Valuing wild pollinators for sustainable crop production

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Summary Abstract

This thesis looks at the role of wild pollinators in providing services to crops. Two data chapters (2 and 3) are accompanied by a modelling chapter (4) which build on the findings of the field studies. The thesis ends with an overview of the trends in pollinator populations and how these relate to the needs of farmers in the UK (chapter 5).

It is often assumed that commercial pollinators are appropriate substitutes of wild pollinators on farms; however this view neglects the differing roles that particular pollinator taxa might play in providing pollination services. For example, crops with a long growing system may require multiple pollinators to ensure pollination throughout the season. Strawberries in Scotland have an extremely long growing season, flowering from April to August. Chapter 2 presents a study showing seasonal complementarity between different pollinating taxa across strawberry farms in Scotland. Pollinators of strawberries also differed in their responses to weather parameters indicating that preserving multiple pollinator taxa could ensure yields under different weather scenarios. The requirements of a long-growing season and adverse weather may be specific to strawberry production in Scotland, but the valuation of multiple taxa can be generalised to systems with differing needs, and also to different ecosystem services.

Wild bees are not only valuable for providing complementary services to commercial pollinators, but are also valuable in the longer term as it is unknown whether commercial pollinators will be available in the future. There are threats to the supply of honeybees which have already triggered price rises; such supply shocks could force farmers to leave production or to seek other ways of providing pollination, including supporting wild pollinators. However farm management pressures, in particular pesticide use, could threaten the ability of wild pollinators to continue to support crop production. The interplay of pesticides and pollination is discussed in chapter 3 and 4. Chapter 3 presents an experiment undertaken on soft-fruit farms which had and had not used the neonicotinoid, thiacloprid, and shows that nests exposed to thiacloprid had higher worker mortality, and lower male production than those at control farms. This has implications both for pollination services now, as worker mortality will reduce the number of bees visiting farms, and also for the maintenance of future pollination services through decreased reproductive capacity of exposed nests. Chapter 4 uses a theoretical model to link pesticide use and habitat use to pollination services, and shows that the use of commercial pollinators could mask the decline in wild populations, making local extinctions more likely.

Chapter 5 sets out the status and extent of pollinators in the UK, along with population trends, trends in habitat and trends in pesticide use to provide an overview of how well pollination services are likely to meet the ongoing needs of crop farmers.

Declaration

I declare that the thesis has been composed by myself and that it embodies the results of my own research. Where appropriate, I have acknowledged the nature and extent of work carried out in collaboration with others.

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Contents

Chapter 1

General Introduction

1.1 Introduction to crop pollination

While many plants are pollinated by wind, the majority of flowering plants are pollinated by insects; estimates based on community level surveys of plant-pollinator interactions suggest that an average of 78% plants in temperate communities are insect-pollinated along with 94% of those in tropical communities (Ollerton et al., 2011). The flowering plants comprise some major crop groups including seed crops such as sunflowers and canola, and fruits. Yields of these crops can be increased by pollen transfer within (for self-pollinated plants) and between plants (for plants requiring cross-pollination). The level of dependency of a crop on insect pollination depends on the reproductive system of the particular plant. For example, melon production is highly dependent on insect pollination as pollen must be transferred between male and female flowers on the same plant for fruit to form (Kremen et al., 2002). Strawberries, on the other hand, are partially self-fertile as the flowers are bisexual so pollen can be moved between stamens and anthers on the same flower by gravity and wind. However they still are still partly dependent on bees; higher quality strawberries are produced when pollen grains are evenly distributed around the flower which is much more likely when pollination is bee-mediated (Chagnon et al., 1993). Both increases in yields and quality of fruit are important to food production; increases in quality can lead to longer storage times and lower perishability as well as increased market value (Garratt et al., 2014, Klatt et al., 2014). While the majority of global food production comes from stable crops such as wheat and rice which do not require pollination, 35% of food crop production has been found to be reliant on insects (Ghazoul, 2005; Klein et al., 2007). Insect pollinated crops have also been found to have higher nutrient content than non-insect pollinated crops, including 98% of vitamin C and cancer-protecting carotenoids as well as 70% of vitamin A (Eilers et al., 2011).

The area of agricultural land dedicated to insect-pollinated crops has increased in recent years; by 70% in developed countries and 100% in developing countries between 1961 and 2006 compared to 40% and 20% respectively for other crops (Aizen & Harder, 2009). The needs of pollinator dependent crops can be met by domesticated pollinators such as the honeybee or wild pollinators such as free-living bumblebees, solitary bees and flies.

1.1.1 Domesticated pollinators

1.1.1.1 *Honeybees*

Honeybees have been used since at least the 1900s for crop pollination, but more recently the honeybee industry has expanded to include long-range transportation of honeybees across the USA (Morse & Calderone, 2000). Honeybees live in vast colonies of (typically) around 50,000 workers. The importance of honeybee pollination differs from country to country; in the UK there are few large-scale honeybee farms, and those present are more focused on honey production than on transportation of bees for pollination. Most UK bee farmers who provide pollination services do so on a reciprocal basis; the bees are able to forage across large areas of flowering plants while pollinating the crop (Breeze et al., 2011). Honeybees are domesticated bees, they live in human-made hives and are managed, but they over-winter within the hive and so are still vulnerable to diseases and changes in the environment surrounding the hive. The sudden losses in honeybees in the United States (Colony Collapse Disorder) has led to concerns about the ability of honeybees to meet farmers' needs into the future. It has not been possible to isolate a cause of Colony Collapse Disorder, but it is likely to be a product of a combination of factors including *Varroa* mites, viruses and poor management (Cox-Foster et al., 2007).

1.1.1.2 Other domesticated bees

Several species of bumblebee *(Bombus* species) have also been domesticated and commercialised (domesticated since the 1970s but not commercialised until 1987) (Velthuis & Van Doorn, 2006). Most commercial production of bumblebees is of *Bombus terrestris* in Europe, North Africa and West Asia, and *B. impatiens* in North America (Velthuis & Van Doorn, 2006). Bumblebees have an annual lifecycle; only the queen survives until the winter and hibernates. Therefore they do not need to store honey for over-wintering like honeybees do, and live in relatively small colonies of around 150 to 300 workers. Commercialised bumblebee hives are housed in cardboard boxes, with a plastic internal area within which the queen builds a nest. As the colonies do not survive over the winter these boxes are disposed of at the end of the growing season, and new ones purchased the following year. The ability of these bees to provide pollination year after year is therefore not vulnerable to external environmental conditions like in the case of honeybees. Within a year commercial bumblebees are still vulnerable to diseases. The use of commercial bumblebees can influence wild bumblebee populations by increasing disease spread between wild bumblebee species (Otterstatter & Thomson, 2008; Whitehorn et al., 2014). There is also evidence that escaped commercial bumblebees can cause damage by competing with wild populations, particularly if used in areas where the commercial species is non-native and more competitive than the local species. For example, a large decline in range of *Bombus dahlbomii*, the endemic Argentine species have been linked to the spread of commercial *Bombus terrestris* from fruit growing areas of Chile (Schmid-Hempel et al., 2014). In response to such threats regulation has begun to evolve; the use of non-native species is now limited in some areas.

Social bees have advantages due to the large number of foragers supported by a nest, but solitary bees are good pollinators of orchard crops and have also been commercialised since the 1970s with *Megachile rotundata* used on alfalfa and *Osmia* species including *O. lignaria*, *O. cornifrons* and *O. rufa* used for orchard fruit (Pitts-Singer & Cane, 2011).

1.1.2 Wild pollinators

While honeybees are considered to be a valuable input to agriculture a consensus is emerging that wild pollinators also contribute substantially to crop pollination. A recent meta-analysis looked at the relationships between pollinator visitation and fruit set and found that relationships were positive for wild bees in all studies and for honeybees in 14% of studies (Garibaldi et al., 2013). Wild pollinators also had a stronger effect on fruit set than honeybees where the relationship was positive (Garibaldi et al., 2013). Wild pollinators are likely to make a large contribution to pollination services in the UK; Breeze et al. (2011) compared areas of crops grown and published pollinator dependencies to the total honeybee stock, and found that honeybees could only provide approximately 34% of the UK pollination needs.

Of wild pollinators bumblebees may be particularly important. Not only are they widespread but they forage at lower temperatures and therefore have a longer window of activity than honeybees (Corbet et al., 1993). Bumblebees have also been found to be more efficient in other ways; they pollinate more flowers per hour and transfer more pollen per visit than honeybees (Willmer et al., 1994). Solitary bees also pollinate crop plants and are abundant early in the year when orchard crops such as cherry and apple are flowering (Bosch et al., 2006; Gruber et al., 2011).

There is also a role for non-bee pollinators in crop pollination. Though not specifically adapted for pollen carrying or transport, butterflies (Lepidoptera) and flies (Diptera) including hoverflies (family: Syrphidae) can transport pollen when moving from flower to flower. Hoverfly pollination is not as well covered in the research literature as that of bees, but visitation by hoverflies was found to increase oil-seed rape yields (Jauker et al., 2012). A higher density (five times) was required to pollinate via hoverflies than with the more efficient pollinator the red mason bee (*Osmia rufa*) (Jauker et al., 2012). It is likely that flies are important in other crop systems perhaps particularly in parts of the world where bumblebees are not widely distributed such as in parts of Africa, where farmers have been known to leave animal carcasses near to mango beds to encourage flies for pollination (B. Gemmill-Herren 2012, pers. comm., December).

1.2 Measuring pollination services

The ability of wild pollinators and/or honeybees to meet the pollination needs of a target crop will depend on external factors such as the availability of forage plants in the landscape and weather conditions during pollination, and biological factors such as diseases. While agronomists have traditionally evaluated the influence of inputs such as fertilisers and fungicides on crop yields, ecologists are best placed to integrate the environmental and biological factors driving pollination success. Studies of the underlying ecology of pollinators, as well as the benefits provided, should contribute to better management decisions for both crop yields and pollinator populations (Kremen & Ostfeld, 2005).

1.2.1 Measuring the contribution of pollinators to crop yields

To measure the yield benefits attributable to pollinators it is important to keep other factors such as fertilisers and crop management constant. This can be achieved through pollination exclusion experiments where pollinators are excluded from some crop plants within a growing area via a fine netting or gauze, and pollinators are allowed to visit other crop plants grown within the same field and under the same growing conditions. The yield difference between these two sets of crops is then calculated and attributed to pollinators. Some experiments of this type also include measurements of the yield from crop plants which are pollinated by hand. The outcome from the hand-pollinated treatment is then assumed to represent the maximum possible yield if full pollination had occurred. If the results from hand pollination are higher than those from open pollination treatments, then this can imply that a lack of pollinator visitation is limiting yield. A review of 482 such experiments has found that 63% of the plants studied exhibited pollen limitation at some sites and in some years (T. Knight et al., 2005). However plants may re-allocate resources between flowers and over-produce ovules, so fruit set by hand pollination is likely to overestimate the yield from natural pollination (T. Knight et al., 2005). Similarly, some bees move around the flower in such a way that most pollen transfer is from the same plant, so experiments which transfer outcross pollen for the hand pollination treatment will again over-estimate the potential yield from “natural” pollination by bees (Aizen & Harder, 2007). Quantity of pollen deposited is not the only factor for successful pollination; some bees show low flower constancy, which means they move frequently between flowers of different plants causing anthers to be clogged with pollen from other species of plant (Chacoff et al., 2008). This will further reduce the average natural pollination compared to hand pollination treatment.

Nonetheless, Knight's review highlights that pollination can be year and context dependent. In experiments on winter oil-seed rape, treatments with honeybees had more pods than those grown with wild bees alone in one year, but this difference disappeared in the following year (Williams et al., 1987). Likewise watermelon flowers were visited by wild bees in California, which provided just sufficient pollination services in one year, and over-supplied services in other years (Kremen et al., 2002). Changes in honeybee numbers from year to year can also impact crops; blackcurrant yields were found to decrease after a harsh winter left honeybee numbers depressed near experimental plots in Poland (Denisow, 2003). There is a clear need to perform studies across multiple sites and time periods to get a full picture of whether crop yields are limited by insufficient pollination services and under what conditions.

1.2.2 Evaluating factors altering pollinator numbers and visitation rates

Management prescriptions have an impact on pollination success, for example Morandin and Winston (2005) found no pollination deficit in organic fields, but one in GM and conventional fields. Native bee communities were sufficient for pollination of watermelons on organic sites with natural habitat nearby but not on conventional farms even when natural habitat was abundant (Kremen et al., 2002). It is not clear whether the organic farms studied had lower pollination deficits because of lower levels of on-farm resources for pollinators, or because of other management factors such as pesticides.

The distance of a crop plant from natural habitat can impact the number of wild pollinators around farms and lead to pollination deficits. Differences can occur even within fields; blueberries in the centre of large fields had lower seed set than those at the edges of fields as pollinators have further to fly from habitat around the edge of the field (Isaacs & Kirk, 2010). A meta-analysis of 23 pollination studies covering 16 crops and 5 continents found a relationship between linear distance from natural habitat patch and pollination visitation and pollen deposition on crops (Ricketts et al., 2008). However there was a high level of variability between studies and the overall relationship was rather weak, suggesting that other factors such as on farm resources and management also play a part. Studies conducted along a habitat gradient from very diverse areas i.e. tropical forest to areas of low diversity such as agricultural monocultures were more likely to show a result than when the difference in habitat was more subtle. Bee visitation rate and pollen deposition fell off sharply with retreating distance from tropical forest patches in Costa Rica (Ricketts, 2004), whereas a relationship between pollination services and habitat resources was not found within the relatively heterogeneous landscapes of Pennsylvania and New Jersey, where native bees were still able to provide the majority of pollination services (Winfree et al., 2008).

In areas where wild bee numbers are low, farmers can encourage wild bees to nest within foraging distance of farmland by providing nesting habitat and providing alternative foraging resources when the crop is not in flower. The effect of such interventions has been found to be strongest in intensively farmed areas. When measured as the increase in bee diversity, effects of organic land management was stronger in simple landscapes with low proportion of natural habitat (Holzschuh et al., 2008). A similar finding was made by Carvell et al. (2011), who measured the differences in species richness between sown areas on farms and non-crop habitat, and found a greater increase in species richness in more intensively farmed landscapes. These studies focused on bee diversity, which may be important for pollination services, but there is a more direct link between bee abundance and pollination. In a meta-analysis of 605 field studies including 23 different crops, Kennedy et al. (2013) found that bee abundance was higher in diversified fields and in landscapes with high quality habitat. It seems reasonable therefore to suggest that field-scale management practices can offset the negative impacts of intensive monoculture agriculture on pollination services to some extent.

The response to habitat and management factors may vary between pollinator groups or species. Steffan-Dewenter and Tscharntke (1999) found that bumblebee numbers decline only slightly with increasing distance to natural habitat whereas the trend was more obvious for solitary bees. Bumblebees have a large foraging range relative to other pollinators, which may make them especially important within the agricultural landscape; they can link between agricultural areas and habitat and provide pollination over a large area (Corbet, 1997). Honeybees are also relatively immune to habitat changes, as they can be placed at any point within the landscape rather than relying on nesting sites. In studies comparing different pollinator guilds, honeybees show a less strong relationship with natural habitat than other guilds (Steffan-Dewenter & Tscharntke, 1999; Steffan-Dewenter et al., 2002; Kremen et al., 2004).

