scheme (Carvell et al. 2016).

5.5 Concluding remarks

This thesis has provided the first national lists of potential bee pollinators for economically important crops. In doing so it has filled a critical knowledge gap, and provided a methodological approach that can be applied to other countries, crops and groups of pollinating insects. Additionally, it builds upon existing knowledge of the capacity of different survey methods to sample bee species in crop areas, which is vital to identify economically important species and monitor their trends in agricultural landscapes. Finally, it has added to our understanding of how pollinator community composition and species richness may influence patterns in crop pollinator occurrence, which can contribute to our understanding of the resilience of crop pollination service provision to environmental changes. The overall findings of this thesis can be used to inform bee species conservation and management in agricultural landscapes.

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7. Appendices

Appendix 1: Bee species database (Chapter 2).

This appendix contains information from the species database of the 229 extant, resident wild bee species in Great Britain that was used in chapter 2 to produce lists of potential pollinators for apple, bean, oilseed and strawberry crops. Table 7.1.1 contains the information collated on flight period (months), sociality (cleptoparasite, eusocial or solitary (regarded as applying to all non-*Bombus* species)), lecty (oligolectic or polylectic, forage (which (if any) of the target crop plant families (Brassicaceae (B), Fabaceae (F), Rosaceae (R)) are visited for pollen and/or nectar) and tongue length (short/long). Table 7.1.2 contains the information collated on distribution and habitat for all bee species.

7.1.1 List of all extant resident bee species in Great Britain with information on flight period, lecty, plant families foraged from, tongue length and sociality.

Species	**Flight Period**	**Lecty**	**Forage**	**Tongue Length**	**Sociality**
Andrena alfkenella	Apr – Aug	Polylectic	B, R	Short	Solitary
Andrena angustior	Apr – Jun	Polylectic	B, R	Short	Solitary
Andrena apicata	Mar – May	Oligolectic (Salix)	B, F, R	Short	Solitary
Andrena argentata	Jul – Aug	Polylectic	B, R	Short	Solitary
Andrena barbilabris	Apr – Jul	Polylectic	B, F, R	Short	Solitary
Andrena bicolor	Mar – Aug	Polylectic	B, F, R	Short	Solitary
Andrena bimaculata	Mar – Aug	Polylectic	B, F, R	Short	Solitary
Andrena bucephala	Apr – Jun	Polylectic	B, R	Short	Solitary
Andrena chrysosceles	Mar – Aug	Polylectic	B, R	Short	Solitary
Andrena cineraria	Mar – Jul	Polylectic	B, F, R	Short	Solitary
Andrena clarkella	Mar – May	Oligolectic (Salix)		Short	Solitary
Andrena coitana	Jun – Aug	Polylectic	R	Short	Solitary
Andrena congruens	Apr – Aug	Polylectic	B, F, R	Short	Solitary
Andrena denticulate	Jun – Sep	Oligolectic or Polylectic	F, R	Short	Solitary

Species	**Flight Period**	**Lecty**	**Forage**	**Tongue Length**	**Sociality**
Andrena dorsata	Mar – Sep	Polylectic	B, F, R	Short	Solitary
Andrena falsifica	Mar – Jul	Polylectic	R	Short	Solitary
Andrena ferox	Apr – Jun	Polylectic	R	Short	Solitary
Andrena flavipes	Mar – Sep	Polylectic	B, F, R	Short	Solitary
Andrena florea	May – Aug	Oligolectic (Cucurbitaceae)	R	Short	Solitary
Andrena fucata	May – Aug	Polylectic	B, F, R	Short	Solitary
Andrena fulva	Mar – Jun	Polylectic	B, R	Short	Solitary
Andrena fulvago	May – Aug	Oligolectic (Asteraceae)		Short	Solitary
Andrena fuscipes	Jul – Sep	Oligolectic (Ericaceae)	F	Short	Solitary
Andrena gravida	Mar – May	Polylectic	B, R, F	Short	Solitary
Andrena haemorrhoa	Mar – May	Polylectic	B, R, F	Short	Solitary
Andrena hattorfiana	Jun – Aug	Polylectic	F	Short	Solitary
Andrena helvola	Apr – Jun	Polylectic	B, R	Short	Solitary
Andrena humilis	May – Jun	Oligolectic (Asteraceae)		Short	Solitary
Andrena labialis	May – Jul	Polylectic	B, F, R	Short	Solitary
Andrena labiata	Apr – Jun	Polylectic	B, R	Short	Solitary
Andrena lapponica	Apr – Jun	Oligolectic (Ericaceae)	F, R	Short	Solitary
Andrena marginata	Jul – Sep	Oligolectic (Dipsacaceae)	R	Short	Solitary
Andrena minutula	Mar – Sep	Polylectic	B, R	Short	Solitary
Andrena minutuloides	Apr – Sep	Polylectic	B, R	Short	Solitary
Andrena nigriceps	Jul – Sep	Polylectic	B, R	Short	Solitary
Andrena nigroaenea	Mar – Jul	Polylectic	B, F, R	Short	Solitary
Andrena nigrospina	May – Jul	Oligolectic (Brassicaceae)	B	Short	Solitary
Andrena nitida	Mar – Jul	Polylectic	B, R	Short	Solitary
Andrena nitidiuscula	Jun – Sep	Oligolectic (Apiaceae)	F, R	Short	Solitary
Andrena niveata	May – Jun	Oligolectic (Brassiceae)	B	Short	Solitary
Andrena ovatula	Mar – Sep	Polylectic	B, F, R	Short	Solitary
Andrena pilipes	Apr – Aug	Polylectic	B, R	Short	Solitary
Andrena praecox	Mar – May	Oliglolectic (Salicaceae)	R	Short	Solitary

Species	**Flight Period**	**Lecty**	**Forage**	**Tongue Length**	**Sociality**
Andrena proxima	May – Jun	Oligolectic (Apiaceae)	B, R	Short	Solitary
Andrena rosae	Mar – Sep	Polylectic	R	Short	Solitary
Andrena ruficrus	Mar – May	Oliglolectic (Salicaceae)		Short	Solitary
Andrena scotica	Mar – Jul	Polylectic	B, F, R	Short	Solitary
Andrena semilaevis	May – Aug	Polylectic	B, R	Short	Solitary
Andrena similis	Apr – Jun	Oligolectic (Fabaceae)	F, R	Short	Solitary
Andrena simillima	Jul – Aug	Polylectic	R	Short	Solitary
Andrena subopaca	Apr – Jun	Polylectic	B, R	Short	Solitary
Andrena synadelpha	Apr – Jun	Polylectic	B, F, R	Short	Solitary
Andrena tarsata	Jun – Aug	Oligolectic (Rosaceae)	R	Short	Solitary
Andrena thoracica	Mar – Aug	Polylectic	B, F, R	Short	Solitary
Andrena tibialis	Mar – Jun	Polylectic	B, R	Short	Solitary
Andrena trimmerana	Mar – Sep	Polylectic	F, R	Short	Solitary
Andrena vaga	Mar – May	Oliglolectic (Salicaceae)		Short	Solitary
Andrena varians	Mar – Jun	Polylectic	B, R	Short	Solitary
Andrena wilkella	Apr – Jul	Polylectic	B, F, R	Short	Solitary
Anthidium manicatum	May – Aug	Polylectic	F, R	Long	Solitary
Anthophora bimaculata	Jun – Sep	Polylectic	F, R	Long	Solitary
Anthophora furcata	May – Aug	Polylectic	R	Long	Solitary
Anthophora plumipes	Mar – Jun	Polylectic	B, F, R	Long	Solitary
Anthophora quadrimaculata	Jun – Aug	Polylectic	F	Long	Solitary
Anthophora retusa	Apr – Jun	Polylectic	B, F	Long	Solitary
Bombus barbutellus	Apr – Sep	No lectic status	F, R	Long	Cleptoparasite
Bombus bohemicus	Apr – Aug	No lectic status	F, R	Long	Cleptoparasite
Bombus campestris	May – Oct	No lectic status	F, R	Long	Cleptoparasite
Bombus distinguendus	May – Oct	Polylectic	F, R	Long	Eusocial
Bombus hortorum	Mar – Oct	Polylectic	B, F, R	Long	Eusocial
Bombus humilis	May – Sep	Polylectic	F, R	Long	Eusocial
Bombus hypnorum	Mar – Sep	Polylectic	F, R	Long	Eusocial

Species	**Flight Period**	**Lecty**	**Forage**	**Tongue Length**	**Sociality**
Bombus jonellus	Mar – Oct	Polylectic	F, R	Long	Eusocial
Bombus lapidarius	Apr – Oct	Polylectic	B, F, R	Long	Eusocial
Bombus monticola	Apr – Oct	Polylectic	F, R	Long	Eusocial
Bombus muscorum	May – Aug	Polylectic	F, R	Long	Eusocial
Bombus pascuorum	Mar – Nov	Polylectic	F, R	Long	Eusocial
Bombus pratorum	Feb – Sep	Polylectic	F, R	Long	Eusocial
Bombus ruderarius	Apr – Oct	Polylectic	F, R	Long	Eusocial
Bombus ruderatus	Apr – Oct	Polylectic	F, R	Long	Eusocial
Bombus rupestris	May – Sep	No lectic status	F	Long	Cleptoparasite
Bombus soroeensis	Jun – Nov	Polylectic	F, R	Long	Eusocial
Bombus sylvarum	May – Sep	Polylectic	F, R	Long	Eusocial
Bombus sylvestris	Apr – Oct	No lectic status	F, R	Long	Cleptoparasite
Bombus terrestris	Jan – Dec	Polylectic	B, F, R	Long	Eusocial
Bombus vestalis	Mar – Aug	No lectic status	B, F, R	Long	Cleptoparasite
Ceratina cyanea	May – Aug	Polylectic	F, R	Long	Solitary
Chelostoma campanularum	Jun – Aug	Polylectic	B, R	Long	Solitary
Chelostoma florisomne	May – Aug	Oligolectic (Ranunculaceae)	R	Long	Solitary
Coelioxys conoideus	Jun – Aug	No lectic status	R	Long	Cleptoparasite
Coelioxys elongata	Jun – Aug	No lectic status	F, R	Long	Cleptoparasite
Coelioxys inermis	May – Sep	No lectic status	R	Long	Cleptoparasite
Coelioxys mandibularis	Jun – Aug	No lectic status	F	Long	Cleptoparasite
Coelioxys quadridentatus	Jun – Aug	No lectic status	F	Long	Cleptoparasite
Coelioxys rufescens	Jun – Aug	No lectic status	F	Long	Cleptoparasite
Colletes cunicularius	Apr – Jun	Polylectic	B, R	Short	Solitary
Colletes daviesanus	Jun – Sep	Oligolectic (Asteraceae)		Short	Solitary
Colletes floralis	Jun – Aug	Polylectic	B, F, R	Short	Solitary
Colletes fodiens	Jun – Sep	Oligolectic (Asteraceae)	R	Short	Solitary
Colletes halophilus	Aug – Oct	Oligolectic (Asteraceae)	B, F	Short	Solitary
Colletes hederae	Sep – Nov	Polylectic	F	Short	Solitary

Species	**Flight Period**	**Lecty**	**Forage**	**Tongue Length**	**Sociality**
Colletes marginatus	Jun – Aug	Polylectic	F, R	Short	Solitary
Colletes similis	Jun – Sep	Oligolectic (Asteraceae)		Short	Solitary
Colletes succinctus	Jul – Sep	Polylectic	F	Short	Solitary
Dasypoda hirtipes	Jun – Aug	Oligolectic (Asteraceae)		Short	Solitary
Epeolus cruciger	Jun – Sep	No lectic status	F	Long	Cleptoparasite
Epeolus variegatus	Jun – Oct	No lectic status	F, R	Long	Cleptoparasite
Eucera longicornis	May – Jul	Oligolectic (Fabaceae)	B, F, R	Long	Solitary
Halictus confusus	Apr – Sep	Polylectic	B, F, R	Short	Solitary
Halictus eurygnathus	May – Sep	Polylectic		Short	Solitary
Halictus rubicundus	Apr – Oct	Polylectic	B, F, R	Short	Solitary
Halictus tumulorum	Apr – Oct	Polylectic	B, F, R	Short	Solitary
Heriades truncorum	Jul – Oct	Oligolectic (Asteraceae)		Long	Solitary
Hoplitis claviventris	May – Aug	Polylectic	F, R	Long	Solitary
Hylaeus annularis	Jun – Aug	Polylectic	B, R	Short	Solitary
Hylaeus brevicornis	May – Sep	Polylectic	F, R	Short	Solitary
Hylaeus communis	May – Sep	Polylectic	B, R	Short	Solitary
Hylaeus confusus	May – Sep	Polylectic	B, F, R	Short	Solitary
Hylaeus cornutus	Jun – Aug	Polylectic		Short	Solitary
Hylaeus dilatatus	Jun – Aug	Polylectic	B, R	Short	Solitary
Hylaeus hyalinatus	May – Sep	Polylectic	B, R	Short	Solitary
Hylaeus incongruous	Jun – Aug	Polylectic	B, F, R	Short	Solitary
Hylaeus pectoralis	Jun – Sep	Polylectic	R	Short	Solitary
Hylaeus pictipes	Jun – Sep	Polylectic	B, R	Short	Solitary
Hylaeus signatus	Jun – Sep	Narrowly Oligolectic (Reseda spp.)	B, R	Short	Solitary
Lasioglossum albipes	Apr – Sep	Polylectic	R	Short	Solitary
Lasioglossum angusticeps	May – Sep	Polylectic	F	Short	Solitary
Lasioglossum brevicorne	May – Aug	Oligolectic (Asteraceae)		Short	Solitary
Lasioglossum calceatum	Mar – Oct	Polylectic	B, F, R	Short	Solitary
Lasioglossum cupromicans	Apr – Oct	Polylectic	B, R	Short	Solitary

Species	**Flight Period**	**Lecty**	**Forage**	**Tongue Length**	**Sociality**
Lasioglossum fratellum	Apr – Oct	Polylectic	R	Short	Solitary
Lasioglossum fulvicorne	Apr – Oct	Polylectic	B, R	Short	Solitary
Lasioglossum laevigatum	Apr – Sep	Polylectic	B, F, R	Short	Solitary
Lasioglossum laticeps	Apr – Sep	Polylectic	B, R	Short	Solitary
Lasioglossum lativentre	Apr – Oct	Polylectic	F, R	Short	Solitary
Lasioglossum leucopus	May – Oct	Polylectic	R	Short	Solitary
Lasioglossum leucozonium	May – Oct	Polylectic	F, R	Short	Solitary
Lasioglossum malachurum	Apr – Oct	Polylectic	B, F, R	Short	Solitary
Lasioglossum minutissimum	Apr – Oct	Polylectic	B, R	Short	Solitary
Lasioglossum morio	Mar – Oct	Polylectic	B, R	Short	Solitary
Lasioglossum nitidiusculum	Mar – Oct	Polylectic	B, R	Short	Solitary
Lasioglossum parvulum	Mar – Sep	Polylectic	R	Short	Solitary
Lasioglossum pauperatum	Apr – Oct	Polylectic		Short	Solitary
Lasioglossum pauxillum	Apr – Oct	Polylectic	B, F, R	Short	Solitary
Lasioglossum prasinum	Apr – Aug	Polylectic		Short	Solitary
Lasioglossum punctatissimum	Apr – Oct	Polylectic	F, R	Short	Solitary
Lasioglossum puncticolle	May – Sep	Polylectic		Short	Solitary
Lasioglossum quadrinotatum	Mar – Sep	Polylectic	B	Short	Solitary
Lasioglossum rufitarse	Apr – Oct	Polylectic	R	Short	Solitary
Lasioglossum semilucens	May – Sep	Polylectic	R	Short	Solitary
Lasioglossum sexnotatum	Apr – Sep	Polylectic	B, R	Short	Solitary
Lasioglossum sexstrigatum	Apr – Sep	Polylectic	R	Short	Solitary
Lasioglossum smeathmanellum	Mar – Sep	Polylectic	R	Short	Solitary
Lasioglossum villosulum	Apr – Oct	Polylectic	R	Short	Solitary
Lasioglossum xanthopus	Apr – Oct	Polylectic	B, F, R	Short	Solitary
Lasioglossum zonulum	Apr – Oct	Polylectic	B, R	Short	Solitary
Macropis europaea	Jul – Sep	Narrowly oligolectic (Primulaceae)	F, R	Short	Solitary
Megachile centuncularis	Jun – Aug	Polylectic	B, F, R	Long	Solitary
Megachile circumcincta	May – Aug	Polylectic	F, R	Long	Solitary