1.3 Impact of pesticides on pollinators

Pesticide use on farms has the potential to affect pollinators foraging within the farms and around the wider landscape. Broad spectrum insecticides are no longer widely used, but more modern systemic pesticides such as the neonicotinoids can be toxic in very small doses (Iwasa et al., 2004). Systemic pesticides are designed to be applied to a seed coat and then to infiltrate all parts of the plant. This leads to efficient and targeted pest control; the farmer no longer needs to rely on repeat spraying of foliage to maintain protection. However, the transfer of the pesticide throughout the plant can led to exposure of pollinators to insecticides when foraging on pollen and nectar. A group of systemic pesticides, the neonicotinoids, have received a great deal of attention in recent years, due to their high potency and widespread use. The most widespread in the EU are the seed treatments clothianidin, imidacloprid and thiamethoxam, which are used on a range of crops including corn, maize, oil seed rape, turf and cereals, and the foliar sprays acetamiprid and thiacloprid which are used on crops including potatoes, brassicas and soft-fruits.

1.3.1 Mode of action

Neonicotinoids work by binding to nicotinic acetylcholine receptors in the nervous systems of insects causing paralysis and death at higher concentrations (Jeschke et al., 2011). Pesticide toxicity is usually measured in terms of LD50, an acute toxicity measure, or the lethal dose (by contact or orally) for 50% of the test population. LD50s are very low for neonicotinoids; oral LD50s for honeybees are 0.0179 – 0.0299 µg/bee for imidacloprid, clothianidin and thiamethoxam, and 7.07 and 14.6 for acetamiprid and thiacloprid respectively (Iwasa et al., 2004). Bumblebees are similarly sensitive to oral exposure and less sensitive to contact though the exact relationship differs between neonicotinoids (Sanchez-Bayo & Goka, 2014). LD50s only reflect the risk of acute exposure whereas bees may be exposed to pesticides over weeks during crop flowering. A pesticide level which is below the LD50 and therefore considered safe may be dangerous if a bee is exposed to this level over a period of time. For example, Sanchez-Bayo and Goka (2014) calculated exposures to neonicotinoids across a bee's lifespan and found that residues of thiamethoxam in honey and pollen in published studies approached the oral LD50, and imidacloprid residues exceeded the LD50 when the likely ingestion levels over the life-span of larvae and workers were considered.

1.3.2 Sub-lethal effects

Doses below the LD50 have also been found to cause changes in behaviour or health which limit a bee's ability to contribute to the maintenance and growth of the nest. Both honeybees and bumblebees are social species; asexual workers collect pollen and feed the larvae of the queen, which are reared into new asexual (workers) or reproductive individuals (new queens and drones). Any deviations in the foraging ability of workers can therefore impact the ability of the nest to reproduce. Honeybees fed pollen and nectar dosed in similar concentrations of imidacloprid to the residues found in treated plants had difficulty in navigating and were lost from hives in higher proportions than from control hives (Henry et al., 2012). Bumblebees are similarly affected; workers were found to forage less efficiently and were more likely to be lost while foraging when exposed to imidacloprid (Gill et al., 2012). Lower foraging efficiency could be the reason that treated nests produced fewer queens than control nests when field-realistic doses of imidacloprid were fed to bumblebee nests which were then allowed to forage freely (Whitehorn et al., 2012).

Interactions with other chemicals and threats such as parasites and fungal infections could increase the detrimental effects of neonicotinoids. The impact on navigation behaviour in Gill et al.'s (2012) study was higher when bumblebees were exposed to a pyrethroid insecticide along with the neonicotinoid. Thiacloprid and acetamiprid have also been found to increase in toxicity when combined with other chemicals; a laboratory study which exposed honeybees to thiacloprid and commonly used plant fungicides found that such compounds increased the potency of thiacloprid up to 1141 fold (for the fungicide triflumizole) decreasing the oral LD50 to 0.0128 mg/bee (Iwasa et al., 2004). The LD50 of acetamiprid was likewise reduced to 0.0290 mg/bee with the same chemical (Iwasa et al., 2004). Other synergists such as DMI fungicides had similar effects on the toxicity of acetamiprid and thiacloprid. There are also interactions with parasites at exposures far below the lethal dose; for example honeybees exposed to doses of thiacloprid of 1/100th of the LD50 died more quickly when infected with the protozoan parasite *Nosema ceranae*, than those infected with the parasite alone (Vidau et al., 2011).

1.3.3 Environmental residues

The impact of neonicotinoids on foraging pollinators will depend on their exposure to neonicotinoids and synergists throughout the environment or through contaminated pollen and nectar. A few large scale studies have looked at neonicotinoid concentrations found in pollen and nectar stores from within honeybee nests and therefore provide an indication of exposure levels near to agricultural areas. The Germany bee monitoring project, which took bee bread samples from 1104 colonies over 4 years (215 bee bread and pollen samples), found thiacloprid in 56% of samples after oil seed rape bloom with a maximum concentration of 199 µg/kg (Genersch et al., 2010). Imidacloprid was found at much lower concentrations of 3µg/kg, and clothianidin and acetamiprid were also found at low concentrations (Genersch et al., 2010).

Samples were also collected from bee hives placed near to fields treated with different neonicotinoids over the course of a year in Poland (Pohorecka et al., 2012). Thiamethoxam was found in 65% of nectar and pollen samples at levels of 4 µg/kg, clothianidin was found in 17% of nectar and honey samples at levels of around 2 µg/kg and imidacloprid at levels of around 1 µg/kg in nectar and honey samples (Pohorecka et al., 2012). Neonicotinoids applied as foliar sprays were found to have quite variable concentrations from <1 to 65 µg/kg for acetamiprid and from 1 to 369 µg/kg for thiacloprid (Pohorecka et al., 2012). Even higher concentrations of thiacloprid were found in pollen from hives within orchards; an average of 646 µg/kg and maximum of 1002 µg/kg (Pohorecka et al., 2012).

Pollen and wax samples taken from apiaries in Florida and California, and apple orchards in Pennsylvania, found two or more pesticides in 98.4% of samples with 60% containing at least one systemic pesticide (Mullin et al., 2010).

1.3.4 Foliar sprays

Detrimental effects of thiacloprid have been found when bees were fed much lower concentration of thiacloprid than was reported in the two European studies. When bumblebees were fed concentrations of 12 µg/kg worker mortality was raised by 17% relative to control bees (Mommaerts et al., 2010). The more toxic (as measured by LD50) pesticides thiamethoxam, imidacloprid and clothianidin are now subject to an EU moratorium banning commercial use for two years from 2014 to 2016. Acetamiprid and thiacloprid has received less attention by policy makers so far but should not be excluded from future consideration.

Despite the effects of neonicotinoids evident in semi-field and laboratory experiments, experiments on free-flying bees have not shown the same impacts. Schmuck et al. (2003) combined pyrethroid applications with thiacloprid in experimental tunnels. While honeybees had increasingly uncoordinated behaviour, there were no hive level effects as measured by pollen stores, hive weight and brood nest size (Schmuck et al., 2003). Sechser and Freuler (2003) fed thiamethoxam onto beds of tomatoes through an irrigation system and observed two bumblebee colonies in treatment tunnels and two in control tunnels for 35 days after spraying. They found more dead bees in the treated tunnels and more dead larvae, however the results were not significant (Sechser & Freuler, 2003). In a field study of fields treated or untreated with clothianidin, 32 colonies were placed in the middle of 4 1ha treatment or control fields during bloom, weight gains and honey yields were not significantly different from those in control fields (Cutler & Scott-Dupree, 2007). While these studies have been cited as evidence against any effect of neonicotinoids in natural conditions, it has been noted that the level of replication in the studies undertaken so far has been too low to have much predictive power, particularly in honeybees where variability between hives is high (Cresswell, 2011). Nonetheless the limited field evidence has led policy makers to question the importance of laboratory based findings. As explicitly stated by the chemical company Bayer Crop Science "while many laboratory studies described sub-lethal effects, no adverse effects to bee colonies were ever observed in field studies at field-realistic exposure conditions". There is a need for well replicated experiments where bees are allowed to forage freely to gain a realistic idea of how neonicotinoids affect bees in natural situations.

1.4 Link between diversity and pollination

The relationship between diversity and ecosystem service level is generally assumed to be positive, though most of the experimental evidence for this relationship is from simple experiments showing "over-yielding" when mixes of grasses are grown versus when a single species is grown (reviewed by Balvanera et al., 2006). For most ecosystem services, some species will contribute little while others over-perform relative to their abundance and so a linear relationship between ecosystem service and number of species is not expected. With this in mind, the academic focus has recently shifted to considering the link between functional diversity and ecosystem function rather than considering diversity in terms of numbers of species or phylogenetic differences (Naeem & Wright, 2003; Cadotte et al., 2011).

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1.4.1 Complementarity

Functional diversity can be defined as the range of traits that influence the functioning of an ecosystem. Species or species groups which contribute to overall ecosystem services in complementary ways will increase functional diversity and can increase ecosystem service provision overall. For example, Hoehn et al. (2008) placed flowering pumpkins at different heights, and found that overall seed yields were higher when more pollinator groups were present if the pollinator groups foraged at different flowering heights, i.e. if they were complementary in their use of space. This type of spatial complementarity has also been observed in pollinators of almond trees; while honeybees tended to forage in the top sections of trees, wild bees were found to prefer foraging in the bottom section so overall nut production was higher when both groups were present (Brittain et al., 2013a). Spatial complementarity can also occur at the fruit scale, for example, strawberry flowers are made up of numerous ovules each of which must be fertilised to produce a well-shaped fruit. Chagnon et al. (1993) showed that visits by both honeybees and bumblebees to strawberries produced the highest quality fruits as they were complementary in the parts of the ovule which they transfer pollen to; honeybees transferred pollen to the apical ovules producing rounded tips, while bumblebees circled around the base of the flower, producing symmetrical sides. Bluethgen and Klein (2011) proposed that complementarity in activity times for different pollinators across the year, or seasonal complementarity, could ensure a supply of pollinators to crops flowering over a number of months and thus increase overall yields.

1.4.2 Redundancy

The general relationship between diversity and ecosystem function tends to be positive but levels off; each additional species only adds to overall function up to a point (Hector & Bagchi, 2007). Some species may have a relatively minor role, or may be similar in functional contribution to other groups of species therefore adding little to overall ecosystem services. Having multiple species with overlapping functions (in contrast to complementary functions) leads to redundancy and can make overall service provision more resilient to change, as not all species will be affected in the same way to stressors (Walker, 1995). Winfree and Kremen (2009) found that pollinator groups responded differently to habitat loss, and the response of different species was across different scales suggesting that the presence of multiple pollinating species could buffer the overall level of service in response to such changes.

For such differences in responses to stressors to stabilise overall function, ideally species should respond in opposite directions; some species should have a positive and some a negative response to the same disturbance. There is little evidence of such an effect (termed density compensation) in pollinators (Winfree & Kremen, 2009), and a meta-analysis of long-term ecological data showed that positive associations between species seems normal in terrestrial assemblages, that is, the abundance of co-occurring species move in parallel, implying that they are impacted in similar ways by stressors (Valone & Barber, 2008). Such positive associations are particularly likely to be found in physiologically similar groups such as insects of a similar size and with similar nutritional requirements; for example 6 out of 7 associations between butterfly group abundances over a 10 year study were found to be positive (Valone & Barber, 2008).

For a species or group to compensate for the loss of another and stabilise services, they also need to provide a similar level of service to the lost species. Unfortunately it is often the case that one species or group provides the vast majority of ecosystem service delivery. In a meta-analysis of 115 experiments linking ecosystem services to function it was found that the biggest loss in productivity was generally associated with the removal of the most productive species (Cardinale et al., 2006). So although there is the potential for species to take over when another species is removed, this could be hindered by 1) positive associations between species in numbers and 2) poor performance of non-dominant groups.

However, while one might expect that at least within pollinating genera (i.e. *Bombus*) associations might be positive, rather than negative and compensating but between less related groups compensation might be more likely. Brittain et al. (2013a) looked at communities under different wind conditions and found that honeybees changed foraging behaviour in high wind conditions, but overall visitation was buffered when other taxa were present. Other taxa in this case included wild bees (non-*Apis* bees) and flies. The differences in responses between honeybees and other taxa to wind speeds suggest that more generally pollination services may be more resilient when multiple pollinator groups are present.

1.4.3 Facilitation

Increasing number of species can also enhance service provision if two species facilitate each other so that services provided by one species are greater in the presence of the other. This has been observed between honeybees and wild bees on sunflowers in California; in the presence of honeybees wild bees moved between flowers more frequently to give higher pollination overall (Greenleaf & Kremen, 2006). Similarly, honeybees moved more frequently between trees when non-*Apis* bees were present, leading to more outcrossing of almond trees and a greater proportion of fruit set when both taxa were present (Brittain et al., 2013b).

1.5 Economic approaches to pollination

1.5.1 Production functions

Economics provides some tools to value the contribution of pollinators to crop yields, with the usual method being the production function approach. The production function approach can be used to value ecosystem services when the final good or service is marketable. The value of the ecosystem service providers (in this case, pollinators) is taken to be the gain in market value of the final good or service from a change in the level of the providers (Barbier, 2007). Production function valuation has been used to value aggregate pollination services over geographical areas including honeybees in the US and pollinators worldwide (Morse & Calderone, 2000; Klein et al, 2007). Alternatively this method has been used to value the uncultivated land area required for sufficient crop pollination for coffee production in Costa Rica and for canola production in Canada (Ricketts et al, 2004; Morandin & Winston, 2006). When used to assess the value of aggregate services, the proportions of yields attributable to pollination (or dependency ratio), are taken from published pollination exclusion experiments (see section 1.2.1) or estimated from expert opinion.

Smith et al took this approach to value pollination services in the UK as part of the National Ecosystem Assessment in the UK. The Natural Ecosystem Assessment sought to assess the value of the benefits from the UK's natural environment. Pollinators were included in this as a "regulating" ecosystem service. Regulating services also include biological pest control and other services which are essential in the production of final goods and services. Through the production function method, using pollinator dependencies across 10 crops, the NEA estimated the value of insect-pollination to crops in the UK at £430bn per year in 2007 (Smith et al., 2011).

Most production functions used have the general form:

$$V = P \times Y \times D$$

V is the value of the service, P is the price per unit, Y is the number of units (yield), D is the proportion of the yield which is attributable to the service providers (the dependency ratio).

This approach gives an estimate of the value of production which would be lost given a total loss of pollinators without substitution. Criticisms have been levelled at this approach; the dependency ratios on which the values are based are often highly uncertain. The equation assumes that total costs are the same with or without pollinators when in fact they will be lower without pollinators if there is a lower yield (due to lower harvesting/packaging costs etc.). The actual loss also depends on the presence of substitutes for wild pollinators; if commercial bees can be used then the loss of pollinators can be offset in production. It is also difficult to assign values to different groups of pollinators. This is important if the objective of the study is to value the contributions of wild and commercial pollinators separately. One approach if there is more than one group of pollinators who contribute to the service is to assign the total production value V, in proportion to the abundance of that group relative to the total pollinator abundance (by the addition of a “p” term in the equation above). This was the approach taken by Isaacs and Kirk (2010) to assign value to different pollinator species on blueberries. The increase in value of blueberries directly due to pollinators was partitioned between the species observed visiting blueberry flowers by abundance and efficiency. While this approach distributes the value between the ecosystem service providers present, it does not allow for the possibility that services could be over provided in the study in question and thus allocates value to pollinators which are superfluous to requirements or which play a very minor role. Winfree et al. (2011) overcame some of these issues by adjusting for lower costs, allowing substitution by commercial pollinators and by assigning a maximum pollination level required; any pollinators contributing to the service after the maximum level was reached were not included in the valuation. In order to do this, however, they had to assign either wild bees or honeybees as “primary” and “residual” providers, with the providers chosen to be in the primary group gaining a higher value (a proportion of the residual group were surplus to requirements).