Species	**Flight Period**	**Lecty**	**Forage**	**Tongue Length**	**Sociality**
Megachile leachella	Jun – Aug	Polylectic	F, R	Long	Solitary
Megachile ligniseca	Jun – Aug	Polylectic	B, F	Long	Solitary
Megachile maritima	Jun – Aug	Polylectic	F, R	Long	Solitary
Megachile versicolor	May – Sep	Polylectic	F, R	Long	Solitary
Megachile willughbiella	May – Aug	Polylectic	F, R	Long	Solitary
Melecta albifrons	Apr – Jun	No lectic status	B, F, R	Long	Cleptoparasite
Melitta dimidiata	Jun – Aug	Oligolectic (Fabaceae)		Short	Solitary
Melitta haemorrhoidalis	Jul – Aug	Oligolectic (Campanulaceae)		Short	Solitary
Melitta leporina	Jun – Aug	Oligolectic (Fabaceae)	F, R	Short	Solitary
Melitta tricincta	Jul – Sep	Oligolectic (Orobanchaceae)		Short	Solitary
Nomada argentata	Jul – Sep	No lectic status		Long	Cleptoparasite
Nomada armata	Jun – Jul	No lectic status	F	Long	Cleptoparasite
Nomada baccata	Jul – Aug	No lectic status	R	Long	Cleptoparasite
Nomada conjungens	May – Jun	No lectic status		Long	Cleptoparasite
Nomada fabriciana	Mar – Aug	No lectic status	R	Long	Cleptoparasite
Nomada ferruginata	Apr – May	No lectic status	R	Long	Cleptoparasite
Nomada flava	Apr – Jun	No lectic status	B, F, R	Long	Cleptoparasite
Nomada flavoguttata	Mar – Aug	No lectic status	B, R	Long	Cleptoparasite
Nomada flavopicta	Jun – Sep	No lectic status	F, R	Long	Cleptoparasite
Nomada fucata	Apr – Aug	No lectic status	B, F	Long	Cleptoparasite
Nomada fulvicornis	Mar – Aug	No lectic status	B, R	Long	Cleptoparasite
Nomada goodeniana	Apr – Aug	No lectic status	B, F, R	Long	Cleptoparasite
Nomada guttulata	May – Jun	No lectic status	R	Long	Cleptoparasite
Nomada hirtipes	Apr – Jun	No lectic status	B	Long	Cleptoparasite
Nomada integra	May – Jul	No lectic status		Long	Cleptoparasite
Nomada lathburiana	Apr – Jun	No lectic status	R	Long	Cleptoparasite
Nomada leucophthalma	Mar – May	No lectic status	R	Long	Cleptoparasite
Nomada marshamella	Apr – Sep	No lectic status	B, R	Long	Cleptoparasite
Nomada obtusifrons	Jun – Aug	No lectic status	R	Long	Cleptoparasite

Species	**Flight Period**	**Lecty**	**Forage**	**Tongue Length**	**Sociality**
Nomada panzeri	Apr – Jun	No lectic status	R	Long	Cleptoparasite
Nomada roberjeotiana	Jun – Aug	No lectic status	R	Long	Cleptoparasite
Nomada ruficornis	Apr – Jun	No lectic status	R	Long	Cleptoparasite
Nomada rufipes	Jul – Sep	No lectic status		Long	Cleptoparasite
Nomada sexfasciata	May – Jul	No lectic status	F	Long	Cleptoparasite
Nomada sheppardana	Apr – Jul	No lectic status		Long	Cleptoparasite
Nomada signata	Apr – May	No lectic status	F	Long	Cleptoparasite
Nomada striata	May – Jul	No lectic status	F, R	Long	Cleptoparasite
Osmia aurulenta	Apr – Aug	Polylectic	F, R	Long	Solitary
Osmia bicolor	Apr – Jul	Polylectic	B, F, R	Long	Solitary
Osmia bicornis	Apr – Jul	Polylectic	B, F, R	Long	Solitary
Osmia caerulescens	Apr – Jul	Polylectic	B, F, R	Long	Solitary
Osmia inermis	May – Jul	Polylectic	F, R	Long	Solitary
Osmia leaiana	May – Aug	Oligolectic (Asteraceae)	B, R	Long	Solitary
Osmia parietina	May – Jul	Polylectic	F, R	Long	Solitary
Osmia pilicornis	Apr – Jun	Polylectic	F, R	Long	Solitary
Osmia spinulosa	May – Sep	Oligolectic (Asteraceae)		Long	Solitary
Osmia uncinata	May – Jul	Polylectic	F, R	Long	Solitary
Osmia xanthomelana	Apr – Jul	Oligolectic (Fabaceae)	F	Long	Solitary
Panurgus banksianus	Jun – Aug	Oligolectic (Asteraceae)		Long	Solitary
Panurgus calcaratus	Jun – Sep	Oligolectic (Asteraceae)		Long	Solitary
Sphecodes crassus	May – Sep	No lectic status		Short	Cleptoparasite
Sphecodes ephippius	Apr – Sep	No lectic status	F, R	Short	Cleptoparasite
Sphecodes ferruginatus	May – Aug	No lectic status	R	Short	Cleptoparasite
Sphecodes geoffrellus	Apr – Oct	No lectic status	F, R	Short	Cleptoparasite
Sphecodes gibbus	Apr – Sep	No lectic status		Short	Cleptoparasite
Sphecodes hyalinatus	Apr – Sep	No lectic status		Short	Cleptoparasite
Sphecodes longulus	May – Sep	No lectic status		Short	Cleptoparasite
Sphecodes miniatus	May – Sep	No lectic status		Short	Cleptoparasite

Species	Flight Period	Lecty	Forage	Tongue Length	Sociality
Sphecodes monilicornis	Apr – Sep	No lectic status	R	Short	Cleptoparasite
Sphecodes niger	Apr – Oct	No lectic status		Short	Cleptoparasite
Sphecodes pellucidus	May – Oct	No lectic status		Short	Cleptoparasite
Sphecodes puncticeps	May – Oct	No lectic status		Short	Cleptoparasite
Sphecodes reticulatus	May – Oct	No lectic status		Short	Cleptoparasite
Sphecodes rubicundus	May – Jul	No lectic status		Short	Cleptoparasite
Sphecodes scabricollis	Jun – Sep	No lectic status		Short	Cleptoparasite
Sphecodes spinulosus	May – Jun	No lectic status	R	Short	Cleptoparasite
Stelis breviuscula	Jun – Aug	No lectic status	R	Long	Cleptoparasite
Stelis ornatula	May – Aug	No lectic status	R	Long	Cleptoparasite
Stelis phaeoptera	May – Aug	No lectic status	F	Long	Cleptoparasite
Stelis punctulatissima	Jun – Aug	No lectic status	F, R	Long	Cleptoparasite

7.1.2 List of all extant resident bee species in Great Britain with information on distribution and habitat.

Species	Distribution	Habitat
Andrena alfkenella	England	Coastal, Heaths, Calcareous grasslands
Andrena angustior	England and Wales	Light sandy soils, especially woodland
Andrena apicata	England and Wales	Woodland, Heath, Moors, Quarries
Andrena argentata	England	Heathland
Andrena barbilabris	Great Britain	Light, sandy soils - heaths and acidic grasslands
Andrena bicolor	Great Britain	Many lowland types
Andrena bimaculata	England and Wales	Light sandy soils, especially heaths, sandpits
Andrena bucephala	England and Wales	Several, especially calcareous grasslands and deciduous woodland
Andrena chrysosceles	Great Britain	Wide range but especially open woodland
Andrena cineraria	Great Britain	Variety of open, usually sandy, sites
Andrena clarkella	Great Britain	Open woodland, heaths and moors

Species	**Distribution**	**Habitat**
Andrena coitana	Great Britain	Open woodland, heaths, moors, coastal
Andrena congruens	England and Wales	Especially sand pits and quarries
Andrena denticulata	Great Britain	Most open habitats, usually sandy
Andrena dorsata	England and Wales	Various habitats
Andrena falsifica	England and Wales	Heaths and moors
Andrena ferox	Southern England	Deciduous woodland
Andrena flavipes	England and Wales	Variety of open habitats
Andrena florea	Southern England	Open, sandy sites
Andrena fucata	Great Britain	Woodland, heaths, moors and coastal dunes.
Andrena fulva	Great Britain	Open sites
Andrena fulvago	Great Britain	Coastal cliffs, grassland, dunes and moors, particularly chalk and sandy soils.
Andrena fuscipes	Great Britain	Heath and moors
Andrena gravida	South-east England	Open habitats with a slight preference for clay-based or sandy soils,
Andrena haemorrhoa	Great Britain	Various habitats
Andrena hattorfiana	England and Wales	Open grassland, mainly on calcareous and sandy soils
Andrena helvola	Great Britain	Deciduous woodland
Andrena humilis	England and Wales	Sandy soils
Andrena labialis	England and Wales	Variety of open habitats
Andrena labiata	England and Wales	Generally open, sandy soils
Andrena lapponica	Great Britain	Open woodland, moors and montane sites
Andrena marginata	Great Britain	Variety of open habitats
Andrena minutula	Great Britain	Various habitats
Andrena minutuloides	Southern England	Sandy heaths and commons and especially calcareous grasslands
Andrena nigriceps	Great Britain	Various open sites
Andrena nigroaenea	Great Britain	Wide range of habitats
Andrena nigrospina	Central and southern England	Various open sites
Andrena nitida	England and Wales	Variety of habitats
Andrena nitidiuscula	Southern England	Open and coastal habitats
Andrena niveata	South-east England	Variety of habitats

Species	**Distribution**	**Habitat**
Andrena ovatula	England and Wales	Heaths, dunes, landslips and cliffs.
Andrena pilipes	Southern England - coastal	Coastal sites
Andrena praecox	England and Wales	Open woodland and heathland
Andrena proxima	England and Wales	Open sites
Andrena rosae	England and Wales - coastal	Not known
Andrena ruficrus	North England and Scotland	Varied, but with Sallows and bare ground
Andrena scotica	Great Britain	Most habitats
Andrena semilaevis	Great Britain	Various open sites
Andrena similis	Great Britain	Various
Andrena simillima	South-west England	Coastal grasslands and cliffs
Andrena subopaca	Great Britain	Various, but especially open deciduous woodland
Andrena synadelpha	Great Britain	Various, but most often deciduous woodland
Andrena tarsata	Great Britain	Various, but mostly heaths and moors
Andrena thoracica	England and Wales	Mostly sand, coastal locations
Andrena tibialis	England and Wales	Variety
Andrena trimmerana	England and Wales	Variety
Andrena vaga	South-east England	Open sites rich in Salix
Andrena varians	England and Wales	Variety
Andrena wilkella	Great Britain	Genrally open grassland and open woodland
Anthidium manicatum	Great Britain	Wide variety
Anthophora bimaculata	Southern England	Light sandy soils i.e., lowland heaths, commons, coastal dunes and landslips
Anthophora furcata	England and Wales	Wide variety
Anthophora plumipes	England and Wales	Wide variety
Anthophora quadrimaculata	Southern England	Open sites
Anthophora retusa	Southern England	Preference for sandy soils – commons, heathlands, coastal dunes and cliffs
Bombus barbutellus	Great Britain	Wide variety
Bombus bohemicus	Great Britain	Wide variety
Bombus campestris	Great Britain	Wide variety
Bombus distinguendus	Northern Scotland and Islands	Flower-rich coastal grasslands

Species	**Distribution**	**Habitat**
Bombus hortorum	Great Britain	Wide variety
Bombus humilis	England and Wales	Tall, open grasslands, dunes, cliffs and occassionally heaths
Bombus hypnorum	Great Britain	Heaths, woods and grasslands
Bombus jonellus	Great Britain	Strongly associated with heathland and moorland, but does occur in other habitats
Bombus lapidarius	Great Britain	Wide variety
Bombus monticola	Great Britain	Associated with mountain, moorland and upland grassland habitat
Bombus muscorum	Great Britain	Large areas of open, flower-rich grassland habitats
Bombus pascuorum	Great Britain	Wide variety
Bombus pratorum	Great Britain	Wide variety
Bombus ruderarius	England and Scotland	Flower-rich calcareous grasslands, coastal dunes and machair
Bombus ruderatus	Southern England	Herb-rich grasslands, flower-rich margins in arable farmland and river banks
Bombus rupestris	England and Wales	Wherever host is, but mostly umimproved grasslands
Bombus soroeensis	England and Wales	Flower rich calcareous grasslands in south, moorland in north
Bombus sylvarum	England and Wales	Tall herb-rich grasslands i.e., salt marshes, healthland, dunes, shingle beaches
Bombus sylvestris	Great Britain	Wide variety
Bombus terrestris	Great Britain	Wide variety
Bombus vestalis	Great Britain	Wide variety
Ceratina cyanea	Southern England	Chalk escarpments, heathland, sand quarries and open rides in deciduous woodland
Chelostoma campanularum	Great Britain	Various open habitats
Chelostoma florisomne	England and Wales	Woodland and meadows
Coelioxys conoideus	England and Wales	Coastal dunes, landslips, inland commons and heaths and chalk grassland.
Coelioxys elongata	Great Britain	Coastal dunes, inland heaths and brownfield sites
Coelioxys inermis	England and Wales	Dune systems
Coelioxys mandibularis	England and Wales	Sandy heaths and coastal dune systems
Coelioxys quadridentatus	South-east England	Dune systems
Coelioxys rufescens	England and Wales	Coastal dunes and inland sandy heaths
Colletes cunicularius	England and Wales	Varied sandy sites, quarries, river banks, coastal cliffs, dunes
Colletes daviesanus	Great Britain	Wide variety
Colletes floralis	England and Scotland	Mainly coastal sites, especially sand grasslands and herb-rich sand dunes

Species	**Distribution**	**Habitat**
Colletes fodiens	England and Wales	Strong preference for sandy sites, dry heaths and coastal dunes
Colletes halophilus	South-east England	Coastal habitats
Colletes hederae	England and Wales	Wherever its pollen source is firmly established
Colletes marginatus	England and Wales	Light sandy soils, predominantly coastal dunes
Colletes similis	England and Wales	Wide variety
Colletes succinctus	Great Britain	Heaths, moorland, occasionaly dunes and other coastal habitats
Dasypoda hirtipes	England and Wales	Sandy soils, particularly on heathlands and coastal dunes
Epeolus cruciger	England and Wales	Inland heaths, moors, coastal sand dunes and undercliffs
Epeolus variegatus	England and Wales	Wherever host is, Open woodland, heathland, coastal dunes, cliffs and salt marshes
Eucera longicornis	England and Wales	Coastal grasslands, open rides in deciduous woodland and, occasionally, heathlands
Halictus confuses	England and Wales	Closely associated with sandy heath and other disturbed sandy situations
Halictus eurygnathus	Confined to East Sussex	Chalk grassland, on or near coast
Halictus rubicundus	Great Britain	Wide variety
Halictus tumulorum	Great Britain	Wide variety
Heriades truncorum	South-east England	Open habitats with a source of dead timber
Hoplitis claviventris	England	Wide variety
Hylaeus annularis	England – coastal	Confined to coastal dunes and shingle
Hylaeus brevicornis	England and Wales	Wide variety
Hylaeus communis	Great Britain	Wide variety
Hylaeus confusus	Great Britain	Particularly open deciduous woodland, also chalk grassland, heaths, fens and coastal
Hylaeus cornutus	Southern England	Wide variety
Hylaeus dilatatus	England and Wales	Calcareous grassland, coastal sites, fens and open woodland
Hylaeus hyalinatus	England and Wales	Coastal sites, quarries, sand pits, stonework
Hylaeus incongruous	Southern England	Mainly open woodland, chalk grassland and heaths
Hylaeus pectoralis	South and eastern England	Associated with stands of the common reed, both in brackish and fresh water
Hylaeus pictipes	England and Wales	Open woodland, fens, chalk grassland, chalk heath, coastal dunes and shingle
Hylaeus signatus	England and Wales	Open habitats, including calcareous grassland, quarries, coastal marshes and beaches
Lasioglossum albipes	Great Britain	Wide variety
Lasioglossum angusticeps	Dorset and east Devon	Mainly rough coastal landslips

Species	**Distribution**	**Habitat**
Lasioglossum brevicorne	Great Britain	Sandy soils - lowland heaths, acidic grasslands, coastal dunes and chalk heaths
Lasioglossum calceatum	Great Britain	Wide variety
Lasioglossum cupromicans	Great Britain	Woodland, moors and coastal sites, occasionally other habitats
Lasioglossum fratellum	Great Britain	Moorland, also woodland and lowland heaths
Lasioglossum fulvicorne	Great Britain	Frequent on calcareous soils such as chalk scarps but also found on other strata
Lasioglossum laevigatum	England and Wales	Calcareous grassland, open woodland on chalk, wooded heathland and fenland
Lasioglossum laticeps	Confined to coast of Devon	South-facing unstable clay and sand sea-cliffs with associated flower-rich grasslands
Lasioglossum lativentre	England and Wales	Wide variety
Lasioglossum leucopus	Great Britain	Wide variety
Lasioglossum leucozonium	Great Britain	Wide variety
Lasioglossum malachurum	Southern England	Wide variety
Lasioglossum minutissimum	England and Wales	Sandy or clay soils, heaths and coastal cliffs, but also found elsewhere
Lasioglossum morio	England and Wales	Wide variety
Lasioglossum nitidiusculum	Great Britain	Sandy sites including sand pits, coastal dunes and landslips
Lasioglossum parvulum	England and Wales	Wide variety
Lasioglossum pauperatum	Southern, eastern England	Preference for sandy soils
Lasioglossum pauxillum	England and Wales	Mainly open sites, including chalk grassland and woodland
Lasioglossum prasinum	England and Wales	Associated with heathy vegetation on sandy soils
Lasioglossum punctatissimum	Great Britain	Light, sandy soils including lowland heaths, coastal cliffs, dunes and acidic grasslands
Lasioglossum puncticolle	England and Wales	Open, broad-leaved woodland, coastal land slips, soft-rock cliffs and estuarine
Lasioglossum quadrinotatum	England and Wales	Heaths, calcareous grassland and in open woodland
Lasioglossum rufitarse	Great Britain	Wide variety
Lasioglossum semilucens	South-east England	Unclear
Lasioglossum sexnotatum	East England	Sandy soils including lowland heaths
Lasioglossum sexstrigatum	South-east England	Sandy soils including dunes, sand pits and light woodland
Lasioglossum smeathmanellum	Great Britain	Open sites, particularly with exposed soil
Lasioglossum villosulum	Great Britain	Wide variety
Lasioglossum xanthopus	Southern England	Calcareous grassland, coastal landslips and cliffs
Lasioglossum zonulum	England and Wales	Variety but preference for woodland