1.5.2 Criticisms of valuation approaches

In addition to the problems with production function approaches described in the previous section, some more fundamental criticisms have been levelled at the ecosystem services approach to valuation. The benefits of ecosystem services are often weighed up against the cost of preservation, meaning that services are lost if the benefits are not sufficient to meet the costs, or when an alternative project with a higher payoff is available for investment. The comparability of the costs and benefits from different investments including natural capital implicitly assumes that natural capital can be substituted with other forms of capital, such as man-made or financial capital, which may be difficult or impossible under normal conditions. Cost-benefit analysis is often carried out in one year and that value is then used to estimate future benefits. Besides the variability in values between years which would not be captured through an estimate from one year, it is impossible to tell what future citizens will value. Any judgement imposed on the needs or values of future citizens is unlikely to be accurate leading to issues of intergenerational equity (Hampicke, 1994). The total benefits, even at one time point, will be higher than the market value implies if there are social or non-use benefits which should be included. More essentially, some disagree that utilitarian valuation is the correct way to weigh up conservation options, and call for nature to be conserved for its intrinsic value rather than any usefulness to humans (Farber et al., 2006).

1.5.3 Precautionary approaches and additional values

Despite these reservations, conservation at any cost may not be feasible and a planner may still need to decide between projects in a systematic way. Thus various compromises have emerged to better incorporate the inherent uncertainties and irreversibilities when evaluating ecosystem processes. Some authors have sought to incorporate ecological limits into the economic decision criteria. Alternatively the wider values associated with ecosystem processes besides the production value can be included within the total value of the service, thus better reflecting the total value.

Ciriacy-Wantrup (1952) proposed a system of "Safe Minimum Standards" to limit economic decisions to those which did not cause irreversible damage to ecological populations. The Safe Minimum Standards approach proposed to maintain species populations above a minimum level, to reduce the maximum possible losses connected with an irreversible decline. This approach tended to skew decisions towards conservation rather than development and was seen as a risk-adverse approach to evaluating whether developments should take place or not, since irreversible change could have extremely large losses but these are highly uncertain (Crowards, 1998). Most other attempts to align economic valuation with ecological principles have sought to quantify in some way the other benefits of conserving species above and beyond the raw use value. For example, species could have a precautionary value or value associated with reducing the probability of a negative state change (Farber, 2006). An example of this was in Barbier's study on Mangrove loss in Thailand between 1979 and 1996. A 1m^2 of decline in Mangrove area was found to increase the vulnerability of these coastal area to natural disasters by 0.36% (Barbier, 2007). A separate value of conserving species comes from the value of maintaining a resource for an (uncertain) future use. Option values were used to justify conservation of California Elk; while the species is not eaten by humans currently, Californian Elk could offer a protein source for humans in the future, in which case there is an option value of maintaining it for the future and conservation is prudent (Ciriacy-Wantrup & Phillips, 1970). While it is extremely difficult to quantify the probability of a species being useful in the future, option valuation does provide an opportunity to take into account the potential use of a species over the long-term and under various scenarios rather than basing the worth of a species on only its known value today (Arrow and Fisher, 1974; Kassar & Lasserre, 2004).

A separate value which has also been used in the literature to justify conservation is the value that additional species bring by stabilising ecosystem services over time, which has been referred to as both the portfolio value and insurance value. The insurance value is the value associated the reduction in variability associated with having an assemblage of species to provide a service rather than relying on one species. While financial theory may suggest that we can construct a portfolio of species to reduce risk and smooth fluctuations in service provision over time (Figge, 2004), as seen in section 1.4.2 uneven production of services and positive covariances potentially render this source of value as lower than it should be intuitively.

These additional values, precautionary values, option values and insurance/portfolio values are all benefits which arise in addition to current production values of ecosystem services. But while assigning value to species or services provides reasons for conservation, these values do not provide information on the limits of the system of how that system might be managed for the future. Though approaches like Safe

Minimum Standards have not held ground in the literature, it has been recognised more recently that the avoidance of thresholds is important for the maintenance of ecosystem services into the future. Considering ecosystem services as a flow from natural capital which must be maintained, incorporates ecological limits in a way which can be understood by those with knowledge of other forms of capital.

1.5.4 Natural Capital Approach

Natural capital can be defined as those natural assets (biological assets, land and water areas) which provide through their existence and/or some combination of their functions, a positive economic or social value (NCAC). Ecosystem services are then considered as a flow from this natural capital, which might deteriorate if not maintained (Barbier, 2011). Framing ecosystem services as a flow from natural capital incorporates the potential for irreversible loss and absolute scarcity. It also places the natural environment in the same language as financial or other assets, which could lead to greater incorporation of the requirements of these assets within government planning. With this in mind, the UK government aims to facilitate the creation of a comprehensive set of Natural Capital Accounts which will provide regular assessments of the quality and extent of natural capital stock as well as the benefits in terms of human well-being (POST, 2011).

If data were available, such a process could track whether an ecosystem asset is being maintained in terms of quantity and quality, and whether the costs of maintenance can be covered by the current price (POST, 2011). For a full evaluation of natural capital, it would be ideal to be able to predict the future flows of benefits from the capital, and to compare these with the projected costs (Barbier, 2011). While monitoring can be reasonably done for some forms of capital such as road networks and buildings, and some natural resources particularly directly marketable ones (e.g. timber) and some reasonable predictions can be made, the majority of systems considered to be natural capital are difficult to measure, complex systems with interacting drivers and inputs. This makes the quantification of the extent of natural capital and flows from it difficult, let alone the prediction of future outcomes. This is no different for pollinators, which can move over wide areas and so are impacted by both local and landscape scale factors. Kremen et al. (2007) provided a conceptual framework for pollination and other Mobile-agent Based Ecosystem Services (MABES) linking the various factors which impact pollination and determine its value. These factors included landscape structure, which incorporates habitat patch size and isolation, and aspects of the plant community including the competitiveness relative to crop plants, with specific pollinator requirements and biotic factors which affect both plants and pollinators (Kremen et al., 2007). Measuring the extent of pollinators and the benefits from them over a wide geographical area would require the integration of these factors with feedback from markets and policy decisions which affect land use (Kremen et al., 2007).

1.5.4.1 Quantitative modelling approaches

The ecological components of the MABES model were used as a basis for a predictive model of pollinator abundance within a landscape. Lonsdorf et al. (2009) developed equations to establish the suitability of habitat cells for nesting and for foraging and combined these to give relative scores of pollinator abundance within a landscape. This abundance score could then be compared with pollinator demand across agricultural cells in the same landscape. A similar approach was taken by Polce et al. (2013) who used data on species distributions to predict the distribution of *Bombus pascuorum*, and related this to demand for field bean pollination across the UK.

These predictive approaches use data and realistic assumptions to estimate pollinator distributions and hence supply of pollination services. The Lonsdorf model was validated across three areas of the USA and was reasonably successful in predicting pollinator visitation for sunflowers and watermelon in California, and coffee in Costa Rica. However, it was not successful in New Jersey where there were fine scale floral and nesting resources and lower variability in pollinators (Lonsdorf et al., 2009). The suitability of the model therefore depends on the particular landscape and the features of it and it is not able to take into account small scale management which will still be an important determinant of pollinator outcomes.

Local habitat management has been modelled using more stylised and simple models. For example, Brosi et al. (2008) used a linear farm to test different habitat configurations within a farm area. Cells in the farm were designated as nesting habitat or crop area and bees had different dispersing and foraging ranges. The optimal configuration of habitat cells within the farm depended on the relationship between dispersal and foraging range (Brosi et al., 2008). Keitt (2009) extended this type of approach to a more realistic grid based design, with varying distributions of converted habitat cells across the grid. The model was more complicated, with pollination and nest success modelled as stochastic processes. Unstable points were found with low plant and pollinator densities, and the points of instability were higher with habitat loss and when mortality parameters were higher (Keitt, 2009). These models looked at generic systems and so are not likely to lead to realistic predictions for a particular design in reality, but can inform about the relationships between factors.

A well validated model of pollinator nests looked at the impacts of sub-lethal chronic doses of neonicotinoids on colony failure (Bryden et al., 2013). In this model, death rate of the colony was related to the effective number of workers (adjusted for impairment). The model was able to predict the path of colony failure in experimental colonies treated with pesticides.

It is not surprising that models like Bryden et al.'s which are specific to the nest type (commercial nests) and species (*Bombus terrestris)*, and predicted growth under controlled conditions, are more successful at predictions than models which attempt to integrate factors across large areas and natural conditions. There is a clear trade-off between the generality (and therefore applicability to a wide variety of circumstances) of the potential results coming out, and the accuracy of the actual results compared to the world they are describing. Models like the Lonsdorf model are the most general and have the potential to be useful in a wide range of scenarios but in reality have only been found to be applicable to a limited set of situations. While quantification may be desirable in an ordered world, there is also the risk that too high an emphasis is placed on numbers these models deliver, when the assumptions underlying them are not strong.

1.5.4.2 Qualitative approaches

Recognising that there is fundamental uncertainty, that quantification is difficult for unmarketable goods and services, and even for marketable goods and services which depend on biological populations, a broad and mostly qualitative framework was used for the follow-on phase of National Ecosystem Assessment. A panel of ecological and economic experts developed a Natural Capital Asset Check. The check was developed to record the likely trends in the use of natural assets across the UK to see whether or not natural assets could be said to be on a sustainable path. The framework was to be broad enough to cover a range of natural assets including site specific estuaries and wider categories such as woodlands and pollinators along with the habitats which support them. The steps required an assessment of uncertainty for each conclusion made, asking whether the evidence for a point is conflicting or if experts are in agreement.

The first step required an assessment of the integrity and extent of the natural asset, and the observable trends in these. This was followed by an assessment of the drivers of change for that asset including political, biophysical and socio-economic drivers. The extent and condition of the asset, combined with current drivers, was used to answer the questions; is the ability of the asset to support ecosystem services being maintained (integrity test), and can an adequate level (given the likely demands) of ecosystem services could be expected from that asset (sustainability test). The final section of the exercise attempted to identify red flags and any signs there might be that thresholds might be reached beyond which irreversible loss of capital would occur. While quantitative data and analysis were used, the framework also encouraged authors to identify knowledge gaps and so undue focus was not put on areas which could be quantified at the expense of other areas.

1.6 Outline of research chapters

While it has been established that pollinators are important to crop yields, the particular contribution of wild pollinators relative to substitutes still requires more research, and will be specific to different crops. It is also important to understand whether diverse pollinator groups are important for overall pollination due to their differences as management recommendations can then be made which support more than one group of pollinators. Knowledge of how wild bees respond to various threats such as weather changes, habitat use and pesticide use will be important to maintaining services in the future. There are multiple ways of carrying out such research, field studies, modelling and qualitative approaches. I start with two field studies, both undertaken on soft-fruit farms in East Scotland. Both raspberries and strawberries require pollination to different extents, and commercial bee use varies between these fruits and between farms. The first field study is an ecological study of the factors which affect wild and commercial pollinators and their delivery of pollination services to strawberries and raspberries (chapter 2). This study also considers whether complementarity in seasonal activity and weather tolerances are important for the pollination of soft-fruits. The second field study was an experiment carried out on the same working farms, and looked at the effect of normal levels of neonicotinoid use on the mortality and reproduction of bumblebee nests within the landscape (chapter 3). The third study uses a simple structural ecological-economic model for a specific crop in Scotland, parameterised using field and published data to model the combined impacts of pesticide use and land use change on pollination services (chapter 4). In the final study a more qualitative approach was taken. The Natural Capital Asset Check for pollinators reviews the literature on pollinators across the UK, to answer the overall question of whether the UK pollinators can sustain crop yields for the future (chapter 5).

Chapter 2

Functional diversity matters: Seasonal complementarity of pollinators ensures fruit production through the growing season

Ciaran Ellis, Hannah Feltham, Kirsty Park, Nick Hanley, Dave Goulson

The fieldwork presented in this chapter was carried out with Hannah Feltham, a PHD student at Stirling University, fieldwork plans were devised as a group and carried out by C. Ellis and H. Feltham with undergraduate volunteers. H.Feltham carried out GIS mapping of the landscape surrounding the farms. All other analyses were carried out by C. Ellis. C. Ellis wrote all parts of the paper. Co-authors commented on drafts of this paper.

2.1 Abstract

Understanding the relative contributions of wild and managed pollinators, and the functional contributions made by a diverse pollinator community, is essential to the maintenance of yields in the 75% of world crops that benefit from insect pollination. Through a field study and pollinator exclusion experiments on two soft-fruit crops in a system with both wild and managed pollinators we have linked seasonal differences in the abundance of pollinator groups to yields across the growing season. Pollinators also responded differently to weather and habitat variables suggesting that diversity can reduce the risk of pollination service shortfalls. These results provide evidence for the link between increased diversity and function in a real crop system.

The functional approach taken here shows that low efficiency pollinators such as flies may be more important to pollination than expected. Flies pollinated in poor weather and at the end of the growing season when other pollinators were scarce, and so made a unique function contribution. Understanding how differences between pollinator groups can enhance pollination services to crops strengthens the case for multiple species management and highlights the risks of replacing all pollinators with managed alternatives.

2.2 Introduction

Insect-mediated pollination increases yield in around 75% of world food crops, which provide ~35% of our food (Klein et al. 2007). The importance of insect pollination has led to the commercialisation of not only the honeybee, but also several species of bumblebee and various solitary bees (Pitts-Singer & Cane 2011). Nonetheless the role of wild pollinators is likely to be greater than was previously assumed: a meta-analysis of pollination data from 41 crop systems found that wild pollinators numbers had a stronger effect on fruit set than honeybees in the majority of crops studied (Garibaldi et al. 2013) and play a significant role in varied crop systems (e.g. Winfree et al. 2008; Breeze et al. 2011; Rader et al. 2012).

Wild species are also important for their contribution to pollinator diversity, which has been shown to positively influence crop success (Klein et al., 2003). Increased diversity increases ecosystem service provision when species contribute slightly different functions (Cadotte et al., 2011). Particularly, functional diversity is increased when species (or species groups) are complementary in the services they provide so the overall scope of service provision is increased when more species are present. For example, pollinator species may be complementary in the heights at which they forage; honeybees and wild bees are complementary in their use of space on almond trees, so having both groups present increases yield overall (Brittain et al. 2013a). Likewise seed set in pumpkins grown at different heights was increased when more pollinator groups with different preferred pollinating heights were available (Hoehn et al. 2008). For crops with long growing seasons, one species or group of species may not be active for the entire growing season, and so complementarity in abundance or activity across time (seasonal complementarity) will be important (Bluethgen & Klein 2011).

Species or species groups that overlap in functional contribution may respond slightly differently to changing conditions, thus buffering the overall service over multiple years (Winfree & Kremen 2009; Brittain et al. 2013a). Differential responses to landscape context or management practices could ensure the service provision continues after land-use alterations (Steffan-Dewenter et al. 2002; Jha & Vandermeer 2009; Tuell & Isaacs, 2010). Maintaining both complementarity functions and response diversity will ensure that future pollination needs are met under a range of circumstances (Elmqvist et al. 2003).

The soft fruit industry in Scotland produces 216,000 tonnes of strawberries (5% of the global total) and 3,000 tonnes of raspberries per year (FAOSTAT, 2013). Both crops are highly reliant on insect pollination for marketable fruit. The pollinator requirements of raspberries and strawberries differ: raspberries are highly attractive to bees and the peak of flowering coincides with the seasonal peak in bee numbers. Strawberries, on the other hand, have a long growing season which may require multiple pollinator groups to ensure pollination across the season. This study examines the importance of diversity in soft-fruit pollination by asking the following questions:

1. What are the relative levels of pollination contributed by different species?
2. Is there complementarity between different pollinator groups enabling strawberry pollination across the season?
3. Are there differences in the response of different pollinator groups to weather and habitat variables which could be important for the continued pollination of these crops?