Species	**Distribution**	**Habitat**
Macropis europaea	England	Wetland sites supporting the main forage plant
Megachile centuncularis	Great Britain	Wide variety, but often gardens
Megachile circumcincta	Great Britain	Coastal dunes and inland heaths
Megachile leachella	England and Wales	Mainly coastal sand dunes and inland sandy soils
Megachile ligniseca	England and Wales	Wide variety
Megachile maritima	England and Wales	Sandy, coastal areas, particularly dune systems
Megachile versicolor	Great Britain	Wide variety
Megachile willughbiella	Great Britain	Wide variety
Melecta albifrons	England and Wales	Open woodland, sand and gravel pits, masonry and cob walls
Melitta dimidiata	Restricted to Wiltshire, England	Open chalk grasslands
Melitta haemorrhoidalis	England	Calcareous and sandy grasslands, heath and open deciduous woodland
Melitta leporina	England and Wales	Open grassland on sandy, calcareous and clay soils
Melitta tricincta	England and Wales	Dry calcareous and sandy grasslands
Nomada argentata	Southern England	Chalk and acidic grasslands
Nomada armata	Southern England	Flower-rich calcareous grasslands
Nomada baccata	Southern England	Lowland and dune heaths
Nomada conjungens	Southern England	Grasslands
Nomada fabriciana	Great Britain	Variety of lowland habitats
Nomada ferruginata	Southern England	Open sites including deciduous woodland, parkland and heaths
Nomada flava	England and Wales	Wide variety
Nomada flavoguttata	Great Britain	Wide variety
Nomada flavopicta	Great Britain	Chalk grasslands
Nomada fucata	Southern Britain	Wherever its host occurs
Nomada fulvicornis	England and Wales	Dry heaths, calcareous grasslands, coastal cliffs and landslips
Nomada goodeniana	Great Britain	Wide variety
Nomada guttulata	England and Wales	Predominantly flower rich grasslands
Nomada hirtipes	England and Wales	Wide variety
Nomada integra	England and Wales	Sandy soils
Nomada lathburiana	England and Wales	Wide variety

Species	**Distribution**	**Habitat**
Nomada leucophthalma	Great Britain	Wide variety
Nomada marshamella	Great Britain	Wide variety
Nomada obtusifrons	Great Britain	Moors, heaths and open woodland
Nomada panzeri	Great Britain	Particularly associated with open broad-leaved woodland
Nomada roberjeotiana	England and Wales	Heaths and moors
Nomada ruficornis	Great Britain	Variety, particularly woodland and grassland
Nomada rufipes	Great Britain	Variety, particularly dry heaths and moorlands
Nomada sexfasciata	England	Coastal cliffs
Nomada sheppardana	England and Wales	Wide variety
Nomada signata	England and Wales	Variety including heaths, grasslands and cliffs
Nomada striata	Great Britain	Particularly flower-rich grasslands
Osmia aurulenta	England and Wales	Calcicolous - coastal dunes and grasslands
Osmia bicolor	England and Wales	Calcicolous - coastal dunes, grasslands, woodlands
Osmia bicornis	Great Britain	Wide variety
Osmia caerulescens	Great Britain	Wide variety
Osmia inermis	Scottish Highlands	Montane grassland
Osmia leaiana	England and Wales	Wide variety
Osmia parietina	England and Wales	Unimproved grassland
Osmia pilicornis	England and Wales	Mainly deciduous woodlands
Osmia spinulosa	England and Wales	Dry calcareous grasslands
Osmia uncinata	Scotland only	Open woodland
Osmia xanthomelana	England and Wales	Coastal cliffs and dunes
Panurgus banksianus	England and Wales	Sandy commons, heaths, acidic grasslands and coastal dunes and landslips
Panurgus calcaratus	England and Wales	Sandy heaths and commons
Sphecodes crassus	England and Wales	Wide variety
Sphecodes ephippius	Great Britain	Wide variety
Sphecodes ferruginatus	England and Wales	Chalk grassland, deciduous woodland and moorland
Sphecodes geoffrellus	Great Britain	Open sunny banks and disturbed ground
Sphecodes gibbus	England and Wales	Wide variety

Species	**Distribution**	**Habitat**
Sphecodes hyalinatus	Great Britain	Calcareous grassland
Sphecodes longulus	England and Wales	Dry, sandy soils
Sphecodes miniatus	Southern England	Dry sandy soils, including heaths and sand pits
Sphecodes monilicornis	Great Britain	Wide variety
Sphecodes niger	England and Wales	Sunny banks
Sphecodes pellucidus	Great Britain	Sandy areas
Sphecodes puncticeps	England and Wales	Wide variety
Sphecodes reticulatus	England and Wales	Sandy sites - heaths, open woodland and chalk grassland
Sphecodes rubicundus	England and Wales	Open woodland, coastal cliffs and marshes
Sphecodes scabricollis	England and Wales	Open woodland and heaths
Sphecodes spinulosus	Southern England	Woodland, chalk and coastal grassland
Stelis breviuscula	South-east England	Open with dead wood
Stelis ornatula	England and Wales	Chalk grassland and Coastal grassland
Stelis phaeoptera	England and Wales	Wide variety
Stelis punctulatissima	England and Wales	Open woodland and coastal grasslands

Appendix 2: Bee species excluded as potential pollinators (Chapter 2)

This appendix lists the 132 bee species that were excluded as potential crop pollinators due to ecological traits that were deemed incompatible with these bees being present in crop fields and/or crop flower visitors. Bees were excluded based upon their flight period (i.e., do not emerge until after the relevant crop has generally ceased flowering), foraging ecology (e.g., oligolectic on non-crop plant families, geographic distribution (e.g., confined to the north of Scotland), habitat requirements (e.g., coastal or healthland species), sociality (e.g., cleptoparasitic) or tongue length (i.e., short tongue species that are oligoletic on *Fabaceae*).

Species	**Exclusion Criteria: Flight Period (FP), (Floral (F), Geographic (G), Habitat (H), Sociality (S) or Tongue Length (T)**	**Details**
Andrena apicata	F	Oligolectic (*Salix spp.)*
Andrena argentata	H	Ericaceous heath
Andrena bimaculate	H	Heathland
Andrena clarkella	F	Oligolectic (*Salix spp.)*
Andrena denticulate	F	Oligolectic (*Asteraceae*)
Andrena falsifica	H	Heathland and moors
Andrena ferox	F	Oligolectic (*Quercus robur*)
Andrena florea	F	Oligolectic (*Bryonia spp.)*
Andrena fulvago	F	Oligolectic (*Asteraceae*)
Andrena fuscipes	F	Oligolectic (*Calluna spp.)*
Andrena hattorfiana	F	Oligolectic (*Dipsacaceae*)
Andrena humilis	F	Oligolectic (*Asteraceae*)
Andrena labialis	T	Oligolectic (*Fabaceae*) / short-tongued
Andrena lapponica	F	Oligolectic (*Vaccinium spp.)*
Andrena marginata	F	Oligolectic (*Dipsacaceae*)
Andrena nitidiuscula	F	Oligolectic (*Apiaceae*)
Andrena ovatula	H	Coastal, heathland and moors
Andrena pilipes	H	Coastal
Andrena praecox	F	Oliglolectic (*Salix spp.)*
Andrena rosae	F	Oligolectic (*Apiaceae*)
Andrena ruficrus	F	Oliglolectic (*Salix spp.)*
Andrena simillima	H	Coastal
Andrena similis	T	Oligolectic (*Fabaceae*) / short-tongued
Andrena tarsata	F	Oligolectic (*Potentilla spp.)*
Andrena vaga	F	Oliglolectic (*Salix spp.)*

Species	**Exclusion Criteria: Flight Period (FP), (Floral (F), Geographic (G), Habitat (H) or Sociality (S) or Tongue Length (T)**	**Details**
Andrena wilkella	T	Oligolectic (*Fabaceae*) / short-tongued
Anthophora furcata	F	Oligolectic (*Lamiaceae*)
Anthophora retusa	H	Coastal, heathland
Bombus barbutellus	S	Cleptoparasite
Bombus bohemicus	S	Cleptoparasite
Bombus campestris	S	Cleptoparasite
Bombus distinguendus	G	North Scotland and islands only
Bombus monticola	H	Upland Habitats
Bombus rupestris	S	Cleptoparasite
Bombus sylvestris	S	Cleptoparasite
Bombus vestalis	S	Cleptoparasite
Chelostoma campanularum	F	Oligolectic (*Campanula spp.)*
Chelostoma florisomne	F	Oligolectic (*Ranunculaceae*)
Coelioxys conoideus	S	Cleptoparasite
Coelioxys elongate	S	Cleptoparasite
Coelioxys inermis	S	Cleptoparasite
Coelioxys mandibularis	S	Cleptoparasite
Coelioxys quadridentatus	S	Cleptoparasite
Coelioxys rufescens	S	Cleptoparasite
Colletes cunicularius	H	Coastal, heathland
Colletes daviesanus	F	Oligolectic (*Asteraceae*)
Colletes floralis	H	Coastal
Colletes fodiens	F	Oligolectic (*Asteraceae*)
Colletes halophilus	F	Oligolectic (*Asteraceae*)
Colletes hederae	FP	Flight Period (August – September)
Colletes marginatus	H	Coastal, heaths
Colletes similis	F	Oligolectic (*Asteraceae*)
Colletes succinctus	FP	Flight Period (July – Sep)
Dasypoda hirtipes	F	Oligolectic (*Asteraceae*)
Epeolus cruciger	S	Cleptoparasite
Epeolus variegatus	S	Cleptoparasite
Halictus confusus	H	Sandy heaths
Halictus eurygnathus	H	Coastal
Heriades truncorum	F	Oligolectic (*Asteraceae*)
Hylaeus annularis	H	Coastal
Hylaeus cornutus	F	Polylectic (non-crop families)
Hylaeus pectoralis	H	Reedbeds
Hylaeus signatus	F	Oligolectic (*Reseda spp*.)
Lasioglossum angusticeps	H	Coastal

Species	**Exclusion Criteria: Flight Period (FP), (Floral (F), Geographic (G), Habitat (H) or Sociality (S) or Tongue Length (T)**	**Details**
Lasioglossum brevicorne	F	Oligolectic (*Asteraceae*)
Lasioglossum laticeps	H	Coastal
Lasioglossum pauperatum	F	Plant families visited unknown
Lasioglossum prasinum	F	Polylectic (non-crop plant families)
Lasioglossum puncticolle	F	Polylectic (non-crop plant families)
Macropis europaea	F	Oligolectic (*Primulaceae*)
Megachile circumcincta	H	Coastal, heaths
Megachile leachella	H	Coastal
Megachile maritima	H	Coastal, heathland
Melecta albifrons	S	Cleptoparasite
Melitta dimidiate	F	Oligolectic (*Onobrychis spp.)*
Melitta haemorrhoidalis	F	Oligolectic (*Campanula spp.)*
Melitta tricincta	F	Oligolectic (*Odontites vernus*)
Nomada argentata	S	Cleptoparasite
Nomada armata	S	Cleptoparasite
Nomada baccata	S	Cleptoparasite
Nomada conjungens	S	Cleptoparasite
Nomada fabriciana	S	Cleptoparasite
Nomada ferruginata	S	Cleptoparasite
Nomada flava	S	Cleptoparasite
Nomada flavoguttata	S	Cleptoparasite
Nomada flavopicta	S	Cleptoparasite
Nomada fucata	S	Cleptoparasite
Nomada fulvicornis	S	Cleptoparasite
Nomada goodeniana	S	Cleptoparasite
Nomada guttulate	S	Cleptoparasite
Nomada hirtipes	S	Cleptoparasite
Nomada integra	S	Cleptoparasite
Nomada lathburiana	S	Cleptoparasite
Nomada leucophthalma	S	Cleptoparasite
Nomada marshamella	S	Cleptoparasite
Nomada obtusifrons	S	Cleptoparasite
Nomada panzer	S	Cleptoparasite
Nomada roberjeotiana	S	Cleptoparasite
Nomada ruficornis	S	Cleptoparasite
Nomada rufipes	S	Cleptoparasite
Nomada sexfasciata	S	Cleptoparasite
Nomada sheppardana	S	Cleptoparasite
Nomada signata	S	Cleptoparasite

Species	**Exclusion Criteria: Flight Period (FP), (Floral (F), Geographic (G), Habitat (H) or Sociality (S) or Tongue Length (T)**	**Details**
Nomada striata	S	Cleptoparasite
Osmia inermis	H	Scottish montane grassland
Osmia leaiana	F	Oligolectic (*Asteraceae*)
Osmia spinulosa	F	Oligolectic (*Asteraceae*)
Osmia uncinate	H	Ancient pine forest
Osmia xanthomelana	H	Coastal
Panurgus banksianus	F	Oligolectic (*Asteraceae*)
Panurgus calcaratus	F	Oligolectic (*Asteraceae*)
Sphecodes crassus	S	Cleptoparasite
Sphecodes ephippius	S	Cleptoparasite
Sphecodes ferruginatus	S	Cleptoparasite
Sphecodes geoffrellus	S	Cleptoparasite
Sphecodes gibbus	S	Cleptoparasite
Sphecodes hyalinatus	S	Cleptoparasite
Sphecodes longulus	S	Cleptoparasite
Sphecodes miniatus	S	Cleptoparasite
Sphecodes monilicornis	S	Cleptoparasite
Sphecodes niger	S	Cleptoparasite
Sphecodes pellucidus	S	Cleptoparasite
Sphecodes puncticeps	S	Cleptoparasite
Sphecodes reticulatus	S	Cleptoparasite
Sphecodes rubicundus	S	Cleptoparasite
Sphecodes scabricollis	S	Cleptoparasite
Sphecodes spinulosus	S	Cleptoparasite
Stelis breviuscula	S	Cleptoparasite
Stelis ornatula	S	Cleptoparasite
Stelis phaeoptera	S	Cleptoparasite
Stelis punctulatissima	S	Cleptoparasite

Appendix 3: Bee species included as potential pollinators (Chapter 2)

This appendix lists the 97 bee species that were considered, based upon their ecological traits, to be potential crop pollinators of one or more of the focal crops. The crop(s) for which they were considered potential pollinators are indicated by a tick in the relevant column - apple (A), bean (B), oilseed (O) and strawberry (S).