2.3 Material and Methods

2.3.1 Sites and Survey

The main domesticated pollinators on soft-fruit farms are commercially-reared bumblebees. Honeybees are also sometimes present though they are not ubiquitous in UK crop systems (Breeze et al., 2011). Seven species of wild bumblebees are common in the study area as well as other pollinators including solitary bees, hoverflies and other Diptera (Lye et al., 2011). Contact was made with soft-fruit farms in autumn 2010 and 29 farms were visited in early 2011. Farm managers were asked about commercial pollinator management; how many bumblebee colonies were used and whether, to their knowledge, honeybees were kept within flight distance of the farm. They were also asked about wild pollinator management e.g. whether wild flower strips were grown. Twenty-five farms spread through Angus, Perthshire and Fife (Fig. 2.1) were then chosen for inclusion in the field study. Of these nine grew only strawberries, four only raspberries and twelve grew both. Most soft-fruits were grown undercover in polythene tunnels (polytunnels). Some of the tunnels were stood on stilts and therefore had entry points for pollinators along the sides of the tunnels (open-sided) while for other tunnels the polythene reached the ground so pollinators could only enter from either end (closed-sided).

2.3.2 Pollinator Activity Transects

For each transect, a tunnel was picked at random from those with flowering crops and walked along at a slow walking pace, recording all pollinator visits to flowers. Transects on each farm ran for a total of 300m and included between two and four adjacent tunnels. *Bombus* species were classified to species level where possible; workers of domesticated *Bombus terrestris*, wild *B. terrestris* and wild *B. lucorum* cannot be reliably distinguished by eye. To split the counts of these species into wild and domesticated classifications, we used the average number of *B. terrestris/ B. lucorum* observed at farms not using commercial bees divided by the average number of *B. terrestris/B. lucorum* seen at farms using commercial bees to estimate the proportion of *B. terrestris/B. lucorum* observed, that could be attributed to wild sources. These proportions (for each fruit and time period) were then applied to the overall counts on farms using commercial bees, to obtain an estimate of the number of *B. terrestris/B. lucorum* from wild populations, and *B. terrestris/B. lucorum* from commercial sources.

Other pollinators were assigned to broad grouping, i.e. solitary bees were all grouped together, as were flies (including hoverflies). Three replicate flowers counts were taken in 1m^2 areas within each tunnel to estimate floral resources provided by the crop. Cloud cover was estimated as a percentage. Wind speed was measured on a three point scale (0 = still, 1 = light breeze, 2 = strong breeze), as was rain (0 = no rain, 1 = light rain, 2 = heavy rain). Days with heavy rain were avoided where possible, but if rain began during a visit the transect was completed. Weather stations closest to each farm were used for daily temperature and humidity data. Transects were all walked between 10 am and 5 pm. The time and type of polythene tunnel (closed-sided or open-sided) were also recorded. Farms were visited six times throughout the season, with approximately three weeks between each visit.

2.3.3 Exclusion experiment

The effect of pollinator visits on fruit quality and weight was evaluated at a subset of the farms (9 raspberry-growing farms and 11 strawberry-growing farms). Pollinators were kept away from flowers using polythene mesh netting (holes 1.35mm^2, Harrod Horticultural Ltd, Lowestoft, UK). The net was chosen to exclude insects without allowing moisture to build up within the net, and to allow wind-blown pollen through. For raspberries, 6 plants were used in each of 3 different polytunnels per farm; on each plant a bunch of approximately 9 unopened flowers were covered with the netting which was secured to the branch with covered wire. The bunches were marked with coloured tape along with a control bunch from the same plant. Strawberry plants were entirely covered with the exclusion mesh which was supported by arches of flexible garden wire and fixed to the bed with metal staples and duct tape. The plants were covered in groups of four (two groups of four were covered in each of two polytunnels). Each group was matched with a group of control plants which were marked with tape and signposted. Excluded and control fruits were picked when ripe. The picked berries were categorised into class I and class II fruit based on European marketing criteria and weighed (European Commission, 2011).

2.3.4 Habitat data

Landscape data was obtained from the OS MasterMap Topography Layer (EDINA Digimap Ordinance Survey Service) and ArcGIS 9.2 was used to create circles 1km around each study site. The feature classes from the topography layers were reclassified into five categories; (i) urban areas (buildings and structures), (ii) farmland, (iii) water (inland and tidal), (iv) linear man-made structures (roads, tracks and paths); and (v) semi natural habitat (rough grassland, scrub and woodland). The proportions of land cover for each of the five categories within each 1km buffer were calculated and used in subsequent analysis.

2.3.5 Statistical Analyses

2.3.5.1 Exclusion experiment

Statistical analyses were conducted using the statistical software R version 2.15.1 using packages lme4 and MASS (R Development Core Team, 2010). Models were fitted to the strawberry and raspberry data sets with fruit quality (with binomial errors) or fruit weight (with Gaussian errors) as response variables. Strawberries had high inter-farm variation and so farm identity was fitted as a random factor within a generalised linear mixed model (GLMM). For the raspberry data the residual deviance after fitting a GLM was approximately equal to the remaining degrees of freedom; there was little remaining variation to explain through random effects and so a GLMM was not used (Crawley, 2002). For all models, treatment (insects excluded vs. not excluded) and the average number of pollinators in the transects walked during the ripening period were included as explanatory variables, the flowering period was taken as the five weeks prior to picking (Lye et al., 2011) . To take into account the differences in ability to transfer pollen and the speed at which pollinators work, the abundance counts were multiplied by efficiency factors to provide efficiency-adjusted counts (Isaacs & Kirk, 2010). Honeybee numbers was reduced by a factor of 0.5 relative to bumblebees (Willmer et al., 1994) and fly numbers were reduced by a factor of 0.2 (Albano et al. 2009; Jauker et al. 2012)

2.3.5.2 Pollinator activity

Counts of each pollinator group were summed along transects for each time period. With abundance of each pollinator group as the response, GLMM models with Poisson errors were fitted to the data with farm identity as a random factor. Data were overdispersed and so observation-level random effects were included in addition to the farm level random effects (Maindonald & Braun, 2010). Potential explanatory variables were split into three sets; observation variables (those variables available for each observation including weather variables, date etc.), management variables and habitat variables (Table 2.1). The analysis therefore took a hierarchical approach, with observation level variables and farm level variables (habitat and management variables) (Gelman & Hill, 2007). A full observation level model was fitted to each pollinator group on each soft-fruit. This model was reduced by removing non-significant terms ($p>0.10$) and comparing the Akaike Information Criterion (AIC) between models until the model with the lowest AIC was achieved. The management variables and habitat variables were then fitted separately to the most informative observational level model and the two-level models were reduced as before. When both day and day squared were included in the final model, orthogonality was tested for by applying the “poly” function in R to the model. If there was no change in the significance level of the parameters the terms were deemed to be orthogonal.

2.3.5.3 Complementarity

Species groups show seasonal complementarity if the peaks of their distributions across the season tend to occur separately. This can be tested for using a variance ratio test (1) (Schluter 1984; Stevens & Carson 2001; Winfree & Kremen 2009), which is based on the relationship between total variance of M elements and the co-variances between them (2). In this case the elements (X) are the abundances of the four pollinator groups through time.

$$C = \frac{Var(\sum_{i}^{M} \llbracket Si) \rrbracket}{\sum_{i}^{M} Var(Xi)} \qquad (1)$$

$$Var(T) = \sum_{i}^{M} Var(Xi) + 2 \sum_{i<l}^{M} Cov(Xi, Xl) \qquad (2)$$

If the species groups do not tend to covary positively or negatively, the total variance will be equal to the sum of the variance of each element, and hence the test statistic (C) will be close to 1. Test statistics less than 1 implies negative covariance and thus that the pollinator groups have different peaks throughout the season. A test statistic (C) across all the farms was calculated from the raw data. Per farm test statistics were not calculated as only one visit per farm was made per time period and weather impacted abundance. We generated farm level complementarity figures by simulating pollinator abundances by group for 6 time periods throughout the season. To control for effects of weather we took the average weather variables for each of 6 time periods and used these to generate 1000 random weather scenarios. These scenarios were used as inputs to the best fitting two-level GLMM model for each pollinator group. The complementary figures for each simulated set of pollinator abundances were then calculated. Sensu Winfree & Kremen (2009) we then compared the complementarity results for the simulated data using the full model, versus the results from the same models but with the day and day squared terms eliminated (the null model) using Wilcoxon signed rank test. As the “day” term represents the number of days since the start of the study, the results from the null model represent the pollinator abundances which would be expected if there is no distinction between the pollinator groups based on the time through the year.

2.3.5.4 Impact of complementarity on yield

To assess the importance of different pollinator groups to fruit yield across the season, the GLMM models for wild bumblebees, honeybees and flies were used to simulate pollinator numbers across the season under average conditions. The outputs were totalled and adjusted for pollinator efficiency and the total adjusted pollinator numbers at each time point were then used as an input for the fruit quality GLMM. On the basis of discussions with farmers, the threshold for profitability was taken to be an average of 80% first class fruit. Pollinator groups were then deleted one by one from the total set, and fruit quality across the season re-evaluated.

2.4 Results

2.4.1 Pollinator Activity Transects

From 15 April to 19 August 2011, we observed 2,478 pollinators visiting strawberries in 129 transects at 21 farms and 4,464 pollinators visiting raspberries in 80 transects at 16 farms. Transects took on average 43 minutes to walk. Pollinators were observed on raspberry transects from mid-May to late July, and on strawberries from mid-April to mid-August. On average four (three to five) raspberry transects were walked on each farm with raspberries, and six (four to six) strawberry transects were walked on each farm with strawberries. Strawberry plants were considerably less attractive to pollinators than raspberry plants, with an average density of 8.9 pollinators per 100m^2 per hour (mean ± s.d. 8.9 ± 8.3 pollinators), and an average of 3,556 flowers per 100m^2. In comparison there were an average of 26.0 pollinators per 100m^2 per hour on raspberries (mean ± s.d. 26.0 ± 35 pollinators) and an average of 1,934 raspberry flowers per 100m^2. Therefore there were 5.3 times more pollinators per flower on raspberries than strawberries (1.34×10^{-2} pollinators per flower per hour for raspberries v 2.51×10^{-3} pollinators per flower per hour for strawberries). Of 21 farms growing strawberries, 18 (86%) used commercial bumblebees on this fruit. While the majority purchased bumblebees for pollination early in the season (late April to June), 3 out of 18 farms restocked with additional colonies midway through the season. In contrast, nine of the 16 farms (56%) growing raspberries used commercial bumblebees on raspberries and these farms only bought bees once at the beginning of the season.

Bombus terrestris/B. lucorum, including commercial bumblebees, provided around half the pollinator visits for both crops averaged across all farms (57% of visits to raspberries and 46% of visits to strawberries, see Table S2.1 in Appendix). We estimated that around 16% of visits to raspberries and 29% of visits to strawberries were by commercial *B. terrestris*, and honeybees contributed approximately a quarter of visits to both crops (Table S2.1). Other bumblebee species together comprised 20% of pollinator visits for raspberries and 10% for strawberries; these included *B. lapidarius, B. pascuorum* and *B. pratorum*. *B. hortorum* was seen on raspberries but not strawberries. Hoverflies and other flies made up around 1% of visits to raspberries and 23% of visits to strawberries. Other pollinators included solitary bees which made 68 visits to strawberries and 23 visits to raspberries, and butterflies which were only observed visiting strawberries (5 visits); these groups were not analysed further. The pollinator counts were subsequently grouped into wild bumblebees (including our estimate of the number of *B. terrestris/B. lucorum* attributable to wild pollinators), commercial bumblebees (the remainder of *B. terrestris/B. lucorum* visits), honeybees and flies (including hoverflies).

A total of 17 of the 25 farms had wild flower strips on the farm with 11 leaving field margins unmowed to assist pollinators. Neither of these variables predicted the number of wild bumblebees on either raspberries or strawberries (Tables 2.2 and 2.3). Farmer management of commercial pollinators did, however, have an effect; commercial bumblebee numbers significantly increased with the number of colonies used on strawberries. Where farmers indicated that there were honeybees within flying distance of the farm, higher numbers of honeybees were seen on both raspberries and strawberries. Honeybees were less likely to be found in polytunnels with closed sides than open sides. Commercial bumblebees, on the other hand, were more abundant in closed sided tunnels, likely reflecting the fact that commercial bees (when used) are more likely to remain within a tunnel with closed sides.

Day (number of days from start of the field study) and day squared terms were found to be orthogonal in all models. The standardised coefficients for these terms gives an indication of how early or late in the season that pollinator group was observed on the transect. Pollinator groups with a positive coefficient for day tended to be observed later in the season, and with a negative coefficient were observed earlier (Table 2.2. Standardised coefficient ± s.e. for predictor “day” for pollinators of strawberries: flies and hoverflies -1.49 ± 0.39, commercial bees 1.35 ± 0.31). Pollinators groups with a negative and significant day squared term peaked towards the middle of the season (Table 2.2. Standardised coefficient ± s.e. for predictor “day squared” for pollinators of strawberries: wild bumblebees -1.31 ± 0.15, honeybees -1.34 ± 0.36). On raspberries wild bumblebees also peaked in the middle of the season whereas honeybees were observed later in the season (Table 2.3. Standardised coefficient ± s.e. for predictor “day squared” for pollinators of raspberries: wild bumblebees: -1.88 ± 0.32, and for predictor “day”: honeybees: 1.55 ± 0.54).

Other factors influencing the abundance of pollinators also differed between pollinator groups (Table 2.2 and 2.3). Wild bumblebees, commercial bumblebees and honeybees had similar responses to weather variables; numbers reduced with increasing cloud, wind and rain, and increased with temperature. Flies, on the other hand, seemed to respond in the opposite way, increasing in number with increasing wind, rain and decreasing temperature. Numbers of flies visiting strawberries increased with the proportion of urban area within 1km of the farm. The probability of presence of honeybees on a farm declined with an increased proportion of natural habitat within 1km of the farm.

2.4.2 Exclusion Experiment

When pollinators were able to access flowers, a higher proportion of raspberries were first class (Table S2.2: mean = 91% first class, s.d. = 0.09), than when pollinators were excluded (Table S2.2: mean = 28% first class, s.d. = 0.09). Raspberries were also heavier when pollinators were allowed to forage (Table S2.2: mean of 3.39g ± 0.68 v 4.70g ± 1.13). Exposure to pollinators was a significant predictor of proportion of first class fruit (table S2.3: $Z = 10.28$, $p < 0.001$) and of weight of raspberries (table S2.3: $t = 2.11$, $p=0.051$). Pollinators numbers were consistently high in the raspberry experiments so no incremental effect of pollinators was detected (fig 2.2b (i))

Excluding pollinators from strawberries caused a decline in fruit quality by approximately 50% (table s2.2: 0.4 vs 0.8 fruits reaching 1st class). There was no significant difference in the weight of the strawberries grown with or without pollinators (Table S2.2: mean = 11.2g ± 1.70 v 10.2g ± 1.57) (table S2.3: Z = -0.29, $p > 0.05$). The interaction between efficiency adjusted pollinator number and pollinator exposure was a significant predictor of the proportion of first class fruit, indicating that additional pollinators increase the proportion of first class fruit (Fig. 2.2b (ii), table S2.3: t = 2.55, p = 0.011).

2.4.3 Seasonal Complementarity

The variance of the abundance over time for all species at all farms ($Var\ (T)$) was 45.3 whereas the sum of the individual variances ($\sum Var(Xi)$) was 80.3, giving a variance ratio of 0.56 (see Table S2.4). A test statistic of below 1 supports the hypothesis that pollinator groups peak at different times across the season. The same conclusion was reached when the simulated values for each farm were analysed: comparing the simulated values with and without individual time components, the simulated values from the full model were 0.77 on average for the closed-sided tunnels (compared to 0.96 for the null model; W= 232183, $p<0.001$) and 0.76 on average for the open sided tunnels (compared to 0.93 for the null model; W = 282753, $p<0.001$).

The results were consistent whether the abundance figures were adjusted for efficiency or not (see Table S2.5).