Species	**Lecty**	**A**	**B**	**O**	**S**
Andrena alfkenella	Polylectic	✓		✓	✓
Andrena angustior	Polylectic	✓		✓	✓
Andrena barbilabris	Polylectic	✓		✓	✓
Andrena bicolor	Polylectic	✓		✓	✓
Andrena bucephala	Polylectic	✓		✓	✓
Andrena chrysosceles	Polylectic	✓		✓	✓
Andrena cineraria	Polylectic	✓		✓	✓
Andrena coitana	Polylectic				✓
Andrena congruens	Polylectic	✓		✓	✓
Andrena dorsata	Polylectic	✓		✓	✓
Andrena flavipes	Polylectic	✓		✓	✓
Andrena fucata	Polylectic	✓		✓	✓
Andrena fulva	Polylectic	✓		✓	✓
Andrena gravida	Polylectic	✓		✓	✓
Andrena haemorrhoa	Polylectic	✓		✓	✓
Andrena helvola	Polylectic	✓		✓	✓
Andrena labiata	Polylectic	✓		✓	✓
Andrena minutula	Polylectic	✓		✓	✓
Andrena minutuloides	Polylectic	✓		✓	✓
Andrena nigriceps	Polylectic				✓
Andrena nigroaenea	Polylectic	✓		✓	✓
Andrena nigrospina	Oligolectic (*Brassicaceae*)			✓	
Andrena nitida	Polylectic	✓		✓	✓
Andrena niveata	Oligolectic (*Brassicaceae*)			✓	
Andrena scotica	Polylectic	✓		✓	✓
Andrena semilaevis	Polylectic	✓		✓	✓
Andrena subopaca	Polylectic	✓		✓	✓
Andrena synadelpha	Polylectic	✓		✓	✓
Andrena thoracica	Polylectic	✓		✓	✓
Andrena tibialis	Polylectic	✓		✓	✓
Andrena trimmerana	Polylectic	✓			✓
Andrena varians	Polylectic	✓		✓	✓
Anthidium manicatum	Polylectic	✓	✓		✓
Anthophora bimaculate	Polylectic	✓			✓
Anthophora plumipes	Polylectic	✓	✓	✓	✓

Species	**Lecty**	**A**	**B**	**O**	**S**
Anthophora quadrimaculata	Polylectic		✓		
Bombus hortorum	Polylectic	✓	✓	✓	✓
Bombus humilis	Polylectic	✓	✓		✓
Bombus hypnorum	Polylectic	✓	✓	✓	✓
Bombus jonellus	Polylectic	✓	✓		✓
Bombus lapidarius	Polylectic	✓	✓	✓	✓
Bombus muscorum	Polylectic	✓	✓		✓
Bombus pascuorum	Polylectic	✓	✓		✓
Bombus pratorum	Polylectic	✓	✓		✓
Bombus ruderarius	Polylectic	✓	✓		✓
Bombus ruderatus	Polylectic	✓	✓		✓
Bombus soroeensis	Polylectic		✓		✓
Bombus sylvarum	Polylectic	✓	✓		✓
Bombus terrestris agg.	Polylectic	✓	✓	✓	✓
Ceratina cyanea	Polylectic	✓	✓		✓
Eucera longicornis	Oligolectic (*Fabaceae*)		✓		
Halictus rubicundus	Polylectic	✓		✓	✓
Halictus tumulorum	Polylectic	✓		✓	✓
Hoplitis claviventris	Polylectic	✓			✓
Hylaeus brevicornis	Polylectic	✓			✓
Hylaeus communis	Polylectic	✓		✓	✓
Hylaeus confusus	Polylectic	✓		✓	✓
Hylaeus dilatatus	Polylectic			✓	✓
Hylaeus hyalinatus	Polylectic	✓		✓	✓
Hylaeus incongruous	Polylectic			✓	✓
Hylaeus pictipes	Polylectic			✓	✓
Lasioglossum albipes	Polylectic	✓			✓
Lasioglossum calceatum	Polylectic	✓		✓	✓
Lasioglossum cupromicans	Polylectic	✓		✓	✓
Lasioglossum fratellum	Polylectic	✓			✓
Lasioglossum fulvicorne	Polylectic	✓		✓	✓
Lasioglossum laevigatum	Polylectic	✓		✓	✓
Lasioglossum lativentre	Polylectic	✓			✓
Lasioglossum leucopus	Polylectic	✓			✓
Lasioglossum leucozonium	Polylectic	✓			✓
Lasioglossum malachurum	Polylectic	✓		✓	✓
Lasioglossum minutissimum	Polylectic	✓		✓	✓
Lasioglossum morio	Polylectic	✓		✓	✓
Lasioglossum nitidiusculum	Polylectic	✓		✓	✓
Lasioglossum parvulum	Polylectic	✓			✓
Lasioglossum pauxillum	Polylectic	✓		✓	✓
Lasioglossum punctatissimum	Polylectic	✓			✓
Lasioglossum quadrinotatum	Polylectic			✓	
Lasioglossum rufitarse	Polylectic	✓			✓
Lasioglossum semilucens	Polylectic	✓			✓

Species	**Lecty**	**A**	**B**	**O**	**S**
Lasioglossum sexnotatum	Polylectic	✓		✓	✓
Lasioglossum sexstrigatum	Polylectic	✓			✓
Lasioglossum smeathmanellum	Polylectic	✓			✓
Lasioglossum villosulum	Polylectic	✓			✓
Lasioglossum xanthopus	Polylectic	✓		✓	✓
Lasioglossum zonulum	Polylectic	✓		✓	✓
Megachile centuncularis	Polylectic		✓	✓	✓
Megachile ligniseca	Polylectic		✓	✓	
Megachile versicolor	Polylectic	✓	✓		✓
Megachile willughbiella	Polylectic	✓	✓		✓
Melitta leporina	Oligolectic (*Fabaceae*)		✓		
Osmia aurulenta	Polylectic	✓	✓		✓
Osmia bicolor	Polylectic	✓	✓	✓	✓
Osmia bicornis	Polylectic	✓	✓	✓	✓
Osmia caerulescens	Polylectic	✓	✓	✓	✓
Osmia parietina	Polylectic	✓	✓		✓
Osmia pilicornis	Polylectic	✓	✓		✓

Appendix 4: Details of datasets used to determine crop flower visitors (Chapter 2)

This appendix lists details for all datasets from British, and other European, crop field studies that were used in analyses to determine the crop flower visitors of apple, bean, oilseed and strawberry. Field studies covered four survey types – aerial netting, observation plots, pan traps and transects walks.

Crop	**Survey Type**	**Description of study or reference for study if published**	**Country**
Apple	Transect Walks	Ardin, S. (2018). *Addressing seasonal vulnerability of orchard pollinators through restoration of floral communities*. [Doctoral dissertation, University of Bristol].	Great Britain
Apple	Transect Walks	Campbell, A.J., Wilby, A., Sutton, P. & Wäckers, F.L. (2017). *Do sown flower strips boost wild pollinator abundance and pollination services in a spring-flowering crop? A case study from UK cider apple orchards*. Agriculture, Ecosystems and Environment, 239, 20-29	Great Britain
Apple	Transect Walks	De Groot, G.A., R. van Kats, M. Reemer, D. van der Sterren, J. C. Biesmeijer & D. Kleijn. (2015). *De bijdrage van (wilde) bestuivers aan de opbrengst van appels en blauwe bessen; Kwantificering van ecosysteemdiensten in Nederland* [Dutch]. Wageningen, Alterra, Alterra report 2636.	Netherlands
Apple	Transect Walks	Klein, A. Unpublished. Bees were surveyed for 7 days in April and May 2015. A 20m transect was walked for 5 minutes at the edge and in the interior of orchards at approximately 30 sites.	Germany
Apple	Transect Walks	Garratt, M.P.D., Breeze, T.D., Boreux, V., Fountain, M.T., Mckerchar, M., Webber, S.M., Coston, D.J., Jenner, N., Dean, R., Westbury, D.B. & Biesmeijer, J.C. (2016). Apple pollination: demand depends on variety and supply depends on pollinator identity. *PloS One*, 11, e0153889.	Great Britain

Crop	Survey Type	Description of study or reference for study if published	Country
Apple	Transect Walks	Kleijn, D., Winfree, R., Bartomeus, I., Carvalheiro, L.G., Henry, M., Isaacs, R., *et al*. (2015). Delivery of crop pollination services is an insufficient argument for wild pollinator conservation. *Nature Communications*, 6, 7414.	Netherlands
Apple	Transect Walks	Hutchinson, L. Unpublished. Bees were surveyed for 2 days in May 2018. An observer walked along successive tree rows in orchards continuously for approximately one hour at 8 sites.	Great Britain
Apple	Observation Plots	Kőrösi, A., Markó, V., Kovács-Hostyánszki, A., Somay, L., Varga, A., Elek, Z., Boreux, V., Klein, A.M., Földesi, R. & Báldi, A. (2018) Climate-induced phenological shift of apple trees has diverse effects on pollinators, herbivores and natural enemies. *PeerJ*, e5269.	Hungary
Apple	Observation Plots	Pufal, G. Unpublished. Bees were surveyed for 2 days in April 2014. 15 x 2 minute observations of two apple tree varieties were carried out per site and apple variety at 16 sites.	Germany
Apple	Transect Walks	Radzeviciute, R. Unpublished Bees were surveyed between 2013 and 2015. 500m x 1.5m transect walked for 30 minutes at 4 sites.	Germany
Apple	Transect Walks	Samnegård, U. Unpublished. Bees were surveyed for 10 days in May 2015. Two 20m transects walked per site at 28 sites.	Sweden

Crop	**Survey Type**	**Description of study or reference for study if published**	**Country**
Apple	Observation Plots Pan Traps (2 datasets) Transect Walks (2 datasets)	Garratt, M. & Potts, S. Unpublished. Bees were surveyed for 4 days in April 2011. Apple trees were observed for 15 minutes at 8 sites. 6 stations of blue, white and yellow pan traps were used for 2 days in April 2011 at 8 sites. 3 x blue, green, red and yellow pan traps were used for 1 day in May 2015 at 3 sites. Bees were surveyed for 4 days in April 2011 and 2 days in May 2013. 6 x 50m transects were walked for 10 minutes at 13 sites.	Great Britain
Apple	Aerial Netting	Vereecken, N. Unpublished Bees were surveyed for 6 days in April and May 2016. Aerial netting was carried out for 120 minutes at 4 sites.	Belgium
Bean	Obervation plots	Bailes, E. J., Pattrick, J. G., & Glover, B. J. (2018). An analysis of the energetic reward offered by field bean (Vicia faba) flowers: Nectar, pollen, and operative force. Ecology and evolution, 8, 3161-3171.	Great Britain
Bean	Observation Plots	Bond, D.A. & Kirby, E.J.M. (1999). Anthophora plumipes (Hymenoptera: Anthophoridae) as a pollinator of broad bean (Vicia faba major). *Journal of Apicultural Research*, 38,199-203.	Great Britain
Bean	Transect Walks	Griffin, H.E. (1997). *Studies of the foraging behaviour, activity patterns and community structure of bumblebees (Bombus spp.) pollinating field beans (Vicia faba) and phacelia (Phacelia tanacetifolia) in Eastern Scotland* (Doctoral dissertation, University of St Andrews).	Great Britain

Crop	Survey Type	Description of study or reference for study if published	Country
Bean	Transect Walks Pan Traps	Carre, G., Roche, P., Chifflet, R., Morison, N., Bommarco, R., Harrison-Cripps, J., Krewenka, K., Potts, S.G., Roberts, S.P., Rodet, G. and Settele, J., 2009. Landscape context and habitat type as drivers of bee diversity in European annual crops. *Agriculture, Ecosystems and Environment*, 133, 40-47.	Great Britain
Bean	Transect Walks	Tasei, J.N. (1976). LES INSECTES POLLINISATEURS DE LA FÉVEROLE D'HIVER (VICIA FABA EQUINA L.) ET LA POLLINISATION DES PLANTES MÂLE-STÉRILE EN PRODUCTION DE SEMENCE HYBRIDE [French]. *Apidologie,* 7, 1-28.	France
Bean	Observation Plots Pan Traps (2 datasets) Transect Walks	Garratt, M. & Potts, S. Unpublished. Bees were surveyed for 7 days in May 2011. Bean plants were observed for 15 minutes at 8 sites. Blue, white and yellow pan traps were used for 7 days in May 2011 at 9 sites. Blue, green, red and yellow pan traps were used for 5 days in May and June 2015 at 3 sites. Bees were surveyed for 7 days in May 2011. 50m transects were walked for 10 minutes at 8 sites.	Great Britain
Oilseed	Transect Walk	Bartomeus, I., Potts, S.G., Steffan-Dewenter, I., Vaissiere, B.E., Woyciechowski, M., Krewenka, K.M., *et al*. (2014). Contribution of insect pollinators to crop yield and quality varies with agricultural intensification. *PeerJ*, 2, 328.	Sweden

Crop	**Survey Type**	**Description of study or reference for study if published**	**Country**
Oilseed	Transect Walks	Holzschuh, A., Dormann, C.F., Tscharntke, T. & Steffan-Dewenter, I. (2011). Expansion of mass-flowering crops leads to transient pollinator dilution and reduced wild plant pollination. *Proceedings of the Royal Society of London B: Biological Sciences*, 278, 3444-3451.	Germany
Oilseed	Pan Traps	Phillips, B. (2016). *Pollinator community and function: in oilseed rape fields and in drought-stressed grassland*. [Dissertation, University of Essex].	Great Britain
Oilseed	Observation Plots	Phillips, B.B., Williams, A., Osborne, J.L. & Shaw, R.F. (2018). Shared traits make flies and bees effective pollinators of oilseed rape (Brassica napus L.). *Basic and Applied Ecology*, 32, 66-76.	Great Britain
Oilseed	Transect Walks	Riedinger, V., Mitesser, O., Hovestadt, T., Steffan-Dewenter, I. & Holzschuh, A. (2015). Annual dynamics of wild bee densities: attractiveness and productivity effects of oilseed rape. *Ecology*, 96, 1351-1360.	Germany
Oilseed	Observation Plots Pan Traps (2 datasets) Transect Walks (2 datasets)	Garratt, M. & Potts, S, Unpublished. Bees were surveyed for 4 days in April 2011. Apple trees were observed for 15 minutes at 8 sites. Blue, white and yellow pan traps were used for 12 days in April and May 2012 at 8 sites. Blue, green, red and yellow pan traps were used for 5 days in April 2015 at 3 sites. Bees were surveyed for 14 days in April and May 2012, 18 days in May and June 2013. 50m transects were walked for 10 minutes at 20 sites.	Great Britain

Crop	**Survey Type**	**Description of study or reference for study if published**	**Country**
Oilseed	Observation Plots Transect Walks	Westphal, C., Bommarco, R., Carré, G., Lamborn, E., Morison, N., Petanidou, T., *et al.* (2008). Measuring bee diversity in different European habitats and biogeographical regions. Ecological monographs, 78, 653-671.	Germany
Oilseed	Observation Plots Transect Walks (5 datasets)	Oilseed field studies conducted by UK CEH (Centre for Ecology and Hydrology). Datasets held by Dr B.A. Woodcock.	Great Britain
Oilseed	Transect Walks	Jauker, F., Diekoetter, T., Schwarzbach, F., & Wolters, V. (2009). Pollinator dispersal in an agricultural matrix: opposing responses of wild bees and hoverflies to landscape structure and distance from main habitat. Landscape Ecology, 24, 547-555.	
Strawberry	Transect Walks	Bartomeus, I., Potts, S.G., Steffan-Dewenter, I., Vaissiere, B.E., Woyciechowski, M., Krewenka, K.M., *et al.* (2014). Contribution of insect pollinators to crop yield and quality varies with agricultural intensification. *PeerJ*, *2*, 328.	Germany
Strawberry	Transect Walks (2 datasets)	Feltham, H. (2014). *Maximising a mutualism: sustainable bumblebee management to improve crop pollination.* [Doctoral dissertation, University of Stirling].	Great Britain
Strawberry	Transect Walks	Klatt, B.K., Holzschuh, A., Westphal, C., Clough, Y., Smit, I., Pawelzik, E. and Tscharntke, T. (2014). Bee pollination improves crop quality, shelf life and commercial value. *Proceedings of the Royal Society of London B: Biological Sciences*, 281, 20132440.	Germany
Strawberry	Observation Plots	Schulze, J., Oeschger, L., Gross, A., Mueller, A., Stoll, P. & Erhardt, A. (2012). Solitary bees–Potential vectors for gene flow from cultivated to wild strawberries. *Flora-Morphology, Distribution, Functional Ecology of Plants*, 207, 762-767.	Switzerland

Crop	**Survey Type**	**Description of study or reference for study if published**	**Country**
Strawberry		Garratt, M. & Potts, S, Unpublished.	Great Britain
	Observation Plots	Bees were surveyed for 15 days in May and June 2011. Strawberry plants were observed for 10 minutes at 8 sites.	
	Pan Traps	Blue, white and yellow pan traps were used for 15 days in May and June 2011 at 8 sites.	
	Transect Walks	Bees were surveyed for 15 days in May and June 2011. 50m transects were walked for 10 minutes at 8 sites.	
Strawberry	Transect Walks	Wietzke, A., Westphal, C., Gras, P., Kraft, M., Pfohl, K., Karlovsky, P., Pawelzik, E., Tscharntke, T. & Smit, I. (2018). Insect pollination as a key factor for strawberry physiology and marketable fruit quality. *Agriculture, Ecosystems and Environment*, 258, 197-204.	Germany

Appendix 5: Bee species recorded in crop studies and excluded from flower visitor categories (Chapter 2)

This appendix lists all bee species that were recorded in British flower visitation, British pan trap and other European flower visitation crop studies that were systematically excluded from one of the three flower visitor categories for apple, bean oilseed and strawberry crops. The reason for the exclusion and subsequent action is also provided.

7.5.1 Bee species recorded in British flower visitation studies that were not categorised as definite apple flower visitors.

Species	Reason for exclusion	Action
Andrena subopaca	Single individual recorded and not recorded in European studies.	Classified as likely flower visitor as classified as potential pollinator
Bombus soreensis	Single individual recorded, not recorded in European studies and not classified as potential pollinator	Excluded entirely

7.5.2 Bee species recorded in pan trap studies that were not categorised as likely apple flower visitors.

Species	Reason for exclusion	Action
Lasioglossum pauperatum	Single individual recorded and not classified as potential pollinator	Excluded entirely
Nomada fabriciana	Not classified as potential pollinator	Excluded entirely
Nomada flavoguttata	Not classified as potential pollinator	Excluded entirely
Nomada fucata	Not classified as potential pollinator	Excluded entirely
Nomada goodeniana	Not classified as potential pollinator	Excluded entirely
Nomada ruficornis	Not classified as potential pollinator	Excluded entirely
Sphecodes ephippius	Not classified as potential pollinator	Excluded entirely

7.5.3 Bee species recorded in pan trap studies that were not categorised as possible apple flower visitors.

Species	Reason for exclusion	Action
Sphecodes monilicornis	Not classified as a potential pollinator	Excluded entirely
Sphecodes niger	Not classified as a potential pollinator	Excluded entirely

7.5.4 Bee species recorded in European flower visitor studies that were not categorised as possible apple flower visitors.