2.4.4 Impact of Complementarity on Strawberry Yields

In both closed and open-sided tunnels there were insufficient pollinators for a high proportion of first class fruit early in the season, which coincides with commercial bumblebee use (Fig. 2.4). The proportion of first class fruit in the mid-season is predicted to be low in closed sided tunnels if wild bumblebees are not present as honeybees (the other pollinator group present in abundance in mid-summer) are not abundant in this type of tunnel.

In open-sided tunnels, both honeybees and wild bumblebees pollinate during the middle of the season. Correspondingly the proportion of first class fruit does not drop as severely if wild pollinators are not present.

Flies were important for pollination at the end of the season for both tunnel types, and predicted aggregate yield fell on the removal of this pollinator group. In neither tunnel type are pollination visits sufficient for 80% pollination across the whole season, but with all pollinator groups present this target was more likely to be hit. Simulations were not run for raspberries as the quality and weight of raspberries was consistently high at all farms sampled, suggesting that pollination services are not limiting raspberry production.

Table 2.1 List of variables used in GLMMs to explain pollinator visitation to strawberries and raspberries

Observation level	**Farm Level**	**Farm Level**
	Management variables	*Habitat variables*
Day	Honeybees within 1km of farm (Yes or No)	% Woodland and scrub within 1km
Day squared	Number of bumblebee colonies used on crop per year	% Urban area within 1km
Time of day	Wild flower strips planted (Yes or No)	% Roads within 1km
Polytunnel type	Field margins left unmowed (Yes or No)	
Wind speed (0, 1, 2)		
Cloud cover (%)		
Humidity (%)		
Temperature (^{0}C)		

Table 2.2 Standardised coefficients and standard errors for variables in the most informative observational model (lowest AIC) explaining number of visits by pollinator groups to strawberry flowers

Strawberries	**Observation level variables in best fit model**				
Pollinator group	*Intercept*	*Day*[a]	*Day squared*[a]	*Polytunnel*[b]	*Flowers*
Wild bumblebees	2.69±0.27***	0.42±0.17*	-1.31 ± 0.15***	-0.20 ± 0.21	0.27 ± 0.11**
Commercial bumblebees	1.35±0.31***	-0.98±0.15***	Ns	0.11 ± 0.23	Ns
Flies and hoverflies	-1.49±0.39***	1.69±0.17***	Ns	0.39 ± 0.30	Ns
Honeybees (presence)	0.20±0.66	Ns	-1.34 ± 0.36***	1.28 ± 0.61*	Ns
Honeybees (when present)	-0.43±0.62	0.61±0.18***	Ns	1.10 ± 0.47*	Ns

Strawberries	**Observation level variables in best fit model**					**Farm level variables in best fit model**	
Pollinator group	*Cloud cover (%)*	*Wind (0,1,2)*[c]	*Rain (0,1,2)*[c]	*Temp (°C)*	*Humidity (%)*	*Management*	*Habitat*
Wild bumblebees	-0.22 ± 0.10*	-0.42 ± 0.13**	-0.84 ± 0.35*	0.20 ± 0.12 .	Ns	Ns	Ns
Commercial bumblebees	Ns	-0.28 ± 0.13*	-1.34 ± 0.41**	0.46 ± 0.12***	0.22 ± 0.12 .	0.0018 ± 0.000826*†	Ns
Flies and hoverflies	Ns	0.61 ± 0.17***	0.41 ± 0.26	-0.34 ± 0.14*	-0.40 ± 0.14**	Ns	0.60 ± 0.21**¶
Honeybees (presence)	-0.69 ± 0.28*	Ns	Ns	Ns	Ns	Ns	-0.16 ± 0.06**§
Honeybees (when present)	-0.41 ± 0.14**	Ns	Ns	Ns	Ns	1.20 ± 0.56*‡	Ns

a. Day and day square terms were found to be orthogonal in all models

b. Polytunnel coefficients compare open-sided tunnels to closed-sided tunnels; a positive coefficient represents an increase in pollinators relative to closed-sided tunnels.

c. Wind/Rain levels were 0 = no wind/rain, 1 = light wind/rain and 2 = high wind/rain, treated as ordinal continuous.

† Number of colonies bought. ‡ Honeybees known to be deployed nearby (yes or no). ¶ Proportion of urban area within 1km. § Proportion of natural habitat within 1km.

Ns denotes non-significant terms which were not included in the model with the lowest AIC. Terms with no period or asterisk were in the lowest AIC model but not significant. Other significance levels are symbolised by: . $P < 0.10$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Table 2.3. Standardised coefficients and standard errors for variables in the most informative observational model (lowest AIC) explaining number of visits by pollinator groups to raspberry flowers

Raspberries	**Observation level variables in best fit model**				
Pollinator group	*Intercept*	*Day*[a]	*Day squared*[a]	*Polytunnel*[b]	*Flowers*
Wild bumblebees	3.4±0.18***	1.48 ± 0.22***	-1.88 ± 0.32***	-0.02 ± 0.20	0.75 ± 0.11***
Commercial bumblebees	0.91±0.64	Ns	Ns	-4.52 ± 1.26***	1.29 ± 0.59*
Honeybees (presence)	-0.08±0.70	Ns	Ns	1.54 ± 0.71*	0.69 ± 0.44
Honeybees (when present)	-1.11±0.58.	1.55 ± 0.54***	Ns	0.19 ± 0.42	1.06 ± 0.26***

Raspberries	**Observation level variables in best fit model**					**Field level variables in best fit model**	
Pollinator group	*Cloud cover (%)*	*Wind (0,1,2)*[c]	*Rain (0,1,2)*[c]	*Temp (°C)*	*Humidity (%)*	*Management*	*Habitat*
Wild bumblebees	-0.36 ± 0.11***	Ns	Ns	Ns	Ns	Ns	Ns
Commercial bumblebees	Ns	Ns	Ns	Ns	Ns	Ns	Ns
Honeybees (presence)	Ns	Ns	Ns	Ns	Ns	Ns	-0.19 ± 0.08*[§]
Honeybees (when present)	-0.52 ± 0.26*	1.15 ± 0.30***	Ns	0.76 ± 0.26**	Ns	1.18 ± 0.58*[†]	Ns

a. Day and day square terms were found to be orthogonal in all models

b. Polytunnel coefficients compare open-sided tunnels to closed-sided tunnels; a positive coefficient represents an increase in pollinators relative to closed-sided tunnels.

c. Wind/Rain levels were 0 = no wind/rain, 1 = light wind/rain and 2 = high wind/rain, treated as ordinal continuous.

† Honeybees known to be deployed nearby (yes or no), § Proportion of natural habitat within 1km.

Ns denotes non-significant terms which were not included in the model with the lowest AIC. Terms with no period or asterisk were in the lowest AIC model but not significant. Other significance levels are symbolised by: . P < 0.10, * P < 0.05, ** P < 0.01, *** P < 0.001.

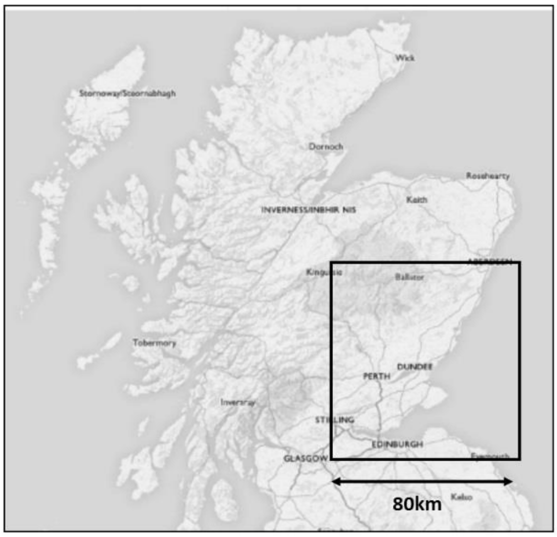

Figure 2.1 Location of study area within East and South-East Scotland.

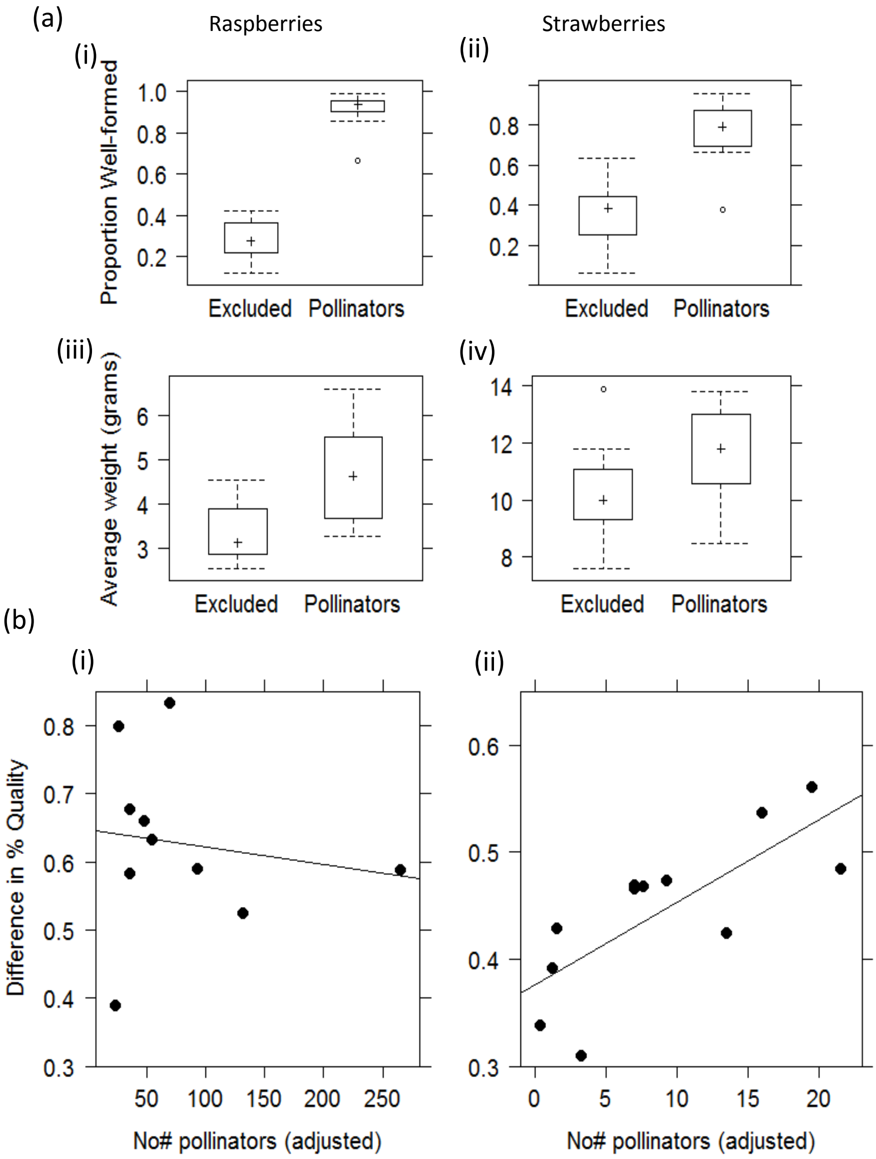

Figure 2.2. Effect of pollinator exposure and numbers of pollinators (adjusted for efficiency) on fruit quality and weight. (a) Proportion of class I fruit was higher when insects could visit flowers of (i) raspberries ($t = 10.28$, $p < 0.0001$) and (ii) strawberries ($t = 10.43$, $p < 0.0001$), weight of fruit was marginally significantly higher when insects could visit (iii) raspberries ($Z = 2.11$, $p = 0.0513$). Strawberry weight was also higher on average but the difference was not significant (iv) strawberries ($Z = 1.60$, $p > 0.05$). (b) Fruit quality increased with the number of pollinators adjusted for efficiency in (ii) strawberries (treatment x adjusted pollinator number, $t = 2.55$, $p = 0.011$) but not (i) raspberries were no relationship was observed ($t = -1.21$, $p > 0.05$).

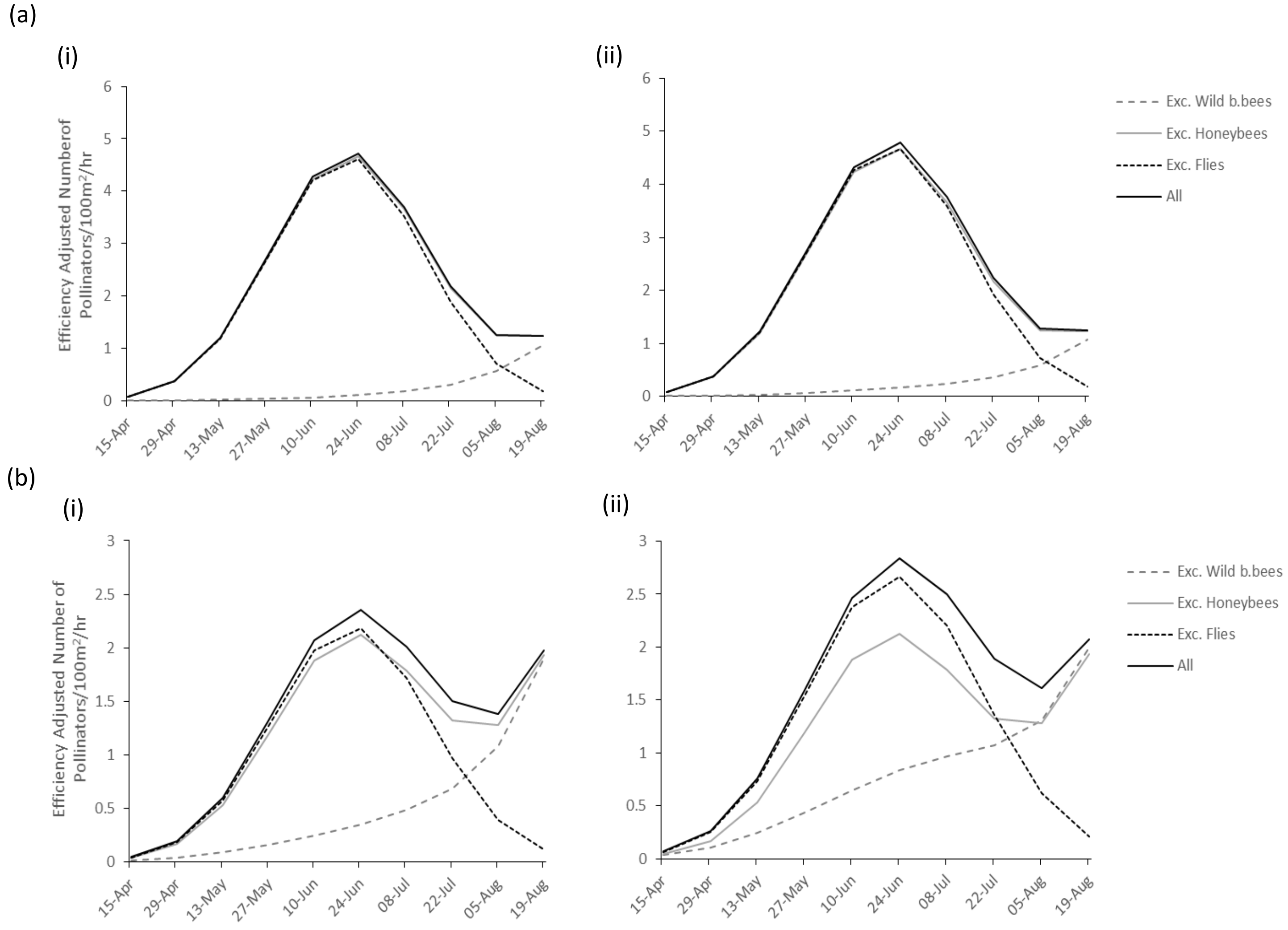

Figure 2.3. Simulated numbers of pollinators (adjusted for efficiency) across the growing season under average conditions, with pollinator groups deleted one-by-one. (a) closed-sided tunnels (i) Honeybees kept in the vicinity and (ii) honeybees are not kept within the vicinity. (b) Open-sided tunnels (i) honeybees kept in the vicinity (ii) honeybees not kept in the vicinity. Honeybees were rarely seen in closed sided tunnels and so the removal of this group does not make a difference to overall pollinator numbers in (a)(i) and (a)(ii). In open-sided tunnels, when all groups were present pollinators were around from mid-May until the end of the season. Removing pollinator groups had an impact: there was a large drop in pollinator numbers in the mid-season when wild bumblebees are removed, and at the end of the season when flies were removed. For both types of tunnel, the gap where no pollinators are present in April can be met by commercial pollinators.

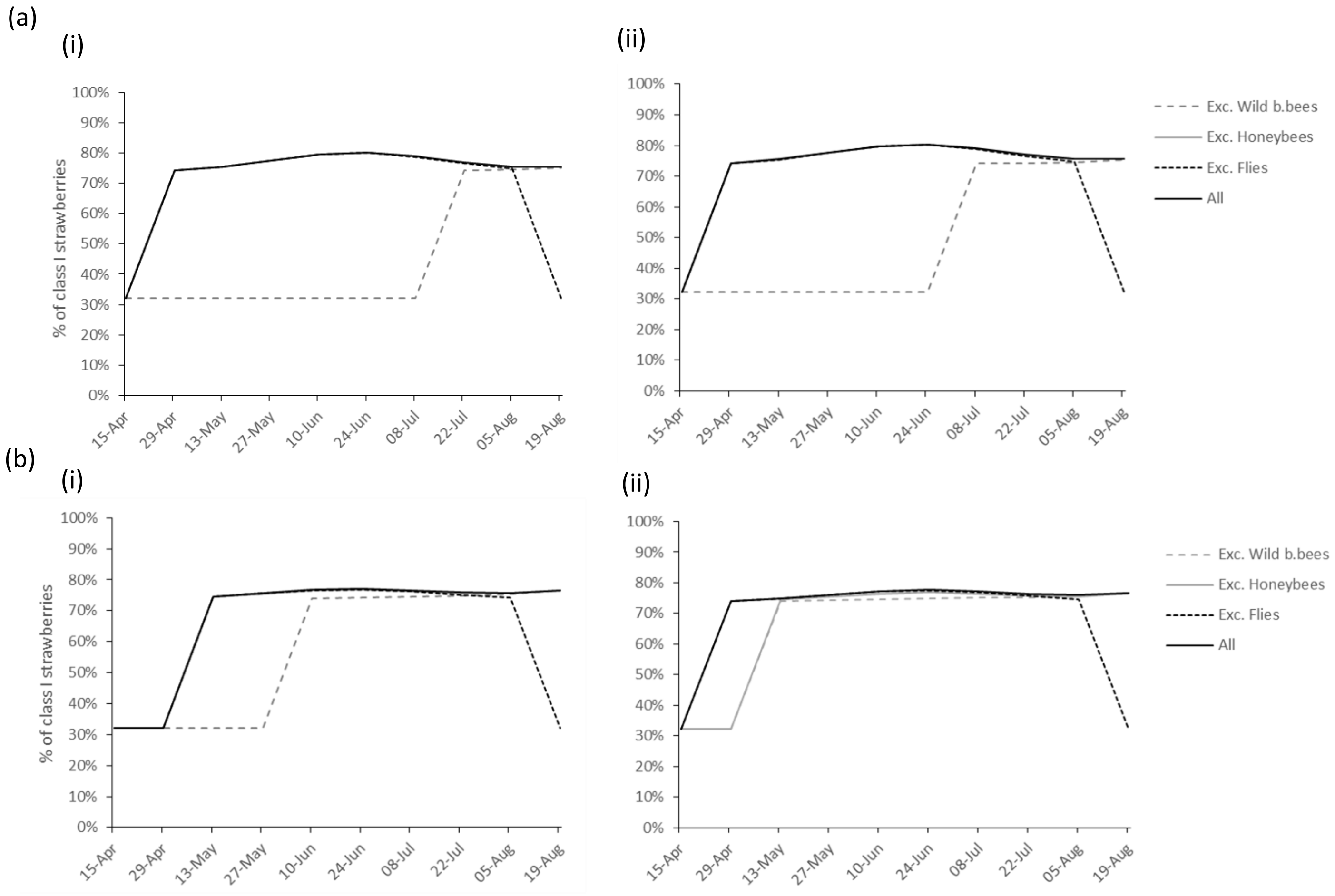

Figure 2.4. Simulated proportions of class I strawberries across the growing season with pollinator groups deleted. Results were generated from efficiency adjusted counts shown in figure 2.3, run through the GLMM model for fruit quality. (a) closed-sided tunnels (i) Honeybees kept in the vicinity and (ii) honeybees are not kept within the vicinity. (b) Open-sided tunnels (i) honeybees kept in the vicinity (ii) honeybees not kept in the vicinity. Honeybees are active at around the same time as wild bees, but were present at lower levels and so the removal of honeybees does not shift quality expectations significantly. The removal of wild bees however causes quality to drop for a large part of the season in closed sided tunnels (a), and in the early part of the season in open-sided tunnels (b) where honeybees are more abundant. In both tunnel types the removal of flies causes a decline in fruit quality at the end of the season.

2.5 Discussion

The pollination of strawberries throughout the year is facilitated by seasonal complementarity among both wild and commercial pollinators. Honeybees and wild bumblebees can provide pollination through the peak of the season, June and July, after which flies provide the bulk of pollination services. The potential for complementarity in seasonal abundance between different pollinator groups was suggested by Bluethgen and Klein (2011), but to our knowledge this is the first experimental evidence for such an effect. Our data supports the suggestion that species diversity can improve ecosystem services by increasing the functional range of the service provided.

Wild bee numbers were sufficient to provide adequate pollination for raspberries. Raspberries are more attractive to pollinators than strawberries and they have a shorter growing season, which coincides with the peak of wild bee activity. Despite this, commercially-reared bumblebees were used on half of the sites which grew raspberries. While commercially-reared bumblebees may not be necessary every year, there can be high variation in pollinator services between years; Lye et al. (2011) found that raspberry pollination was limited by lack of wild pollinators in an experiment in the same area in 2009. The relative abundance of different species can change dramatically between years as observed on watermelon and oil-seed rape

(Kremen et al., 2002). Smoothing out interannual variability in pollination services might be a justification for using domesticated bees on the farms studied.

There is no reliable way to distinguish commercial *Bombus terrestris* and wild *Bombus terrestris/lucorum* in the field. The proportions of *Bombus terrestris/lucorum* observed that were wild bees were estimated based on data from farms which do not use commercial bumblebees. This assumes that commercial bumblebee use itself does not reduce the number of wild bumblebees seen at a farm, and that there are not fundamental differences between farms that do and do not deploy commercial bumblebees that might affect wild bee abundance. We would expect commercial bumblebees to have an impact on wild bumblebees if densities of bees were high enough for competition to occur. This is unlikely on strawberries as the overall pollinator density was low. Densities were far higher on raspberries, so it is possible that the use of commercial bees could have affected the numbers of wild bees observed here. However any competition would presumably also affect *B. pascuorum* and *B. pratorum;* there were no differences in densities of these species between raspberry farms which used commercial bees and those that did not. It is reasonable to conclude that significant competition did not occur on the farms observed and that there are not major differences in wild bee fauna between farms that do and do not deploy commercial bees.

There were differences in the responses of the pollinator groups to weather experienced during the field study. Information on response diversity could be critical to managing pollination services over time; if a species of pollinator were to decline in abundance or reduce activity due to poor weather conditions, pollination may fall below the threshold required for a profitable harvest. In our system, this is particularly important for strawberries; even during May and June, the threshold for a profitable strawberry harvest was only just met by wild pollinators on the average farm. If different pollinator groups respond differently to weather conditions, the risk of pollination falling too low could be reduced by ensuring the presence of a diversity of species (Elmqvist et al., 2003). However the bees in our study responded in the same way to weather variables; both bumblebee and honeybee activity was reduced with higher wind, rain and cloud cover. The ability of these bee groups to buffer the activity of the other in varying weather conditions is therefore limited. Conversely, flies seemed to respond in the opposite way to both *Bombus* and *Apis* bees, and were more likely to be seen on transects in wet weather and higher winds. Both *Bombus* and *Apis* species are sensitive to weather conditions experienced while leaving the nest, and may not forage in unfavourable conditions. *B. terrestris* were observed to cease foraging within tunnels when rain began, despite the polythene covering. In contrast, flies may seek shelter within the tunnels in poor weather (since they have no nest to retreat to), increased numbers of flies on the crop.

Different pollinator groups also responded differently to habitat surrounding the farms. Similar to Steffan-Dewenter and Tscharntke (1999), we found that honeybees were less likely to be observed on a transect with increasing natural habitat in the 1km surrounding the farm. This relationship might be because natural habitat provides floral resources that are more attractive to honeybees. No habitat variable tested influenced the numbers of bumblebees in our study. While some studies have found a declining relationship between social bee abundance and habitat isolation (reviewed by Ricketts et al., 2008), other studies found no relationship between bumblebees and semi-natural habitat at any scale (Westphal et al., 2006). Another study in the same region of Germany found a trend of increasing bumblebee numbers with more natural habitat at large scales, though this was not significant (Steffan-Dewenter et al., 2002) . There was also no relationship between wild bee visitation and proportion of natural habitat around watermelon crops across Pennsylvania and California, with the suggestion that other features in the farming landscape can provide bee habitat which can mitigate loss of semi-natural areas (Winfree et al., 2007). Bumblebees also have relatively large home ranges (M. Knight et al., 2005; Osborne et al., 2008) which could account for their insensitivity to natural habitat within 1km in this study and others (Greenleaf et al., 2007).

Fly abundance was positively related to the proportion of urban areas in the surrounding environment. Some fly species are strongly associated with human activity, breeding in organic waste in refuse and compost heaps which may explain this relationship (Goulson et al., 2002). Gardens within urban areas may also provide floral resources that support pollinators (Goulson et al., 2010), though it was notable that only flies showed a relationship with urban areas in this study.

While farmers could increase the number of commercial pollinators by buying more bumblebee boxes, or keeping honeybees near to the farm, the wild pollinator management prescriptions (wild flower strips and unmowed field margins) did not increase the visitation rate of any of the pollinator groups. Increasing floral resources has been seen to boost queen numbers in some bumblebees (Lye et al., 2009), and is well known to attract large numbers of worker bumblebees (Kells et al, 2001; Carvell et al., 2007), but the link to increased pollination of nearby crops is less clear (Klein et al., 2012). The pollinator management parameters we used were self-reported from the farm managers. Many of the farms that had wild flower strips were part of supermarket schemes to boost pollinators. However, the area requirement was generally very small (~0.2 ha) and it could be far away from the crop, with farmers reporting poor germination of some seed mixes. While such actions, if successful, may contribute to the abundance of pollinators on the farm (Haaland & Bersier, 2011), they are unlikely to significantly boost the number of bees on a crop unless they encompass a sizeable area, establish to provide a flower-rich sward, and are near to the crop plant requiring pollination.

Our data suggest that flies are important pollinators of strawberries in late season. Methods to increase fly populations or those of other non-bee pollinators have rarely been studied (although see Hickman & Wratten, 1996), but there is anecdotal evidence of mango farmers positioning animal carcasses near to crops to encourage flies, suggesting they are important in other fruit systems (Barbara Gemmill-Herren *pers comm*). It would be useful to investigate in more detail the particular species involved in strawberry pollination. For example, provision of breeding habitat for flies (which might include dung heaps for many calyptrate flies or butts of stagnant water for hoverflies such as *Eristalis* sp.) would require little space and minimal maintenance.

While flies are generally assumed to be less efficient pollinators than bees, they increase overall pollination services to strawberries through their unique contribution to functional diversity; they increase the seasonal spread of pollinators and widen the range of weather conditions in which pollination can occur. Developing methods of evaluating the benefit of increasing number of species, which take into account the increase in function diversity will be important if the true contribution of species groups is to be appreciated.

2.6 Acknowledgments

The authors wish to thank the farmers and farm workers who allowed access to their land and participated in the survey. We are also grateful to Stuart Bence, Stuart Morrison, Andreia Penado, Emilie Ploquin and Bryony Wallace for their assistance in the field.

2.7 Appendix

Table S2.1

Overall number and percentage of total visits observed by different species of pollinator, and different pollinator groups, bold entries are pollinator groups used in analysis

	Raspberries		***Strawberries***	
	Visits to flowers	Percent of total visits (%)	Visits to flowers	Percent of total visits (%)
B. terrestris/B. lucorum	2502	57%	1141	46%
Of which commercial	**697**	**16%**	**706**	**29%**
Of which wild	1805	41%	441	18%
B. pascuorum	160	4%	21	1%
B. pratorum	487	11%	65	3%
B. lapidaries	131	3%	134	5%
B. hortorum	24	1%	0	0%
All wild bumblebees	**2607**	**59%**	**661**	**19%**
A. mellifera	**1029**	**23%**	**477**	**27%**
Solitary bees	15	0%	68	3%
Flies	55	1%	**561**	**23%**
Total	**4403**		**2473**	

Table S2.2

Mean and standard errors for % of class one fruit with and without pollinators, and individual fruit weight with and without pollinators, for both fruits.

	Raspberries	Mean ± S.E
% Class I	With pollinators	0.91 ± 0.03
	Pollinators excluded	0.27 ± 0.03
Weight	With pollinators (g)	4.70 ± 0.36
	Pollinators excluded (g)	3.39 ± 0.22

	Strawberries	Mean ± S.E
% Class I	With pollinators	0.77 ± 0.04
	Pollinators excluded	0.35 ± 0.05
Weight	With pollinators (g)	11.5 ± 0.49
	Pollinators excluded (g)	10.2 ± 0.45

Table S2.3

GLM (raspberries) and GLMM (strawberries) for the effect of efficiency adjusted pollinator numbers on percentage of first class fruit (binomial model) and fruit weight (Gaussian model). Models were fitted to include the dependent variables treatment (pollinators present versus pollinators excluded), and the interaction between treatment and number of pollinators observed prior to fruit formation. A significant interaction between the treatment and the adjusted number of pollinators signifies that increasing pollinator abundance has an influence on the fruit set. The interaction was significant and positive in strawberries; increasing number of pollinators increases the proportion of good quality fruits. In the case of raspberries, the interaction was not significant but the treatment effect was, therefore we can conclude that raspberry quality does depend on pollinators but the fruit set was not increased with increasing numbers of pollinators.

	Raspberries	Coefficient ± s.e.	Z/t	P=value
% Class I	Intercept	-1.42 ± 0.11	-13.1	<0.0001
	Treatment (pollinators allowed)	1.35 ± 0.13	10.28	<0.0001
	Treatment x Adj. Number of pollinators	0.00 ± 0.00	-1.21	Ns
Weight	Intercept	3.46 ± 0.49	7.07	<0.0001
	Treatment (pollinators allowed)	1.46 ± 0.69	2.11	0.0512
	Treatment x Adj. Number of pollinators	0.00 ± 0.00	-0.29	Ns

	Strawberries	Coefficient ± s.e.	Z/t	P=value
% Class I	Intercept	-0.74 ± 0.33	-2.23	0.026
	Treatment (pollinators allowed)	1.78 ± 0.17	10.43	<0.0001
	Treatment x Adj. Number of pollinators	0.04 ± 0.02	2.55	0.0109
Weight	Intercept	10.12 ± 0.80	12.56	<0.0001
	Treatment (pollinators allowed)	0.46 ± 0.66	0.69	Ns
	Treatment x Adj. Number of pollinators	0.09 ± 0.06	1.60	Ns

Table S2.4

Table showing average number of each pollinator group per transect of strawberries, data used to calculate complementarity statistic.