Species	Reason for exclusion	Action
Andrena bimaculata	Not documented as potential pollinator	Excluded entirely
Andrena coitana	Not documented as potential pollinator	Excluded entirely
Andrena humilis	Not documented as potential pollinator	Excluded entirely
Andrena ovatula	Not documented as potential pollinator	Excluded entirely
Andrena pilipes	Not documented as potential pollinator	Excluded entirely
Bombus vestalis	Not documented as potential pollinator	Excluded entirely
Colletes cunicularis	Not documented as potential pollinator	Excluded entirely
Hylaeus annularis	Not documented as potential pollinator	Excluded entirely
Megachile centuncularis	Not documented as potential pollinator	Excluded entirely
Melecta albiforns	Not documented as potential pollinator	Excluded entirely
Nomada ferruginata	Not documented as potential pollinator	Excluded entirely
Nomada flava	Not documented as potential pollinator	Excluded entirely
Nomada fulvicornis	Not documented as potential pollinator	Excluded entirely
Nomada marshamella	Not documented as potential pollinator	Excluded entirely

7.5.5 Bee species recorded in British flower visitation studies that were not categorised as definite bean flower visitors, reason for exclusion and subsequent action.

Species	Reason for exclusion	Action
Andrena cineraria	Single individual recorded, not recorded in European studies and not classified as potential flower visitor	Excluded entirely
Andrena scotica	Single individual recorded, not recorded in European studies and not classified as potential flower visitor	Excluded entirely
Bombus sylvestris	Single individual recorded, not recorded in European studies and not classified as potential flower visitor	Excluded entirely
Bombus vestalis	Single individual recorded, not recorded in European studies and not classified as potential flower visitor	Excluded entirely
Halictus rubicundus	Single individual recorded, not recorded in European studies and not classified as potential flower visitor	Excluded entirely

7.5.6 Bee species recorded in pan trap studies that were not categorised as possible bean flower visitors, reason for exclusion and subsequent action.

Species	**Reason for exclusion**	**Action**
Andrena bicolor	Not documented as potential pollinator	Excluded entirely
Andrena chrysosceles	Not documented as potential pollinator	Excluded entirely
Andrena dorsata	Not documented as potential pollinator	Excluded entirely
Andrena fucata	Not documented as potential pollinator	Excluded entirely
Andrena fulva	Not documented as potential pollinator	Excluded entirely
Andrena minutula	Not documented as potential pollinator	Excluded entirely
Andrena minutuloides	Not documented as potential pollinator	Excluded entirely
Andrena nigroaenea	Not documented as potential pollinator	Excluded entirely
Andrena nitida	Not documented as potential pollinator	Excluded entirely
Andrena semilaevis	Not documented as potential pollinator	Excluded entirely
Andrena subopaca	Not documented as potential pollinator	Excluded entirely
Bombus barbutellus	Not documented as potential pollinator	Excluded entirely
Bombus campestris	Not documented as potential pollinator	Excluded entirely
Bombus rupestris	Not documented as potential pollinator	Excluded entirely
Coelioxys elongata	Not documented as potential pollinator	Excluded entirely
Halictus tumulorum	Not documented as potential pollinator	Excluded entirely
Lasioglossum albipes	Not documented as potential pollinator	Excluded entirely
Lasioglossum calceatum	Not documented as potential pollinator	Excluded entirely
Lasioglossum cupromicans	Not documented as potential pollinator	Excluded entirely
Lasioglossum lativentre	Not documented as potential pollinator	Excluded entirely
Lasioglossum leucopus	Not documented as potential pollinator	Excluded entirely
Lasioglossum leucozonium	Not documented as potential pollinator	Excluded entirely
Lasioglossum malachurum	Not documented as potential pollinator	Excluded entirely

Lasioglossum minutissimum	Not documented as potential pollinator	Excluded entirely
Lasioglossum parvulum	Not documented as potential pollinator	Excluded entirely
Lasioglossum pauxillum	Not documented as potential pollinator	Excluded entirely
Lasioglossum punctiolle	Not documented as potential pollinator	Excluded entirely
Lasioglossum quadrinotatum	Not documented as potential pollinator	Excluded entirely
Lasioglossum semilucens	Not documented as potential potential pollinator	Excluded entirely
Lasioglossum villosulum	Not documented as potential pollinator	Excluded entirely
Lasioglossum xanthopus	Not documented as potential pollinator	Excluded entirely
Nomada flavoguttata	Not documented as potential pollinator	Excluded entirely
Nomada ruficornis	Not documented as potential potential pollinator	Excluded entirely
Nomada striata	Not documented as potential pollinator	Excluded entirely
Sphecodes ephippius	Not documented as potential pollinator	Excluded entirely

7.5.7 Bee species recorded in European flower visitor studies that were not categorised as possible bean flower visitors.

Species	Reason for exclusion	Action
Andrena ovatula	Not documented as potential pollinator	Excluded entirely

7.5.8 Bee species recorded in British flower visitation studies that were not categorised as definite oilseed flower visitors, reason for exclusion and subsequent action.

Species	Reason for exclusion	Action
Andrena angustior	Single individual recorded and not recorded in European studies	Classified as likely flower visitors as documented as potential pollinator
Andrena congruens	Single individual recorded and not recorded in European studies	Classified as likely flower visitors as documented as potential pollinator

Species	Reason for exclusion	Action
Andrena nigrospina	Single individual recorded and not recorded in European studies	Classified as likely flower visitors as documented as potential pollinator
Andrena niveata	Single individual recorded and not recorded in European studies	Classified as likely flower visitors as documented as potential pollinator
Andrena synadelpha	Single individual recorded and not recorded in European studies	Classified as likely flower visitors as documented as potential pollinator
Halictus rubicundus	Single individual recorded and not recorded in European studies	Classified as likely flower visitors as documented as potential pollinator
Lasioglossum leucopus	Single individual recorded and not recorded in European studies	Classified as likely flower visitors as documented as potential pollinator
Lasioglossum zonulum	Single individual recorded and not recorded in European studies	Classified as likely flower visitors as documented as potential pollinator
Bombus bohemicus	Single individual recorded and not recorded in European studies and not documented as potential flower visitor	Excluded entirely
Andrena wilkella	Single individual recorded and not recorded in European studies and not documented as potential flower visitor	Excluded entirely
Lasioglossum albipes	Single individual recorded and not recorded in European studies and not documented as potential flower visitor	Excluded entirely
Lasioglossum leucozonium	Single individual recorded and not recorded in European studies and not documented as potential flower visitor	Excluded entirely
Lasioglossum smeathmanellum	Single individual recorded and not recorded in European studies and not documented as potential flower visitor	Excluded entirely
Nomada goodeniana	Single individual recorded and not recorded in European studies and not documented as potential flower visitor	Excluded entirely

7.5.9 Bee species recorded in pan trap studies that were not categorised as possible oilseed flower visitors, reason for exclusion and subsequent action.

Species	Reason for exclusion	Action
Andrena apicata	Not documented as potential pollinator	Excluded entirely
Andrena praecox	Not documented as potential pollinator	Excluded entirely
Bombus barbutellus	Not documented as potential pollinator	Excluded entirely
Bombus ruderatus	Not documented as potential pollinator	Excluded entirely
Nomada fabriciana	Not documented as potential pollinator	Excluded entirely
Nomada flavoguttata	Not documented as potential pollinator	Excluded entirely
Nomada leucophthalma	Not documented as potential pollinator	Excluded entirely
Nomada ruficornis	Not documented as potential pollinator	Excluded entirely

7.5.10 Bee species recorded in European flower visitor studies that were not categorised as possible oilseed flower visitors.

Species	Reason for exclusion	Action
Andrena falsifica	Not documented as potential pollinator	Excluded entirely
Andrena proxima	Not documented as potential pollinator	Excluded entirely
Bombus humilis	Not documented as potential pollinator	Excluded entirely
Bombus sylvarum	Not documented as potential pollinator	Excluded entirely
Chelostoma florisomne	Not documented as potential pollinator	Excluded entirely
Halictus confusus	Not documented as potential pollinator	Excluded entirely
Hylaeus signatus	Not documented as potential pollinator	Excluded entirely
Lasioglossum laticeps	Not documented as potential pollinator	Excluded entirely
Nomada lathburiana	Not documented as potential pollinator	Excluded entirely
Osmia aurulenta	Not documented as potential pollinator	Excluded entirely

7.5.11 Bee species recorded in British flower visitation studies that were not categorised as definite strawberry flower visitors, reason for exclusion and subsequent action.

Species	Reason for exclusion	Action
Andrena bicolor	Only single individual recorded in 1 study and not recorded in European study	Classified as likely flower visitor as documented as potential flower visitor

7.5.12 Bee species recorded in pan trap studies that were not categorised as likely strawberry flower visitors, reason for exclusion and subsequent action.

Species	Reason for exclusion	Action
Bombus rupestris	Single individual recorded in European study and not documented as potential pollinator	Excluded entirely

7.5.13 Bee species recorded in pan trap studies that were not categorised as possible strawberry flower visitors, reason for exclusion and subsequent action.

Species	Reason for exclusion	Action
Andrena humilis	Not documented as potential pollinator	Excluded entirely
Bombus barbutellus	Not documented as potential pollinator	Excluded entirely
Bombus sylvestris	Not documented as potential pollinator	Excluded entirely
Bombus vestalis	Not documented as potential pollinator	Excluded entirely

7.5.14 Bee species recorded in European flower visitor studies that were not categorised as possible strawberry flower visitors.

Species	Reason for exclusion	Action
Andrena nitiduscula	Not documented as potential pollinator	Excluded entirely
Lasioglossum laticeps	Not documented as potential pollinator	Excluded entirely
Nomada fabriciana	Not documented as potential pollinator	Excluded entirely
Nomada marshamella	Not documented as potential pollinator	Excluded entirely
Sphecodes ephippius	Not documented as potential pollinator	Excluded entirely

Appendix 6: Published studies used to review the survey methods employed to sample bee communities in crops (Chapter 3).

This appendix lists all published studies used in a review of the methods most commonly employed to sample bee communities in apple, bean, oilseed and strawberry crops. Information on sampling protocols is included: how species were identified - visual observations (O), netting for later identification (N) or mixture of both methods (B); the area and/or time sampled, or pan trap colour(s) used; time (minutes) that each sampling unit was carried out for. Site, as used here, denotes a single field survey unit and refers to a farm, field, plot or polytunnel, depending upon the relevant study. The level to which to bees were identified e.g., species or guilds (i.e., bumblebee, solitary bee) is also included.

Crop(s)	Sampling Methodology	Reference	Identification Level
Apple	Fixed Transect Walks (B) – 50m x 0.5-2m, 10 mins. 7 – 15 transects per site at 8 sites.	Campbell, A.J., Wilby, A., Sutton, P. & Wäckers, F.L. (2017). Do sown flower strips boost wild pollinator abundance and pollination services in a spring-flowering crop? A case study from UK cider apple orchards. Agriculture, Ecosystems & Environment, 239, 20-29.	Species
Apple	Observation Plots (B) – 2m x 2m, 15 mins.16 trees per site at 12 sites.	Földesi, R., Kovács-Hostyánszki, A., Kőrösi, Á., Somay, L., Elek, Z., Markó, V., Sárospataki, M., Bakos, R., Varga, Á., Nyisztor, K. & Báldi, A. (2016). Relationships between wild bees, hoverflies and pollination success in apple orchards with different landscape contexts. Agricultural and Forest Entomology, 18(1), 68-75.	Species
Apple	Observation Plots (O) – 1 tree, 10 mins. 6 – 24 observations per site at 11 sites; Fixed Transect Walks (N) – 50m, 10 mins. 3 transects per site at 23 sites; Variable transects, 30 mins. 1 transect per site at 6 sites.	Garratt, M.P.D., Breeze, T.D., Boreux, V., Fountain, M.T., Mckerchar, M., Webber, S.M., Coston, D.J., Jenner, N., Dean, R., Westbury, D.B. & Biesmeijer, J.C. (2016). Apple pollination: demand depends on variety and supply depends on pollinator identity. PloS one, 11(5), e0153889.	OP – Guild (Bombus to species) TW – Species

Crop(s)	Sampling Methodology	Reference	Identification Level
Apple	Observation Plots (B) – 1 tree, 15 mins. 182 trees observed twice each at 3 sites.	Kőrösi, Á., Markó, V., Kovács-Hostyánszki, A., Somay, L., Varga, Á., Elek, Z., Boreux, V., Klein, A.M., Földesi, R. & Báldi, A. (2018). Climate-induced phenological shift of apple trees has diverse effects on pollinators, herbivores and natural enemies. PeerJ, 6, e5269.	Species
Apple	Pan Traps (White UV). 15 pan traps per orchard left out for 24 hours at 31 sites.	Marini, L., Quaranta, M., Fontana, P., Biesmeijer, J.C. & Bommarco, R. (2012). Landscape context and elevation affect pollinator communities in intensive apple orchards. Basic and Applied Ecology, 13(8), 681-689.	Species
Apple	Observation Plots (O) – 1 tree, 5 mins. 5 trees observed three times at 26 sites; Fixed Transect Walks (N) – tree row, 10 mins. 3 transects per orchard at 26 sites.	Miñarro, M. & García, D. (2018). Complementarity and redundancy in the functional niche of cider apple pollinators. Apidologie, 49(6), 789-802.	OP – Guilds TW – Species
Apple	Observation Plots (O) – 1 tree, 10 mins. 100 minutes of observations per cultivar (5 cultivars) at 1 site.	Quinet, M., Warzée, M., Vanderplanck, M., Michez, D., Lognay, G. & Jacquemart, A.L. (2016). Do floral resources influence pollination rates and subsequent fruit set in pear (Pyrus communis L.) and apple (Malus x domestica Borkh) cultivars? European Journal of Agronomy, 77, 59-69.	Guilds
Bean	Variable Transect Walks (N) – 5.5m x 2.5m, 5 mins. 4 transects per site at 28 sites.	Banaszak-Cibicka, W., Takacs, V., Kesy, M., Langowska, A., Blecharczyk, A., Sawinska, Z., Sparks, T.H. & Tryjanowski, P. (2019). Manure application improves both bumblebee flower visitation and crop yield in intensive farmland. Basic and applied ecology, 36, 26-33.	Species (only Bombus sampled)

Crop(s)	Sampling Methodology	Reference	Identification Level
Bean	Fixed Transect Walks (O) – 30-50m x 1.5m, 7-12 mins. 54 transects at 2 sites.	Marzinzig, B., Brünjes, L., Biagioni, S., Behling, H., Link, W. & Westphal, C. (2018). Bee pollinators of faba bean (Vicia faba L.) differ in their foraging behaviour and pollination efficiency. Agriculture, ecosystems & environment, 264, 24-33.	Species
Bean	Pan Traps (blue, yellow, white UV). 2 sets of three pan traps left out for 6 hours at 10 sites; Fixed Transect Walks (B) – 150m x 4m, 30 mins. 40 transects at 10 sites.	Nayak, G.K., Roberts, S.P., Garratt, M., Breeze, T.D., Tscheulin, T., Harrison-Cripps, J., Vogiatzakis, I.N., Stirpe, M.T. & Potts, S.G. (2015). Interactive effect of floral abundance and semi-natural habitats on pollinators in field beans (Vicia faba). Agriculture, Ecosystems & Environment, 199, 58-66.	Species
Bean, Oilseed, Strawberry	Fixed Transect Walks (B) – 150m x 4m, 30 mins. 40 transects at 10 sites.	Bartomeus, I., Potts, S.G., Steffan-Dewenter, I., Vaissiere, B.E., Woyciechowski, M., Krewenka, K.M., Tscheulin, T., Roberts, S.P., Szentgyörgyi, H., Westphal, C. & Bommarco, R. (2014). Contribution of insect pollinators to crop yield and quality varies with agricultural intensification. PeerJ, 2, e328.	Species
Bean, Oilseed	Observation Plots (O) – 2m x 1-2m, 15 mins. 3 observation plots at 8 sites per crop.	Garratt, M.P., Coston, D.J., Truslove, C.L., Lappage, M.G., Polce, C., Dean, R., Biesmeijer, J.C. & Potts, S.G. (2014). The identity of crop pollinators helps target conservation for improved ecosystem services. Biological Conservation, 169, pp.128-135.	Species where possible, rest to guilds or genus.
Oilseed	Pan Traps (Yellow UV). 3 pan traps per site at 28 sites.	Bailey, S., Requier, F., Nusillard, B., Roberts, S.P., Potts, S.G. & Bouget, C. (2014). Distance from forest edge affects bee pollinators in oilseed rape fields. Ecology and evolution, 4(4), 370-380.	Species
Oilseed	Observation Plots (O) – 0.5m^2, 5 mins. 3 observation plots per site at 15 sites.	Bartomeus, I., Gagic, V. & Bommarco, R. (2015). Pollinators, pests and soil properties interactively shape oilseed rape yield. Basic and Applied Ecology, 16(8), 737-745.	Guilds

Crop(s)	Sampling Methodology	Reference	Identification Level
Oilseed	Fixed Transect Walks (B) – 150m x 4m, 30 mins. 4 transects per site at 10 sites.	Bommarco, R., Marini, L. & Vaissière, B.E. (2012). Insect pollination enhances seed yield, quality, and market value in oilseed rape. Oecologia, 169(4), pp.1025-1032.	Species
Oilseed	Pan Traps (Blue, Yellow UV, White). 4 sets of 3 pan traps left out for 4 days at 85 sites; Fixed Transect Walks (B) – 50m, 10 mins. 2 transects per site at 85 sites.	Catarino, R., Bretagnolle, V., Perrot, T., Vialloux, F. & Gaba, S. (2019). Bee pollination outperforms pesticides for oilseed crop production and profitability. Proceedings of the Royal Society B, 286(1912), 20191550.	Species or Genus
Oilseed	Fixed Transect Walks (O) – 75m x 4m, 15 mins. 3 rounds of 4 transects per site at 9 sites.	Garratt, M.P., Brown, R., Hartfield, C., Hart, A. & Potts, S.G. (2018). Integrated crop pollination to buffer spatial and temporal variability in pollinator activity. Basic and Applied Ecology, 32, 77-85.	Guilds
Oilseed	Fixed Transect Walks (B) – 100m x 1m, 15 mins. 2 rounds of 2 transects at 34 sites.	Holzschuh, A., Dormann, C.F., Tscharntke, T. & Steffan-Dewenter, I. (2011). Expansion of mass-flowering crops leads to transient pollinator dilution and reduced wild plant pollination. Proceedings of the Royal Society B: Biological Sciences, 278(1723), 3444-3451.	Species
Oilseed	Fixed Transect Walks (O) – 150 x 1m, 15 mins. 2 rounds of 2 transects at 15 sites.	Holzschuh, A., Dainese, M., González-Varo, J.P., Mudri-Stojnić, S., Riedinger, V., Rundlöf, M., Scheper, J., Wickens, J.B., Wickens, V.J., Bommarco, R. & Kleijn, D. (2016). Mass-flowering crops dilute pollinator abundance in agricultural landscapes across Europe. Ecology letters, 19(10), 1228-1236.	Guilds

Crop(s)	Sampling Methodology	Reference	Identification Level
Oilseed	Observation Plots (O) – 2 x 2m for 5 mins. 8 observation plots per site at 27 sites. Fixed Transect Walks (N) – 50 x 2m, 10 mins. 2 transects per site at 27 sites.	Krimmer, E., Martin, E.A., Krauss, J., Holzschuh, A. & Steffan-Dewenter, I. (2019). Size, age and surrounding semi-natural habitats modulate the effectiveness of flower-rich agri-environment schemes to promote pollinator visitation in crop fields. Agriculture, Ecosystems & Environment, 284, 106590.	OP – Guilds Transects - Species
Oilseed	Pan Traps (blue, white, yellow UV). 1 set of pan traps left out for 25 hours per site at 15 sites.	Le Féon, V., Burel, F., Chifflet, R., Henry, M., Ricroch, A., Vaissière, B.E. & Baudry, J. (2013). Solitary bee abundance and species richness in dynamic agricultural landscapes. Agriculture, Ecosystems & Environment, 166, pp.94-101.	Species
Oilseed	Pan Traps (blue, yellow UV, white). Pan traps left out for 4 days; Fixed Transect Walks (N) - . 50m, 10 mins. 2 transects per site at 71 sites.	Perrot, T., Gaba, S., Roncoroni, M., Gautier, J.L. & Bretagnolle, V. (2018). Bees increase oilseed rape yield under real field conditions. Agriculture, Ecosystems & Environment, 266, 39-48.	Species or Genus
Oilseed	Fixed Transect Walks (B) – 150m^2, 15 mins. 2 transects per site at 16 sites.	Riedinger, V., Mitesser, O., Hovestadt, T., Steffan-Dewenter, I. & Holzschuh, A. (2015). Annual dynamics of wild bee densities: attractiveness and productivity effects of oilseed rape. Ecology, 96(5), 1351-1360.	Species
Oilseed	Fixed Transect Walks (N) – 50m x 2m, 15 mins. 1 transect per site at 143 sites.	Rollin, O., Bretagnolle, V., Decourtye, A., Aptel, J., Michel, N., Vaissière, B.E. & Henry, M. (2013). Differences of floral resource use between honey bees and wild bees in an intensive farming system. Agriculture, Ecosystems & Environment, 179, 78-86.	Species
Oilseed	Fixed Transect Walks (N) - 50m x 2m, 15 mins. 1 transect per site at 143 sites.	Rollin, O., Bretagnolle, V., Fortel, L., Guilbaud, L. & Henry, M. (2015). Habitat, spatial and temporal drivers of diversity patterns in a wild bee assemblage. Biodiversity and Conservation, 24(5), 1195-1214.	Species

Crop(s)	Sampling Methodology	Reference	Identification Level
Oilseed	Pan Traps (Yellow). 247 pan traps left out for 3 days at 10 sites.	Scherber, C., Beduschi, T. & Tscharntke, T. (2019). Novel approaches to sampling pollinators in whole landscapes: a lesson for landscape-wide biodiversity monitoring. Landscape Ecology, 34(5), 1057-1067.	Species
Oilseed	Observation Plots (O) – 6 patches of flowers, 5 mins. 7 observation plots per site at 3 sites; Pan Traps (blue, white, yellow UV). 3 triplets of pan traps left out for 48 hours per site at 10 sites.	Stanley, D.A., Gunning, D. & Stout, J.C. (2013). Pollinators and pollination of oilseed rape crops (Brassica napus L.) in Ireland: ecological and economic incentives for pollinator conservation. Journal of Insect Conservation, 17(6), 1181-1189.	OP – Guild (Bombus to species) PT – Species
Oilseed	Pan Traps (blue, white, yellow UV). 3 triplets of pan traps left out for 48 hours at 10 sites; Fixed Transect Walks (B). 100m x 2m. 12 transects per site at 5 sites.	Stanley, D.A. & Stout, J.C. (2013). Quantifying the impacts of bioenergy crops on pollinating insect abundance and diversity: a field-scale evaluation reveals taxon-specific responses. Journal of Applied Ecology, 50(2), 335-344.	PT – Species TN – Species TW – Species (Bombus), Genus (Solitary)
Oilseed	Observation Plots (O). 30cm x 30cm, 5 mins. 7 observation plots per site at 2 sites.	Stanley, D.A. & Stout, J.C. (2014). Pollinator sharing between mass-flowering oilseed rape and co-flowering wild plants: implications for wild plant pollination. Plant Ecology, 215(3), 315-325.	OP – Species (Bombus), Genus (Solitary)
Oilseed	Observation Plots (O). 1m x 2m, 7 mins. 2 observation plots per site at 24 sites; Pan Traps (yellow UV). 2 traps per site left out for 48 hours at 24 sites; Fixed Transect Walks (O).50m x 2m, 30 mins. 16 transects per site at three sites.	Woodcock, B.A., Edwards, M., Redhead, J., Meek, W.R., Nuttall, P., Falk, S., Nowakowski, M. & Pywell, R.F. (2013). Crop flower visitation by honeybees, bumblebees and solitary bees: Behavioural differences and diversity responses to landscape. Agriculture, Ecosystems & Environment, 171, 1-8.	OP – Guilds PT – Species TW – Species (Bombus, some *Andrena*), Genus (Solitary)

Crop(s)	Sampling Methodology	Reference	Identification Level
Oilseed	Fixed Transect Walks (O). 200m. 2 transects per site at 3 sites.	Woodcock, B.A., Bullock, J.M., McCracken, M., Chapman, R.E., Ball, S.L., Edwards, M.E., Nowakowski, M. & Pywell, R.F. (2016). Spill-over of pest control and pollination services into arable crops. Agriculture, Ecosystems & Environment, 231, 15-23.	Guilds
Strawberry	Pan Traps (white, yellow UV). 3 sets of pan traps left out for 5 to 15 days at 12 sites.	Ahrenfeldt, E.J., Klatt, B.K., Arildsen, J., Trandem, N., Andersson, G.K.S., Tscharntke, T., Smith, H.G. & Sigsgaard, L. (2015). Pollinator communities in strawberry crops– variation at multiple spatial scales. Bulletin of entomological research, 105(4), 497-506.	Species
Strawberry	Pan Traps (white). 5 traps left out for 10 days on 4 occasions per site at 12 sites.	Ahrenfeldt, E.J., Kollmann, J., Madsen, H.B., Skov-Petersen, H. & Sigsgaard, L. (2019). Generalist solitary ground-nesting bees dominate diversity survey in intensively managed agricultural land. Journal of Melittology, (82), 1-12.	Species
Strawberry	Fixed Transect Walks (O). 300m. 6 transects per site at 21 sites.	Ellis, C.R., Feltham, H., Park, K., Hanley, N. & Goulson, D. (2017). Seasonal complementary in pollinators of soft-fruit crops. Basic and Applied Ecology, 19, pp.45-55.	Species (Bombus) Guild (Solitary)
Strawberry	Fixed Transect Walks (O). 100m x 2m. 2 to 6 transects per site at 6 sites.	Feltham, H., Park, K., Minderman, J. & Goulson, D. (2015). Experimental evidence that wildflower strips increase pollinator visits to crops. Ecology and evolution, 5(16), 3523-3530.	Species (Bombus) Guild (Solitary)
Strawberry	Fixed Transect Walks (N). 80m x 2m, 20 mins. 12 transects per site at 19 sites.	Ganser, D., Mayr, B., Albrecht, M. & Knop, E. (2018). Wildflower strips enhance pollination in adjacent strawberry crops at the small scale. Ecology and evolution, 8(23), 11775-11784.	Species
Strawberry	Observation Plots (O). 3m x 6m, 10 mins. 6 observation plots per site at 10 sites.	Hodgkiss, D., Brown, M.J. & Fountain, M.T. (2019). The effect of within-crop floral resources on pollination, aphid control and fruit quality in commercial strawberry. Agriculture, ecosystems & environment, 275, 112-122.	Guilds

Crop(s)	Sampling Methodology	Reference	Identification Level
Strawberry	Fixed Transect Walks (N). Row of plants, 10 mins. 16 transects over 12 sites.	Klatt, B.K., Holzschuh, A., Westphal, C., Clough, Y., Smit, I., Pawelzik, E. & Tscharntke, T. (2014). Bee pollination improves crop quality, shelf life and commercial value. Proceedings of the Royal Society B: Biological Sciences, 281(1775), 20132440.	Species
Strawberry	Fixed Transect Walks (O). 1 row of plants, 30 mins. 23 transects over 2 sites.	Lui, B., Hall, A.M. & Davies, K. (2014). Factors contributing to sustainable strawberry production. Aspects of applied Biology, 127,301-311.	Guilds
Strawberry	Fixed Transect Walks (B). 1 polytunnel, 30 mins. 6 - 8 transects per site at 9 sites.	Martin, C.D., Fountain, M.T. & Brown, M.J. (2019). Varietal and seasonal differences in the effects of commercial bumblebees on fruit quality in strawberry crops. Agriculture, ecosystems & environment, 281, 124-133.	Species (Bombus) Genus (*Andrena*)
Strawberry	Observation Plots (O). 4m^2, 20 mins. 21 observation plots over 5 sites.	Schulze, J., Oeschger, L., Gross, A., Mueller, A., Stoll, P. & Erhardt, A. (2012). Solitary bees–Potential vectors for gene flow from cultivated to wild strawberries. Flora-Morphology, Distribution, Functional Ecology of Plants, 207(10), 762-767.	Guilds (Subsequent random netting to species level)
Strawberry	Fixed Transect Walks (N). 100m. 4 transects per site at 4 sites.	Wietzke, A., Westphal, C., Gras, P., Kraft, M., Pfohl, K., Karlovsky, P., Pawelzik, E., Tscharntke, T. & Smit, I. (2018). Insect pollination as a key factor for strawberry physiology and marketable fruit quality. Agriculture, Ecosystems & Environment, 258, 197-204.	Species

Appendix 7: Generalised linear mixed models and tukey test results (Chapter 3).

This appendix sets out the model and post hoc test results for the generalised linear mixed models described in section 3.3.3 - ‘Abundance of bumblebees and solitary bees detected by different sampling methods.’ The table provides information on the chi-squared (Chi^2), degrees of freedom (Df) and P values (P) for the GLMM’s for apple, oilseed and strawberry, and the estimate (Est), standard error (SE), z value (Z value) and P values (P) for the Tukey Tests.

Crop	**GLMM**	**Chi^2**	**Df**	**P**	**Tukey Test**	**Est**	**SE**	**Z**	**P**	**Sig**
Apple	Guild*Method	22.3	2	0.00001432***						
					Bombus Obs < Solitary Obs	1.33	0.48	2.78	0.0593	
					Bombus Pan < Solitary Pan	3.85	0.42	9.15	<0.001	***
					Bombus Tran < Solitary Tran	1.19	0.40	2.99	0.0325	*
					Bombus Obs < Bombus Pan	0.49	0.51	0.96	0.9292	
					Bombus Obs < Bombus Tran	1.00	0.49	2.04	0.3167	
					Bombus Pan < Bombus Tran	0.50	0.45	1.12	0.8703	
					Solitary Obs < Solitary Pan	3.01	0.38	7.96	<0.001	***
					Solitary Obs < Solitary Tran	0.85	0.38	2.23	0.2224	
					Solitary Pan > Solitary Tran	-2.16	0.35	-6.11	<0.001	***

Crop	GLMM	Chi^2	Df	P	Tukey Test	Est	SE	Z	P	Sig
Oilseed	Guild*Method	16.54	2	0.0002563 ***						
					Bombus Obs > Solitary Obs	- 1.70	0.62	2.74	0.06289	
					Bombus Pan < Solitary Pan	0.31	0.38	0.34	0.99933	
					Bombus Trans < Solitary Trans	-2.43	0.56	- 4.38	<0.001	***
					Bombus Obs < Bombus Pan	0.49	0.41	1.21	0.82153	
					Bombus Obs < Bombus Tran	0.95	0.39	2.42	0.13955	
					Bombus Pan < Bombus Tran	0.50	0.37	1.24	0.80626	
					Solitary Obs < Solitary Pan	2.38	0.60	3.85	0.00148	**
					Solitary Obs < Solitary Tran	0.22	0.74	0.30	0.99963	
					Solitary Pan > Solitary Tran	-2.10	0.56	-3.75	0.00236	**
Strawberry	Guild*Method	75.90	2	2.2e-16***						
					Bombus Obs > Solitary Obs	3.83	0.63	-6.11	<0.001	***
					Bombus Pan > Solitary Pan	-0.16	0.27	-0.60	0.990	
					Bombus Tran > Solitary Tran	-4.46	0.35	-12.63	<0.001	***
					Bombus Obs < Bombus Pan	-0.36	0.26	-1.40	0.707	

Crop	**GLMM**	**Chi^2**	**Df**	**P**	**Tukey Test**	**Est**	**SE**	**Z**	**P**	**Sig**
					Bombus Obs < Bombus Tran	2.11	0.24	8.95	<0.001	***
					Bombus Pan < Bombus Tran	2.47	0.25	10.04	<0.001	***
					Solitary Obs < Solitary Pan	3.31	0.63	5.22	<0.001	***
					Solitary Obs < Solitary Tran	1.49	0.68	2.19	0.224	
					Solitary Pan > Solitary Tran	0.38	0.38	-4.86	<0.001	***

Appendix 8: Mean abundance and species richness of bee genera sampled per site (Chapter 3).

This appendix details the mean abundance and species richness ±SE of bee genera sampled per site in apple (A), field bean (B), oilseed rape (O) and strawberry (S) crops (datasets 1.1a – 1.1c and 1.2a – 1.2d). Pan trap standardised data (dataset 1.1b) represents where the total abundance and species richness of each genus sampled per site was divided by 8 before calculating the mean, in order to estimate the mean abundance and species richness of each genus that would be sampled if survey effort was equal to that of transect walks.