Average number of pollinators per transect

Time Period	C bumblebees	W bumblebees	Honeybees	Flies	Sum
1	12.6	0.8	1.6	0.0	15.0
2	5.5	1.9	1.0	1.5	9.9
3	5.5	10.8	6.4	1.0	23.6
4	6.6	10.6	9.1	3.0	29.3
5	3.1	5.2	3.1	3.9	15.3
6	1.9	1.8	1.9	19.2	24.8
Variance	11.5	17.1	8.6	43.1	
				V of the sums	45.3
				S of the variances	80.3
				Complementarity	**0.56**

Table S2.5

Table showing summary statistics for complementary values from 1,000 simulations of pollinators using the full GLMM model, and the null model with day and day squared terms removed. For each tunnel type the mean complementary statistic was lower when pollinators were generated from the full model (implying that pollinator groups did peak at different times). This difference was observable whether or not the abundances were adjusted by efficiency.

	Tunnel type	**Model**	**Mean**	**Variance**	**Wilcox statistic**	**P-value**
Pollinator abundance	Closed-sided	Full model	0.77	0.059	232183	<0.0001
		Null model	0.96	0.037		
	Open-sided	Full model	0.76	0.059	282753	<0.0001
		Null model	0.93	0.056		
Pollinator abundance adjusted by efficiency	Closed-sided	Full model	0.83	0.044	227422	<0.0001
		Null model	0.99	0.028		
	Open-sided	Full model	0.84	0.038	245408	<0.0001
		Null model	0.98	0.027		

Chapter 3

Neonicotinoid Impacts Upon Bumble Bee Colony Development Under Field Conditions

Ciaran Ellis, Kirsty Park, Dave Goulson

All fieldwork, analyses and writing were carried out by C. Ellis, with undergraduate assistance in the field. Co-authors commented on drafts of this paper.

3.1 Abstract

Previous studies linking neonicotinoid insecticides to impaired colony performance in social bees have been criticised for using doses that were unrealistic, or because bees were forced to consume contaminated food under laboratory conditions. Here we exposed colonies of the bumblebee *Bombus terrestris* to the neonicotinoid thiacloprid by placing them adjacent to recently sprayed raspberry crops (or control crops) for two weeks. Thiacloprid is routinely used as a foliar spray for horticulture and is sold in garden centres for consumer use; it is generally regarded as one of the most benign neonicotinoids for bees. Bees were free-flying at all times and thus free to choose where to forage.

Exposed colonies reached a lower final weight, produced 46% fewer reproductives, and had a 25% higher proportion of dead bees in the colony at the end of the season than colonies placed at control farms.

This is the first study to demonstrate significant impacts on free-flying bees of neonicotinoid use following normal farm practices. The observed effects on colonies in a natural setting raise concerns as to the long-term impacts of neonicotinoid use for wild bee populations surrounding farms, and knock-on impacts on pollination services both on and off farms.

3.2 Introduction

The link between neonicotinoids and the health of bee colonies remains controversial. Recent studies describe negative impacts on foraging, navigation and learning in honeybees and bumblebees, and on fecundity and colony success in bumblebees, but these have attracted criticism in some quarters because they were partly conducted in a laboratory setting, because bees were forced to consume treated food, and/or because bees were exposed to unrealistic concentrations of neonicotinoids). Nevertheless, in 2013 the European Union voted to suspend use of the three most widely used neonicotinoids (imidacloprid, thiamethoxam and clothianidin) for use as seed dressings on flowering crops for 2 years.

Relatively little attention has been paid to neonicotinoids applied as a foliar sprays such as thiacloprid. Thiacloprid has considerably lower toxicity to honeybees than some other neonicotinoids; for example the LD_{50} by topical application is 14,600 ng/bee for thiacloprid compared to 18 ng/bee for imidacloprid (Iwasa et al., 2004). As a result it has been described as “bee-safe” and hence suitable for use on flowering crops; it is widely used in horticulture and is also the predominant insecticide sold for garden use in Europe (Jeschke et al., 2011). However, spray application rates are much higher than those used in seed dressings (Goulson, 2013), and so bees can be exposed to high concentrations of thiacloprid. For example, concentrations of up to 199 µg/kg were found in pollen in honeybee hives in Germany (Genersch et al., 2010), and a mean concentration of 89.1 µg/kg of thiacloprid was found in apple pollen within honeybee hives in Poland (Pohorecka et al., 2012). Enhanced worker mortality has been found in laboratory studies when bumblebees were fed thiacloprid at the much lower concentration of 12 µg/kg (Mommaerts et al., 2010), suggesting that foliar sprays should be treated with the same caution as other neonicotinoids.

Here we present a field study designed to examine the impact of foliar applications of thiacloprid on mortality and reproduction of freely foraging bees. Thiacloprid (formulation "Calypso", Bayer Crop Science) is applied responsively to raspberries during flowering if the pest, raspberry beetle, is detected. The recommended application rate followed by farmers is 120g of active ingredient / ha in a dilute spray. Bumblebees are the main pollinators of raspberries throughout the study region (Scotland, UK) and wild bees are present in high densities during bloom (Lye et al, 2011).

Colonies of the bumblebee *B. terrestris* were placed adjacent to a raspberry crop that had been sprayed with thiacloprid in batches of six colonies per farm (five treated farms and four unsprayed control farms, see Appendix, table S3.1 and fig. S3.1). Colonies were left in situ for two weeks, and then removed from the raspberry farms and divided three per treatment between a flower-rich habitat (moorland with extensive flowering of Ericaceae, henceforth "flower-rich") and a less flower-rich site (a mix of improved grassland, amenity grassland, woodland and some ornamental gardens - henceforth "flower-poor"). Their performance was monitored for a total of eight weeks from commencement of the experiment; colonies that died during the experiment were removed and frozen, and all other nests were destructively sampled at the end of the experiment before all nests were dissected.

3.3 Material and Methods

3.3.1 Colony placement and monitoring

Commercially reared colonies of *Bombus terrestris audax* (Biobest N.V., Belgium) were obtained on 15 June 2012 and randomly assigned to treatments in a full factorial design (controls or exposed to thiacloprid, flower-poor or flower-rich habitats). There was no difference in weight between the colonies at the beginning of the experiment (week 1) (Likelihood Ratio Test location, $\chi^2 = 0.99$, d.f. =1, p=0.319; Likelihood Ratio Test treatment, $\chi^2 = 0.39$, d.f.=1, p = 0.53). Colonies were initially kept in the grounds of the University of Stirling campus in an area comprising woodland, amenity grasslands, improved pasture and ornamental gardens.

A network of raspberry farmers in Perthshire and Angus (central Scotland) were asked to take part in the study. They informed us when they were about to spray a flowering raspberry crop. Six nests were placed at the ends of the rows of raspberries, within 1m of the flowering crop, as soon as possible after spraying (between 1 and 5 days, table S3.2), and on the same day another six colonies were placed next to raspberries on a different farm that were not spraying within the next two weeks (and had not previously applied an insecticide in 2012), which served as a control site. Controls were chosen from the remaining farms and matched by size of soft fruit operation and where possible, geographical area (fig. S3.1, table S3.1). Some of the raspberries were in polytunnels, but all tunnels were open ended and/ or open sided at this time of year, and bee colonies were placed at the end of tunnels so they were not confined to the crop. Between 15th June and 5th July five batches of six nests were deployed on treated farms, and four batches of nests simultaneously placed adjacent to unsprayed raspberries on control farms (table S3.2). The numbers of control and treatment deployments for the first placement date were uneven as only two suitable control farms were available within the required geographical area, and of a similar farm size and management style to the three treatment sites. Bees in nests were allowed to forage at the farms for two weeks. After the two week exposure period colonies were removed from farms and split equally between the University campus and a site on flowering heather moorland approximately 5 km from the University. Nests from different farms were placed at least 30m apart to minimise drifting between the nests. The University campus is probably reasonably typical of lowland UK, having relatively few floral resources in July and August, while the moorland site provided extensive dense patches of flowering *Calluna vulgaris* and *Erica* spp..

Colonies were all weighed at the beginning of the experiment and weekly throughout the experiment, apart from during the exposure period at the farms when they were not disturbed for two weeks. Weighing was conducted at night to ease handling, minimise disturbance and to ensure that most bees were present in the nest. The nests were also checked for signs of poor health and 15 nests (11 treatment, 4 control) were removed from the experiment because they became heavily infested with wax moths (*Aphomia sociella*) (details in table S3.3). Wax moths are common pests of bumblebee nests and are extremely destructive, encasing the nest and any bees in a sticky web before caterpillars hatch and fed on the wax cells, pollen and nectar.

3.3.2 Dissections

At termination of the experiment nests were dissected and the following recorded: numbers of adult bees of each caste; numbers of pupae identifiable as future queens, males or workers; other pupae; empty pupal cells; numbers of dead bees. Reproductive output was calculated as the sum of queens and queen pupae plus 0.5 times the number of males and male pupae (since males are haploid).

3.3.3 Statistical analysis

All statistics analyses were conducted using the statistical software R version 2.15.1 (R Development Core Team, 2010). To assess the impact of treatment on measures of nest success, generalised linear mixed models (GLMMs) were fitted to the data using packages lme4 and MASS with farm identify as a random factor. Explanatory factors within the model were treatment, location during the post-exposure period ("flower-rich" versus "flower-poor") and the interaction between these. Response variables were number of workers and reproductive success (as described above), and number of empty pupal cells. To assess the effect of the pesticide on bee mortality, the number of dead bees within each nest was divided by the total number of bees within the nest. All models except proportion of dead bees were fitted with Poisson errors and were overdispersed and so observation-level random effects were included (Main-Donald & Braun, 2010). The response variable "proportion of dead bees" was fitted as a two vector response variable (dead bees in nest and all bees in nest) with binomial errors and the same dependent variables as the models above. The interaction term was removed from models if it was not significant at the 5% level, models were not reduced further. The effect of treatment on colony weight was analysed similarly, but using a linear mixed model with farm identity as a random factor and treatment, location and treatment*location interaction as fixed effects. Parameter significance in this case was determined using likelihood ratio tests comparing models with and without the parameter.

A Kaplan-Meier survival analysis was conducted used packages Survival and KMsurv to check for differences in colony survival and propensity to suffer from heavy wax moth infestation between treatment and control colonies.

3.4 Results

Overall, there were strong effects of both exposure and site on colony performance, with exposed colonies and those at the flower-poor site performing poorly and, for several measures of performance, there was a significant interaction between these two factors (Table 3.1, Fig. 3.1). For example, there was a significant treatment x site interaction on final colony weight (LR, Chi-square = 6.13, 1 d.f., p = 0.013); at the flower rich site the control colonies were 10% heavier than the exposed nests (mean ± s.e. of 780g ± 27.0 versus 709g ± 14.7), whereas at the flower poor site colony weights were low in both exposed and control colonies (overall mean of 701 g ± 16.6; Fig. 3.1a). Similarly, there was a significant treatment x site interaction for the reproductive output of the nests (measured as the number of new adult queens and queen pupae plus half the number of males and male pupae; Table 3.1). Overall, reproductive output was 46% lower in treated nests compared to controls (mean ± s.e. 23.9 ± 4.6 versus 13.0 ± 3.3, respectively), but the difference was more marked at the flower-rich site (Fig. 3.1b). When analysed separately, the same pattern was observed for male production, but not for queens; queen production was very low in all colonies (Fig. S3.3 d, overall mean ± s.e.; new queens = 1.66 ± 0.47, queen pupae = 3.48 ± 0.59). There were no treatment or site effects on the numbers of workers remaining in the nests at the end of the experiment (Fig. 3.1c). However, the proportion of bees within nests that were already dead at termination of the experiment had a significant treatment x site interaction (Table 3.1), with a 25% increase in proportion of dead bees in exposed nests compared to controls, and a slightly more marked difference between pesticide treatments at the flower-poor site (Fig. 3.1d) (bees that were dead before freezing are readily distinguished as they have matted fur, are often partly decayed, and are invariably located away from the comb around the periphery of the nest box, whereas live bees cluster together in the centre of the nest as the temperature drops). There was no difference in overall colony mortality, measured as the number of nests that died before the end of the experiment (n=12), between exposed and control nests (Fig. S3.2, $\chi^2 = 0.4$, d.f.=1, p=0.546). Overall more exposed colonies were infected with wax moths than control ones (n = 11 v n = 4) though the survival curves were not significantly different (Fig. S3.2, $\chi^2 = 3.8$, d.f.=1, p=0.052).

Table 3.1. Coefficients of GLMM models for colony level parameters and significance levels

Response variable	**Treatment**	**Location**[a]	**Treatment x Location**[b]	**Errors**
Colony weight (initial)	Ns	Ns	Ns	Normal
Colony weight (final)	Ns	Ns	-1.289*	Normal
Number of Bees (overall)	-0.39.	Ns	Ns	Poisson
Number of Workers	Ns	Ns	Ns	Poisson
Reproductive output	Ns	1.39**	-1.438*	Poisson
Number of Queens	Ns	Ns	Ns	Poisson
Number of Males	-0.9037*	1.28***	Ns	Poisson
Proportion of dead bees	Ns	Ns	0.36*	Binomial

a. Location compares flower-rich relative to flower-poor (positive indicates high values at the flower-rich site)

b. Treatment x location shows the treatment effect at the flower-rich site (positive indicates higher values at the flower-rich site)

Ns denotes non-significant terms. Interaction terms were removed and the model refitted if non-significant.

Other significance levels are symbolised as follows: . $P < 0.10$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

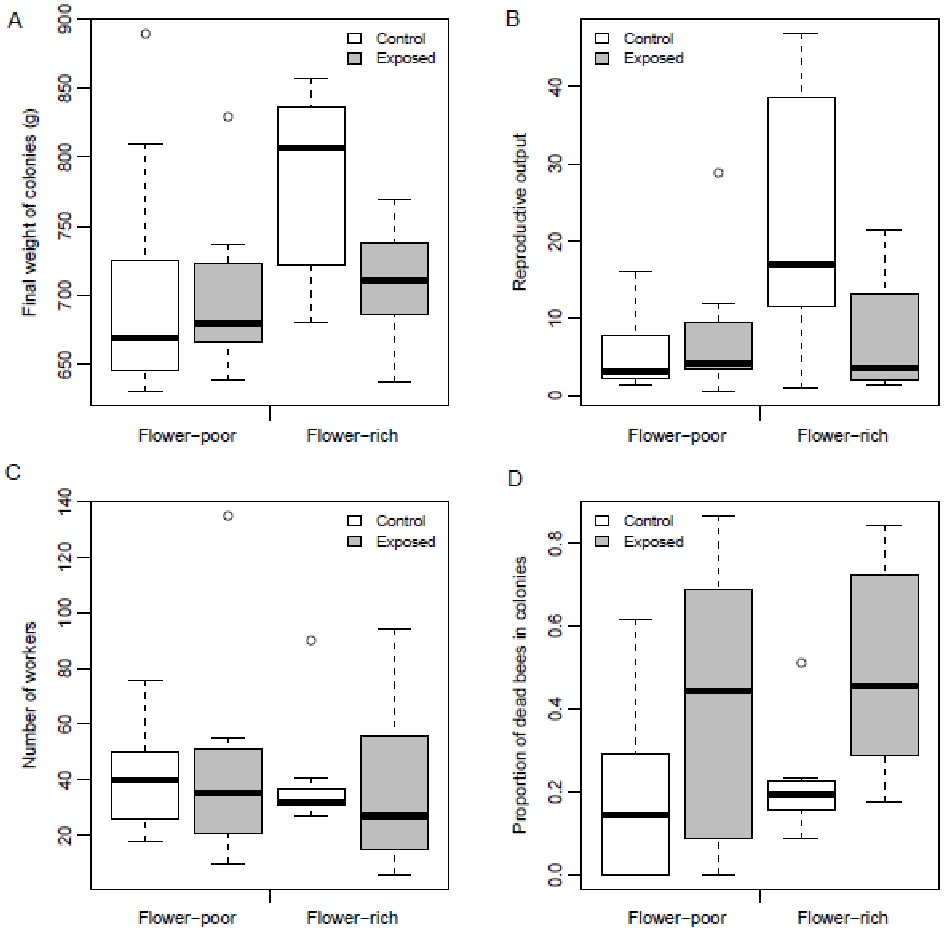

Figure 3.1. Colony effects of exposure to thiacloprid for two weeks, and of the habitat in which colonies were subsequently placed (flower-rich or flower-poor). Data are represented as medians and interquartile ranges. See also figure S3.3. A. Final weight of colonies; B. Reproductive output, measured as the number of queens plus half the number of males; C. the number of workers remaining in colonies at the end of the experiment; D. the proportion of dead bees within nests at the end of the experiment.