7.8.1. Datasets 1.1a – 1.1d.

Crop	Survey Type	Diversity	*Andrena*	*Bombus*	*Halictus*	*Lasioglossum*	*Osmia*	Unidentified Solitary
A	**Observation Plots**	**Abundance**	0.6 ±0.3	1.8 ± 0.4	NA	NA	0.1 ± 0.1	5.1 ± 1.0
	Pan Traps	**Abundance**	66.6 ± 19.8	2.5 ± 0.4	2.8 ± 1.2	54.8 ± 27.6	0.6 ± 0.4	-
		(Standardised)	8.3 ± 2.5	0.3 ± 0.1	0.3 ± 0.1	6.8 ± 3.5	0.08 ± 0.05	-
		Species Richness	7.6 ± 0.4	2.0 ± 0.5	0.6 ± 0.2	3.8 ± 0.6	0.3 ± 0.2	-
		(Standardised)	1.0 ± 0.1	0.3 ± 0.1	0.1 ± 0.1	0.5 ± 0.1	0.03 ± 0.02	-
	Transect Walks	**Abundance**	3.1 ± 1.0	4.4 ± 1.0	-	0.1 ± 0.1	-	10.8 ± 2.7
		Species Richness	1.9 ± 0.4	2.1 ± 0.4	-	0.1 ± 0.1	-	-
B	**Observation Plots**	**Abundance**	-	14.0 ± 5.2	-	-	-	0.3 ± 0.2
	Pan Traps	**Abundance**	-	14.8 ± 5.6	-	-	-	-
		(Standardised)	-	1.8 ± 0.7	-	-	-	-
		Species Richness	-	3.3 ± 0.3	-	-	-	-
		(Standardised)	-	0.4 ± 0.1	-	-	-	-
	Transect Walks	**Abundance**	0.4 ± 0.2	63.8 ± 9.7	-	-	-	-
		Species Richness	0.4 ± 0.2	5.3 ± 0.4	-	-	-	-

Crop	**Survey Type**	**Diversity**	***Andrena***	***Bombus***	***Halictus***	***Lasioglossum***	***Osmia***	**Unidentified Solitary**
O	**Observation Plots**	**Abundance**	-	5.5 ± 2.2	-	-	0.3 ± 0.3	1.0 ± 0.7
	Pan Traps	**Abundance**	4.5 ± 1.2	4.5 ± 1.2	0.1 ± 0.1	0.9 ± 0.5	-	-
		(Standardised)	0.6 ± 0.1	0.6 ± 0.1	0.01 ± 0.01	0.1 ± 0.06	-	-
		Species Richness	2.0 ± 0.5	2.4 ± 0.4	0.1 ± 0.1	0.4 ± 0.2	-	-
		(Standardised)	0.3 ± 0.1	0.3 ± 0.1	0.02 ± 0.02	0.05 ± 0.02	-	-
	Transect Walk	**Abundance**	0.3 ± 0.2	7.1 ± 2.5	-	-	-	0.4 ± 0.3
		Species Richness	0.3 ± 0.2	2.3 ± 0.5	-	-	-	-
S	**Observation Plots**	**Abundance**	-	19.4 ± 6.2	-	-	-	0.4 ± 0.2
	Pan Traps	**Abundance**	8.0 ± 2.1	12.4 ± 5.3	0.3 ± 0.2	1.6 ± 0.8	-	-
		(Standardised)	1.0 ± 0.3	1.5 ± 0.7	0.03 ± 0.02	0.2 ± 0.1	-	-
		Species Richness	2.6 ± 0.7	2.4 ± 0.3	0.3 ± 0.2	0.5 ± 0.2	-	-
		(Standardised)	0.3 ± 0.1	0.3 ± 0.1	0.03 ± 0.02	0.06 ± 0.02	-	-
	Transect Walk	**Abundance**	0.3 ± 0.2	147.3 ± 32.3	-	0.1 ± 0.1	-	1.4 ± 0.5
		Species Richness	0.3 ± 0.2	3.9 ± 0.4	-	0.1 ± 0.1	-	-

7.8.2 Datasets 1.2a – 1.2d.

Crop	Survey Type	Diversity	*Andrena*	*Bombus*	*Halictus*	*Lasioglossum*
B	**Pan Traps**	**Abundance**	0.9 ± 0.3	1.4 ±0.6	-	-
		Species Richness	0.6 ± 0.2	1.1 ± 0.4	-	-
	Transect Walks	**Abundance**	0.9 ± 0.5	8.3 ± 1.8	-	-
		Species Richness	0.4 ±0.2	3.0 ±0.5	-	-
O	**Pan Traps**	**Abundance**	23.5 ± 7.7	6.0 ± 2.0	0.3 ± 0.3	2.0 ± 1.4
		Species Richness	6.0 ± 1.2	3.3 ± 0.9	0.3 ± 0.3	1.6 ± 0.9
	Observation Plots	**Abundance**	4.8 ± 3.1	2.5 ±1.0	-	0.3 ±0.3
		Species Richness	2.0 ±1.1	1.5 ±0.5	-	0.3 ± 0.3

7.8.3 Number of bee species sampled by observation plots (OP), pan traps (PT) and transect walks (TW) in datasets 1.1a – 1.1c (top row) and 1.2a – 1.2d where applicable (bottom row).

Species	**Apple**			**Bean**			**Oilseed**			**Strawberry**		
	OP	**PT**	**TW**	**OP**	**PT**	**TW**	**OP**	**PT**	**TW**	**OP**	**PT**	**TW**
Andrena sp.	5		6									
							1					
Bombus sp.			2	1		63	4		13	1		156
Lasioglossum sp.							1					
Osmia sp.	1						2					
Solitary sp.	41		6			3	8			3		11
Andrena bicolor		2						6			1	1
								4				
Andrena chrysosceles		42	1						1		8	1
								7				
Andrena cineraria		20	1					1			9	
								1				
Andrena dorsata		18	12									
Andrena flavipes		261					1					
								2				
Andrena fulva												
							1	13				
Andrena gravida		1										
Andrena haemorrhoa		67	5					11			20	
							13	18				
Andrena helvola		5										
Andrena labialis												
					1	2						
Andrena labiata		2										

Species	Apple			Bean			Oilseed			Strawberry		
	OP	PT	TW	OP	PT	TW	OP	PT	TW	OP	PT	TW
Andrena minutula		44									4	
Andrena nigroaenea		36					1	12			9	
								21				
Andrena nitida		29	4									
							2	17				
Andrena scotica		4	1								13	
							1	3				
Andrena subopaca		1										
Andrena tibialis								1				
Andrena trimmerana		1										
Andrena wilkella												
							1	7				
Bombus hortorum		4	1	1		78		2				
					3	46		11				
Bombus hypnorum		1			2	5	4		2	4	1	19
Bombus lapidarius	3	5	10	2	28	97	12	15	18	86	57	549
					3	12	6	3				
Bombus pascuorum	1	2	1		3	14	1	3	2	2		9
						7		4				
Bombus pratorum	1	4	3		3	7		3	3	1	6	9
					1	1		2				
Bombus ruderatus						5						
Bombus terrestris	9	4	12	45	48	250	22	11	19	61	35	436
					9	17	4	4				
Halictus rubicundus								1			2	
								1				
Halictus tumulorum		22										

Species	**Apple**			**Bean**			**Oilseed**			**Strawberry**		
	OP	**PT**	**TW**	**OP**	**PT**	**TW**	**OP**	**PT**	**TW**	**OP**	**PT**	**TW**
Lasioglossum calceatum		10						7			13	1
								3				
Lasioglossum fulvicorne		1										
								1				
Lasioglossum leucopus		3										
Lasioglossum malachurum		187										
								2				
Lasioglossum morio		105										
Lasioglossum parvulum		2										
Lasioglossum pauxillum		129	1									
Lasioglossum xanthopus		5						2				
Osmia bicornis		5										

Appendix 9: Generalised linear mixed models and tukey test results (Chapter 3).

This appendix sets out the model and post hoc test results (7.10.1) for the generalised linear mixed models in section 3.3.8 - ‘Effects of trap colour on bee guilds and species sampled by pan traps.’ The table provides information on the chi-squared (Chi^2, degrees of freedom (Df) and P values (P) for the GLMM’s for apple, oilseed and strawberry, and the estimate (Est), standard error (SE), z value (Z value) and P values (P) for the Tukey Tests. Also included the number of bee species caught in each pan trap colour during IPI (7.10.2) and ALARM field studies (7.10.3).

7.9.1 Model and post hoc test results for generalised linear models

Crop	**GLMM**	**Chi^2**	**Df**	**P**	**Tukey Test**	**Est**	**SE**	**Z**	**P**	**Sig**
Apple	Guild*Colour	18.12	3	0.000116 ***						
					Bombus Blue < Solitary Blue	1.14	0.31	3.72	0.002584	**
					Bombus White < Solitary White	2.19	0.30	7.30	< 1e-04	***
					Bombus Yellow > Solitary Yellow	3.17	0.31	10.33	< 1e-04	***
					Bombus Blue > Bombus White	- 0.06	0.36	- 0.16	0.999985	
					Bombus Blue > Bombus Yellow	-0.21	0.38	-0.57	0.992378	
					Bombus White > Bombus Yellow	-0.15	0.37	-0.41	0.998388	
					Solitary Blue < Solitary White	1.00	0.24	4.20	0.000377	***
					Solitary Blue < Solitary Yellow	1.81	0.23	7.90	< 1e-04	***
					Solitary White < Solitary Yellow	0.82	0.21	3.88	0.001386	***

7.9.2 Number of bee species sampled by each colour pan traps in crops (IPI datasets).

Species	Pan Trap Colour														
	Blue					White					Yellow				
	A	B	O	S	Total	A	B	O	S	Total	A	B	O	S	Total
A.bic			5	1	6	1		1		2	1				1
A. chr			2		2	13		1	2	16	29		4	6	39
A. cin	1			2	3	3			3	6	16		1		17
A. dor	1				1	3				3	14				14
A. flav	17				17	56		2		58	186				186
A. ful			1		1			2		2			3		3
A. grav					0	1				1					0
A. haem	2		2	1	5	19		3	3	25	46		6	16	68
A. hel	2				2					0	3				3
A. lab					0	1				1	1				1
A. min	2				2	14			1	15	28			3	31
A. nig	11		1		12	11		8	4	23	14		3	2	19
A. nit	3		1	3	7	10		4		14	16		12		28
A. scot				1	1			1	2	3	4		2	10	16
A. sub					0					0	1				1
A. tib					0			1		1					0
A. trim					0					0	1				1
A. wil			2		2			1		1			4		4
B.hort	2	20	1		23		2	1		3	2	12			14
B.hyp		2			2	1				1				1	1
B.lap	3	13	4	5	25	2	5	8	14	29		10	3	38	51
B. luc	1	3		4	8	1		4	4	9		3	3	6	12
B. pasc	1	3	2		6					0	1		1		2
B. prat	1		1	2	4	2		1	1	4	1	2	1	3	7
B. ter	1	17	1	3	22	1	14	5	9	29		10	2	9	21
H. rub					0					0			1		1
H. tum	3				3	3				3	16				16
L. calc	3		1		4	4		6	6	16	3		1	7	11
L. fulv	1				1			1		1					0
L. leuc					0					0	3				3
L. mala	12				12	31				31	144		2		146
L. mor	24				24	53				53	28				28
L. parv					0	1				1					1
L. paux	11				11	30				30	87				87
L. punc					0					0	1				1
L. xan			1		1					0			1		1
O.bic					0	1				1	4				4

7.9.3 Number of bee species sampled by each colour pan traps in crops (ALARM datasets).

Species	Pan Trap Colour								
	Blue			White				Yellow	
	B	O	Total	B	O	Total	B	O	Total
A.bic		4	4			0			0
A. chr		2	2		1	1		4	4
A. cin			0			0		1	1
A. flav			0		2	2			0
A. ful	1		1		5	5		7	7
A. haem		2	2		5	5		11	11
A. nig		5	5		2	2		14	14
A. nit		1	1		4	4		12	12
A. scot			0		1	0		2	2
A. wil		2	2		1	1		4	4
B.hort			0	1		1	1	1	2
B.lap			0			0	2		0
B. pasc			0			0		1	1
B. prat			0			0	1		1
B. ter	4		4	1		1		1	1
H. rub			0			0		1	1
L. calc		1	1		1	1		1	1
L. fulv			0		1	1			0
L. mala			0			0		2	2
L. xan		1	1			0		1	1

Appendix 10: Bee species and flower visitor category to which they were assigned (Chapter 4).

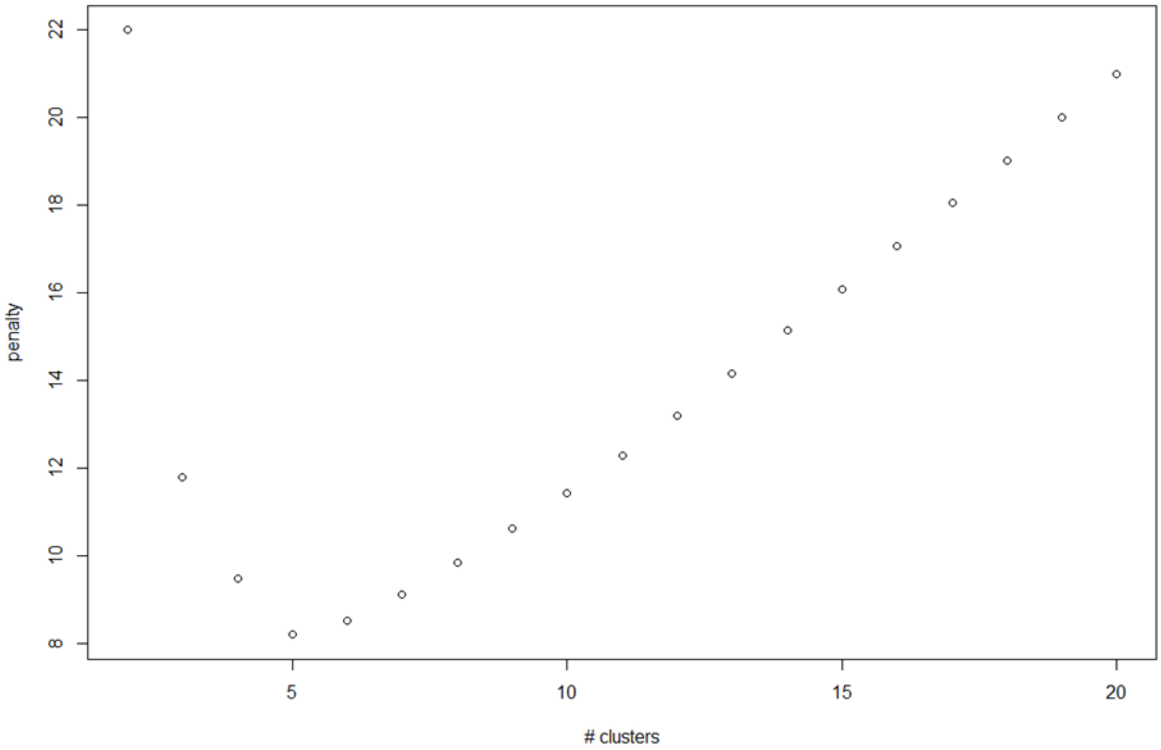
This appendix lists how bee species were categorised as outlined in sections '4.3.1 and 4.4.1 Stability of pollinator occupancy', and the flower visitor category to which they were assigned for each crop. Species labelled as 'Primary' were included in all analyses. Species labelled as 'Core' where included in analyses for both the 'core' and 'all' categories of flower visitors. Species labelled as 'All' where only included in analyses incorporating the 'all' flower visitor category.

Species	**Apple**	**Bean**	**Oilseed**	**Strawberry**
Andrena angustior			All	
Andrena bicolor	Core		Core	All
Andrena chrysosceles	Core		Core	Core
Andrena cineraria			Primary	All
Andrena congruens			All	
Andrena dorsata	Primary		Core	
Andrena flavipes	Core		Core	
Andrena fucata			Core	
Andrena fulva	Core		Core	
Andrena haemorrhoa	Primary	Core	Primary	Core
Andrena helvola	Core		Core	
Andrena labialis		Core		
Andrena labiata	All		Core	
Andrena minutula	Core		Core	All
Andrena nigroaenea	Primary		Primary	All
Andrena nitida	Primary		Core	
Andrena scotica	Core		Primary	All
Andrena subopaca	All		Core	
Andrena synadelpha			All	
Andrena tibialis			All	
Andrena trimmerana	All			
Andrena wilkella		Core		
Anthophora plumipes		Core	Core	
Bombus hortorum	Primary	Primary	Core	
Bombus jonellus			Core	
Bombus lapidarius	Primary	Primary	Primary	Primary
Bombus muscorum			Core	
Bombus pascuorum	Primary	Primary	Core	Core
Bombus pratorum	Core	Core	Core	Core
Bombus ruderatus		Core		
Bombus soroeensis			Core	
Bombus terrestris	Primary	Primary	Primary	Primary
Colletes daviesanus				Core
Halictus rubicundus			All	All
Halictus tumulorum	All		Core	

Species	**Apple**	**Bean**	**Oilseed**	**Strawberry**
Lasioglossum calceatum	Core		Core	Core
Lasioglossum cupromicans			All	
Lasioglossum fulvicorne	All		Core	
Lasioglossum leucopus	All		All	
Lasioglossum malachurum	All		Core	
Lasioglossum morio	All		Core	
Lasioglossum parvulum	All		Core	
Lasioglossum pauperatum			Core	
Lasioglossum pauxillum	Core		Core	
Lasioglossum punctatissimum	All			
Lasioglossum puncticolle			Core	
Lasioglossum xanthopus			Core	
Lasioglossum zonulum			All	
Osmia bicolor			Core	
Osmia bicornis	Core		Core	

Appendix 11: Kelly–Gardner–Sutcliffe (KGS) penalty function plot (Chapter 4).

This appendix shows the output plot for the Kelly–Gardner–Sutcliffe (KGS) penalty function outlined in sections 4.3.2 and 4.4.2 ‘Inter-annual changes in occupancy’.



Appendix 12: Order in which bee species were removed from each crop dataset (Chapter 4).

This appendix details the order in which bee species were removed from each crop dataset in the analyses for sections 4.3.3 and 4.4.3 ‘Stability of pollinator occupancy’.

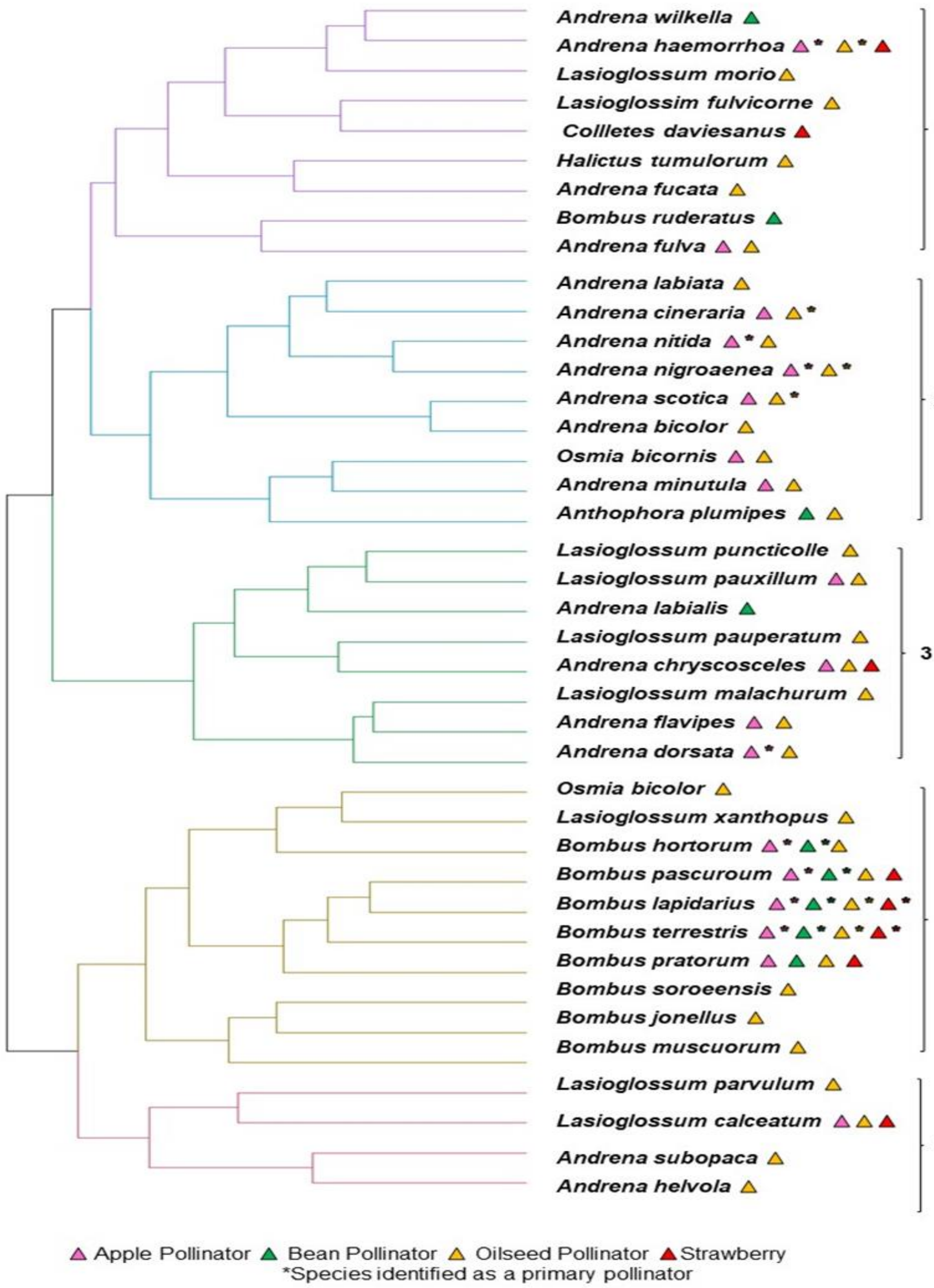
Species	**Apple**	**Bean**	**Oilseed**	**Strawberry**
Andrena angustior			11	
Andrena bicolor	16		30	5
Andrena chrysosceles	11		23	2
Andrena cineraria	13		26	3
Andrena congruens			2	
Andrena dorsata	20		34	
Andrena flavipes	14		27	
Andrena fucata			14	
Andrena fulva	21		35	
Andrena haemorrhoa	26		40	10
Andrena helvola	6		17	
Andrena labialis		2		
Andrena labiate	5		16	
Andrena minutula	19		33	7
Andrena nigroaenea	18		32	6
Andrena nitida	15		29	
Andrena scotica	23		37	8
Andrena subopaca	10		22	
Andrena synadelpha			9	
Andrena tibialis			6	
Andrena trimmerana	3			
Andrena wilkella		3		
Anthophora plumipes		4	24	
Bombus hortorum	24	5	38	
Bombus jonellus			20	
Bombus lapidarius				
Bombus muscorum			7	
Bombus pascuorum	29	8	43	13
Bombus pratorum	27	6	41	11
Bombus ruderatus		1		
Bombus soroeensis			1	
Bombus terrestris	28	7	42	12
Colletes daviesanus				1
Halictus rubicundus			28	4
Halictus tumulorum	22		36	
Lasioglossum calceatum	25		39	9
Lasioglossum cupromicans			8	
Lasioglossum fulvicorne	2		13	
Lasioglossum leucopus	9		21	
Lasioglossum malachurum	4		15	
Lasioglossum morio	17		31	

Species	**Apple**	**Bean**	**Oilseed**	**Strawberry**
Lasioglossum parvulum	7		18	
Lasioglossum pauperatum			5	
Lasioglossum pauxillum	8		19	
Lasioglossum punctatissimum	1			
Lasioglossum puncticolle			4	
Lasioglossum xanthopus			3	
Lasioglossum zonulum			12	
Osmia bicolor			10	
Osmia bicornis	12		25	

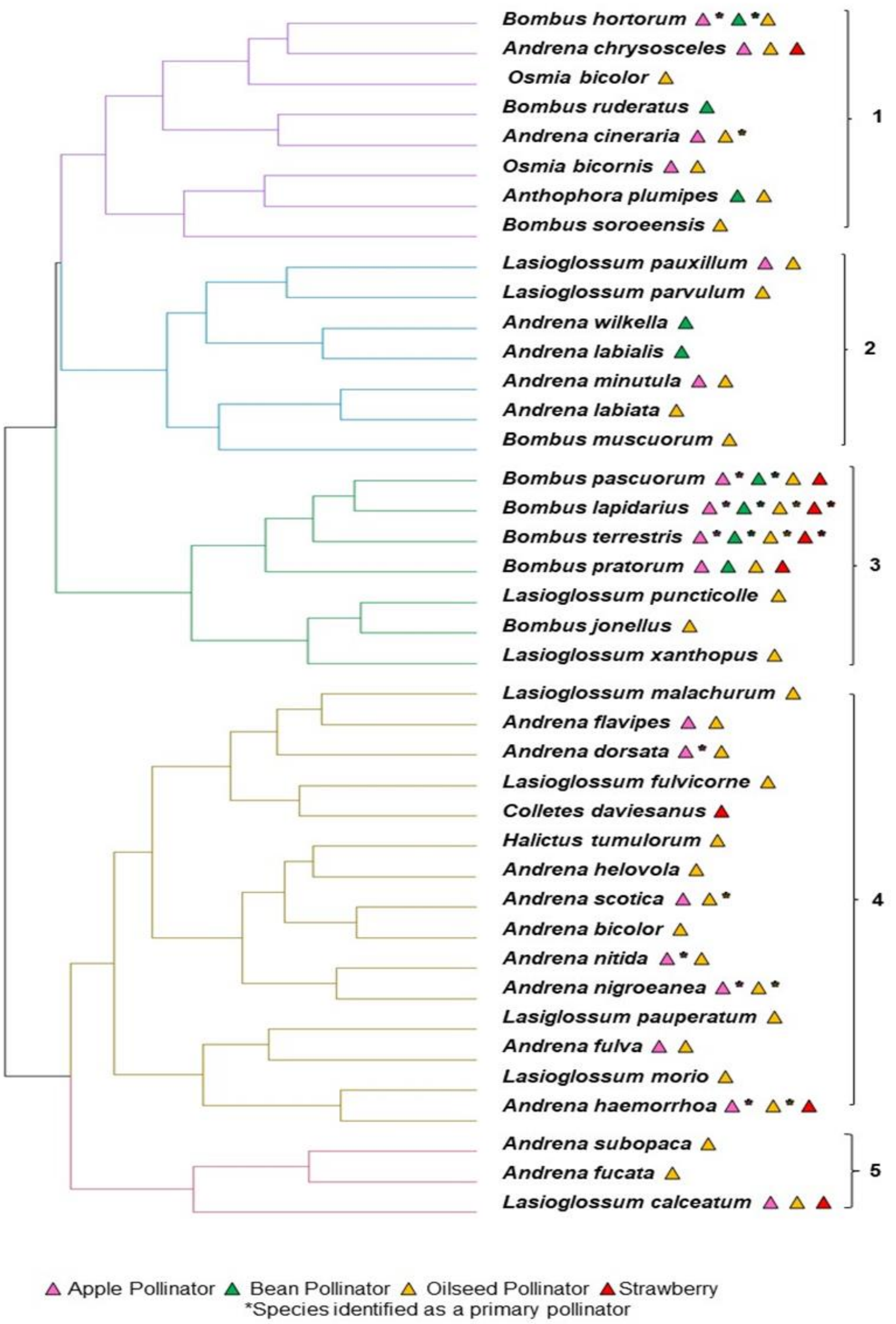
Appendix 13: Dendrogram showing the hierarchical relationships amongst five clusters of bee crop pollinators for the lower 2.5 and upper 97.5 confidence limit occupancy estimates (Chapter 4).

This appendix shows the dendrogram for the lower 2.5 and upper 97. 5 confidence limit occupancy estimates in sections 4.3.4 and 4.4.3 'Occupancy uncertainty confidence limits'.

7.13.1 Lower 2.5 confidence limit occupancy estimates.



7.13.2 Upper 97.5 confidence limit occupancy estimates.



Appendix 14: Pearson's r correlation scores for bee species pairs identified as primary crop pollinators crops using the lower 2.5 and upper 97. 5 confidence interval occupancy estimate data (Chapter 4).

This appendices provides the Pearson's r correlation scores for the analysis using the lower 2.5 and upper 97. 5 confidence interval occupancy estimate data in sections 4.3.2 and 4.4.2 'Inter-annual changes in occupancy' (positive scores in blue and negative scores in red, *indicates a significant (P≤0.05) correlation).

7.14.1 Lower 2.5 confidence interval occupancy estimate data.

	Andena cineraria (O)	*Andrena dorsata* (A)	*Andrena haemorrhoa* (A,O)	*Andrena nigroaenea* (A,O)	*Andrena nitida* (A)	*Andrena scotica* (O)	*Bombus hortorum* (A,B)	*Bombus lapidarius* (A, B,O,S)	*Bombus pascuorum* (A,B)	*Bombus terrestris* (A,B,O,S)
Andrena cineraria	**1**	**0.24**	**0.08**	**0.32***	**0.38***	**0.23**	**-0.11**	**-0.32***	**-0.05**	**-0.06**
Andrena dorsata		**1**	**0.24**	**0.25**	**0.43***	**0.43***	**0.05**	**-0.11**	**-0.05**	**-0.14**
Andrena haemorrhoa			**1**	**0.09**	**0.21**	**0.54***	**0.02**	**-0.11**	**-0.06**	**-0.30**
Andrena nigroaenea				**1**	**0.61***	**0.44***	**0.02**	**-0.22**	**-0.24**	**-0.38***
Andrena nitida					**1**	**0.56***	**0.33**	**-0.06**	**0.09**	**-0.17**
Andrena scotica						**1**	**0.15**	**-0.19**	**0.03**	**-0.36***
Bombus hortorum							**1**	**0.43***	**0.38***	**0.19**
Bombus lapidarius								**1**	**0.55***	**0.49***
Bombus pascuorum									**1**	**0.42***
Bombus Terrestris										**1**

7.14.2 Upper 97.5 confidence interval occupancy estimate data.

	Andena cineraria (O)	*Andrena dorsata* (A)	*Andrena haemorrhoa* (A,O)	*Andrena nigroaenea* (A,O)	*Andrena nitida* (A)	*Andrena scotica* (O)	*Bombus hortorum* (A,B)	*Bombus lapidarius* (A, B,O,S)	*Bombus pascuorum* (A,B)	*Bombus terrestris* (A,B,O,S)
Andrena cineraria	**1**	**0.18**	**0.01**	**0.31***	**0.44***	**0.27**	**-0.03**	**-0.34***	**-0.03**	**-0.10**
Andrena dorsata		**1**	**0.04**	**0.20**	**0.48***	**0.31***	**0.20**	**-0.01**	**0.04**	**-0.16**
Andrena haemorrhoa			**1**	**0.11**	**0.20**	**0.51***	**-0.10**	**-0.08**	**-0.05**	**-0.24**
Andrena nigroaenea				**1**	**0.54***	**0.43***	**-0.05**	**-0.09**	**-0.18**	**-0.25**
Andrena nitida					**1**	**0.55***	**0.32***	**0.01**	**0.17**	**-0.11**
Andrena scotica						**1**	**0.15**	**-0.05**	**0.06**	**-0.35***
Bombus hortorum							**1**	**0.50***	**0.35***	**0.21**
Bombus lapidarius								**1**	**0.60***	**0.55***
Bombus pascuorum									**1**	**0.44***
Bombus terrestris										**1**

Appendix 15: Standard deviation of mean occupancy for primary, core and all flower visitors per crop for the lower 2.5 and 97. 5 confidence limit occupancy estimate data. (Chapter 4).

This appendix provides the standard deviation of mean occupancy (lower 2.5 and upper 97. 5 occupancy estimate data) for each category of flower visitor and crop data for the analysis described in sections 4.3.3 and 4.4.3 ‘Stability of pollinator occurrence’ (number of species in brackets).

7.15.1 Lower 2.5 confidence limit occupancy estimate data.

Crop	Primary Flower Visitors	Core Flower Visitors	All Flower Visitors
Apple	0.016 (n=8)	0.012 (n=18)	0.010 (n=30)
Bean	0.027 (n=4)	0.015 (n=9)	0.015 (n=9)
Oilseed	0.015 (n=6)	0.008 (n=36)	0.007 (n=44)
Strawberry	0.034 (n=2)	0.015 (n=8)	0.010 (n=14)

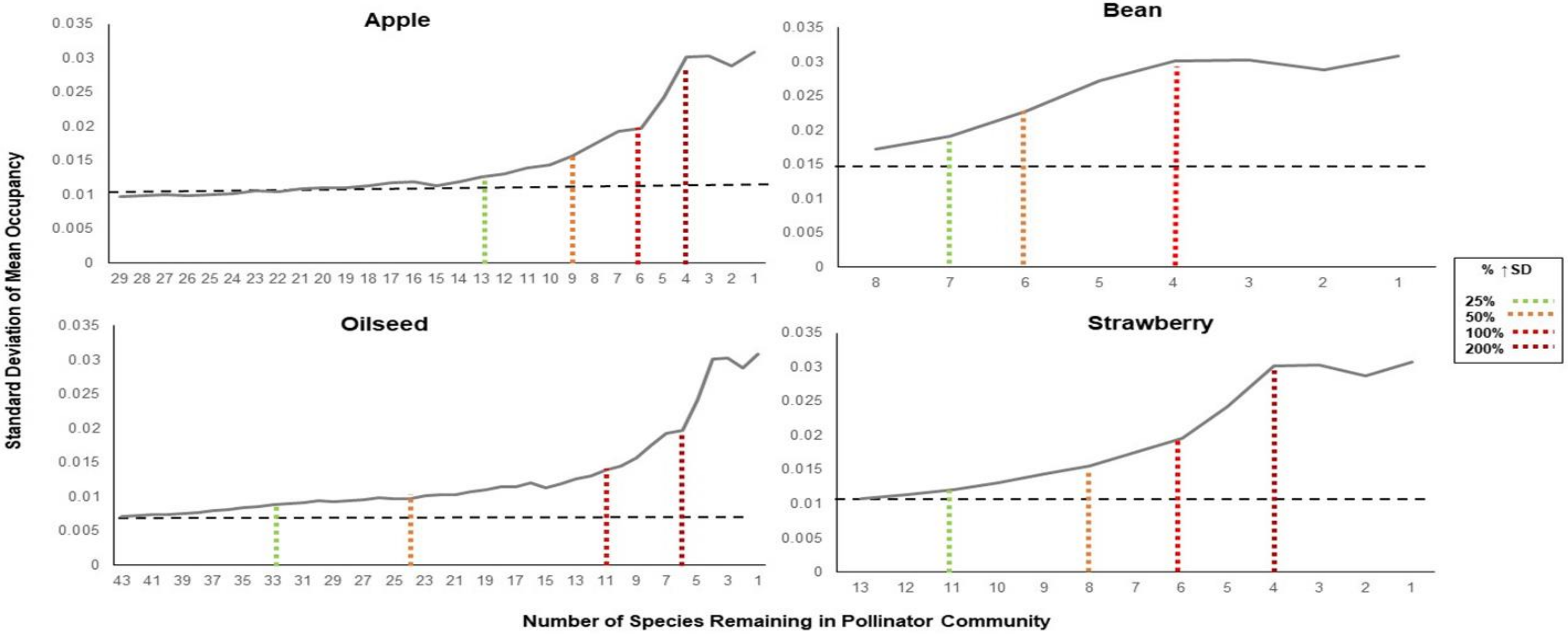
7.15.2 Upper 97. 5 confidence limit occupancy estimate data.

Crop	Primary Flower Visitors	Core Flower Visitors	All Flower Visitors
Apple	0.016 (n=8)	0.011 (n=18)	0.010 (n=30)
Bean	0.024 (n=4)	0.015 (n=9)	0.015 (n=9)
Oilseed	0.016 (n=6)	0.008 (n=36)	0.007 (n=44)
Strawberry	0.031 (n=2)	0.013 (n=8)	0.011 (n=14)

Appendix 16: Standard deviation of mean occupancy (lower 2.5 and upper 97.5 occupancy estimates) for bee crop pollinator communities as successive species are removed (Chapter 4).

This appendix provides the standard deviation of mean occupancy for the lower 2.5 and upper 97. 5 occupancy estimates for (a) apple, (b) bean, (c) oilseed and (d) strawberry crops in sections 4.3.3 and 4.4.4 ‘Stability of pollinator occupancy’.

7.16.1 Lower 2.5 occupancy estimates.



7.16.2 Upper 97.5 occupancy estimates.