3.5 Discussion

This experiment is the first to study the impacts of neonicotinoids on bee colony performance where the bees were free-flying throughout, the crop was of a realistic size, and the pesticide application followed normal farming practice at working farms. The study thus mimics what would happen if a wild bumblebee nest were situated close to a commercial raspberry crop, or when commercial nests are placed next to such crops. The only manipulation carried out for the experiment which was not representative of the real world was the moving of the nests; normally, nests would be exposed to the treated crop for longer than two weeks, and might be subject to further pesticide applications. They would also be present when the crops were actually sprayed, rather than being placed next to crops after spraying. As our sites were working farms, we could not always anticipate when a farm would use thiacloprid and so colonies were exposed to thiacloprid up to 4 days after the spray day (Table S3.2), which again would reduce the expected exposure relative to naturally occurring nests. Thus our study is likely to underestimate impacts of exposure to thiacloprid.

Our study builds on evidence of the impacts of neonicotinoids on bumblebees gained in laboratory and semi-field settings. By monitoring bees which were free to forage either on the crop or elsewhere we can better infer the impacts of neonicotinoids on colonies in natural settings. However we cannot be sure that control nests were not also exposed to neonicotinoids by foragers travelling to nearby farms; although the average foraging distance of bees is modest in rewarding landscapes (~750m; Carvell et al., 2012), foragers can travel considerable distances (M. Knight et al., 2005; Osborne et al., 2008; Hagen et al., 2011). Soft-fruit farms can be considered "rewarding" landscapes particularly as raspberries are extremely attractive to bees, with high densities of wild bumblebees recorded on raspberries plants within the study region (Lye et al., 2011). Farms were matched for size and management type, and all study fields were located within mixed farmland, so differences in background exposure between treatment and control farms are likely to be minimal. Once again, any such exposure would also be experienced by wild bumblebee nests in this landscape.

The results of the study are the first to show colony-level effects of neonicotinoids on bees in a free-flying setting. A study monitoring foraging honeybees exposed to thiacloprid in polythene tunnels found a drop in foraging activity after thiacloprid was sprayed, but this did not lead to hive level effects (Schmuck et al., 2003). It has, however, been noted that the power to detect differences in this study was low due to a small number of replicates (Cresswell, 2011). In addition, honeybee hives may be expected to be more resilient to short-term perturbations than bumblebee nests, as honeybees nests typically hold over 20,000 workers, compared to perhaps 50 to 200 in bumblebee nests.

While thiacloprid has a lower LD_{50} than other neonicotinoids when tested on bees in isolation, there is evidence that it is particularly potent when combined with other stressors (Iwasa et al., 2004; Vidau et al., 2011). Such an environment is likely to be the norm for free-flying bees; 97.3% of samples from wax, pollen and bee bread from North American honeybees contained two of more pesticides (Mullin et al., 2010). Additional stressors including fungicides and parasites can increase the potency of thiacloprid dramatically; a laboratory study that exposed honeybees to thiacloprid and the commonly-used plant fungicide triflumizole found that this compound increased the potency of thiacloprid by 1,141 fold, decreasing the LD_{50} to 12.8 ng/bee (Iwasa et al., 2004). Honeybees exposed to doses of thiacloprid of 1/100th of the LD_{50} died more quickly when infected with the protozoan parasite *Nosema ceranae* than those with the parasite alone (Vidau et al., 2011).

It is notable that all nests produced few queens. A similar study using the same "flower-poor" site in 2011 recorded a mean of ~14 queens per control nest (Whitehorn et al., 2012), but the weather in the summer of 2012 was the wettest in the UK for 100 years (Met Office, 2012), which may account for this difference. Our nests were also subject to the dual disturbance of movement to and from the raspberry farms, which might have impaired their performance compared to those in Whitehorn et al. (2012).

We did not investigate the mechanisms by which thiacloprid reduced colony performance in our study, but previous studies on other neonicotinoids may shed light on this. Exposure to thiamethoxam was found to impair navigation in honeybees (Henry et al., 2012), while exposure to imidacloprid has been found to reduce pollen collection (Gill et al., 2012; Feltham et al., 2014) and reduce egg laying (Laycock et al., 2012). Our finding that the effects of pesticide exposure were more pronounced at the 'flower-rich' site may be because, despite very poor weather in the study year, the control colonies were able to gather sufficient food and hence performed relatively well, while the treated colonies performed poorly because they were unable to efficiently harvest these resources. Whereas in the flower-poor site even bees which had not been exposed to pesticides where unable to forage sufficiently to maintain a colony, so the difference between treatment and control could not be observed here. In addition to any impairment in foraging ability, the increased within-nest mortality will have further reduced the capacity of the colonies to gather food by reducing the work force.

The current study adds to the growing literature highlighting the detrimental effects of neonicotinoids, and is the first study to find effects on freely foraging bees. It also shows that types of neonicotinoids regarded as "bee safe" because of their relatively low toxicity are used at concentration that can harm bumblebees foraging freely. It raises concerns as to the long-term impacts of such use on wild bee populations and the pollination services they provide in fruit-growing areas. The wisdom of allowing thiacloprid to be freely sold for use on flowers by gardeners must also now be questioned.

3.6 Acknowledgments

The authors are grateful to the farmers and landowners for their participation in this study. We also wish to thank Jim Struthers, Stuart Bence and Paul Taylor for assistance at sites; Alistair Hall, Christopher Coates and Allan Drewette for help with bee- handling; Sienna Gray, Ben Conlon, Madalyn Watkins, Andreia Penado and Karlien Gootzen, for assistance with dissections and Stephanie O'Connor for advice.

3.7 Appendix

Table S3.1

Farm site details

Placement Group	Area of soft-fruit grown (ha)	Placement Date
A	80	15th June
A	85	15th June
A	85	15th June
A	40	15th June
A	80	15th June
B	7	3rd July
B	9	3rd July
C	65	6th July
C	65	6th July

Table S3.2

Details of treatment farms within each placement group, in placement group A there were three treatment sites, and one treatment and one control site in each of groups B and C.

Placement Group	Treatment	Spray date	Placement date
AT1	Thiacloprid	11th June	15th June
AT2	Thiacloprid	13th June	15th June
AT3	Thiacloprid	11th June	15th June
BT	Thiacloprid	2nd July	3rd July
CT	Thiacloprid	6th July	6th July

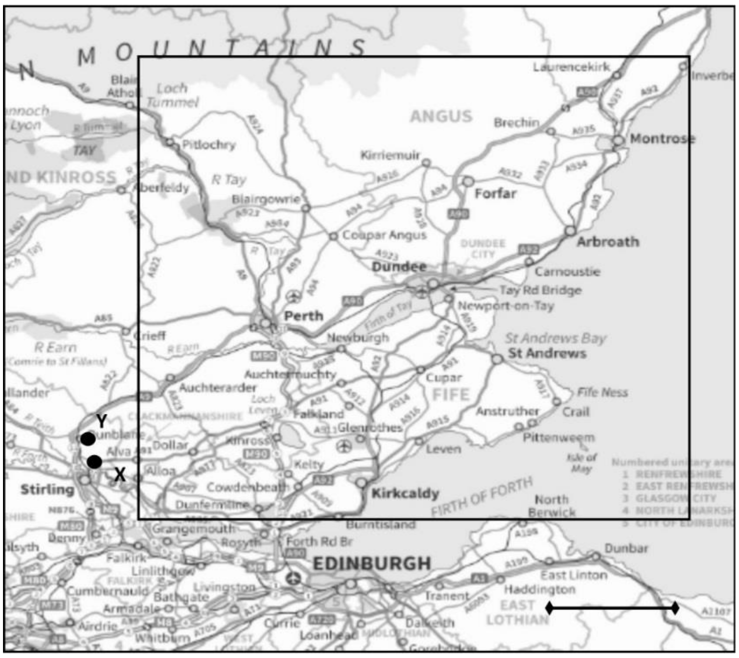

Figure S3.1

Map showing study area in East Scotland. All farm-sites were within the boxed area. X and Y show the locations of the flower-poor and flower-rich post exposure locations respectively.

Table S3.3

Details of removals from experiment due to early death and wax moth infestation, T and C refer to whether the removed colony was from a treatment site or a control site respectively.

	Removal time (day)	**No. dead colonies**	**No. wax moth infested**
13/07/2012	28	2 (T, C)	3 (T, T, T)
18/07/2012	33		2 (T, C)
20/07/2012	35	5 (T, T, T, T, C)	1 (T)
24/07/2012	39		8 (T, T, T, C, C, C)
27/07/2012	42		1 (T)
02/08/2012	48	5 (T, C, C, C, C)	

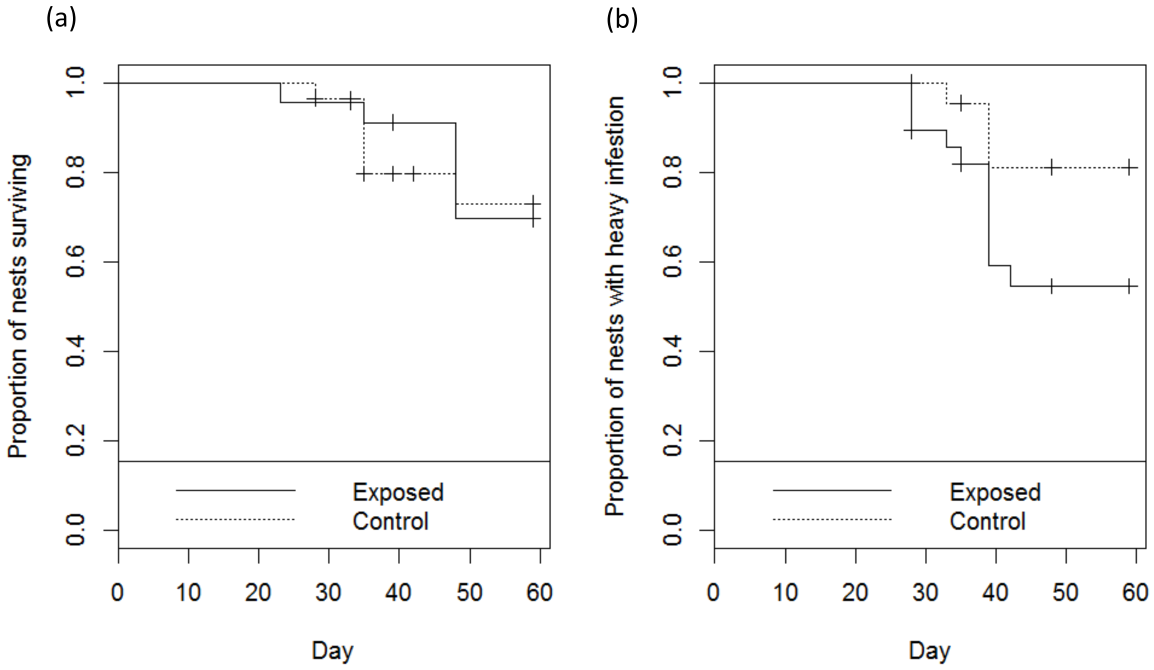

Figure S3.2

Kaplan-Meier survival curves based on a) proportion of colonies not removed from the experiment due to early death b) proportion of colonies not removed from the experiment due to heavy wax moth infestation. The proportion of surviving colonies was not significantly different between the exposed and control colonies $\chi^2= 0.4$, d.f.=1, p=0.546. While more exposed colonies were infected with wax moths than control colonies (11 infected exposed colonies vs 4 infected control colonies), the difference between the curves was not significant; $\chi^2= 3.8$, d.f.=1, p=0.052.

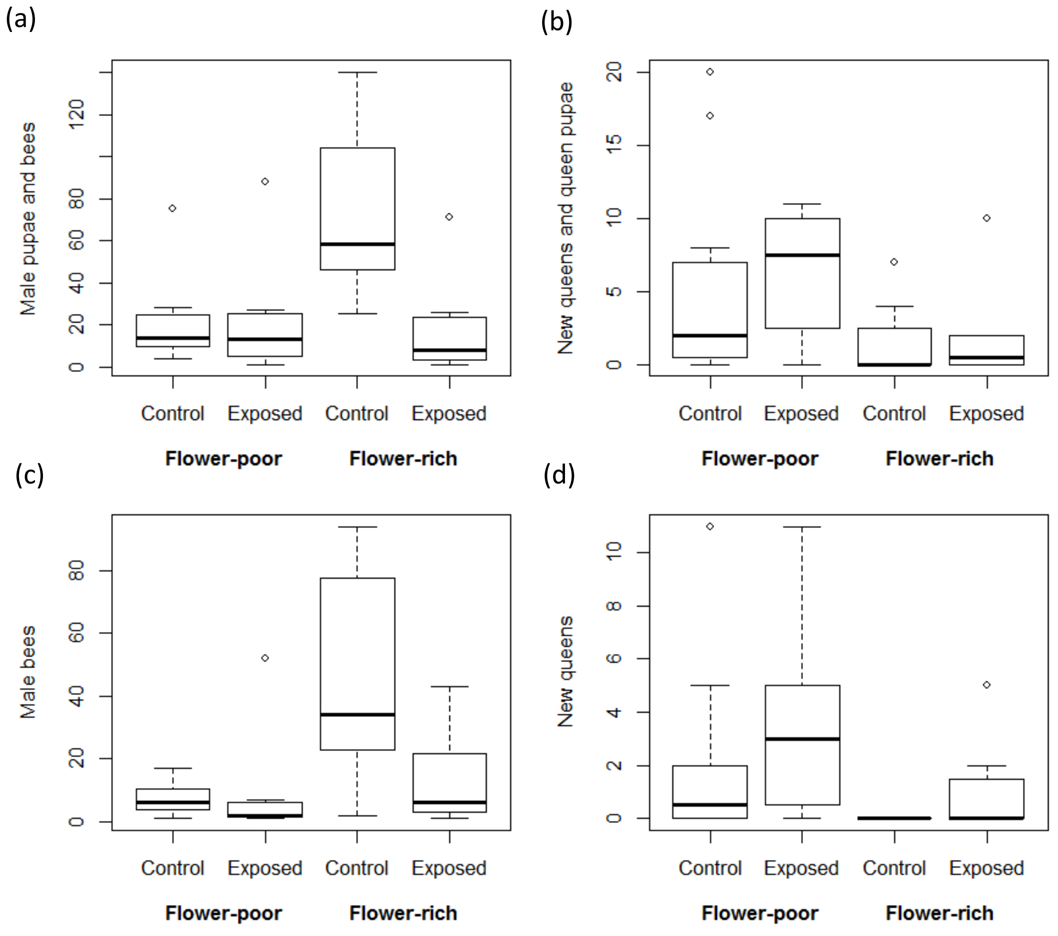

Figure S3.3

Effects of exposure to thiacloprid for two weeks, and of the habitat in which colonies were subsequently placed (flower-rich or flower-poor) on a) Number of male pupae and male bees combined; b) Number of queen pupae and new queens combined; c) the number of male bees remaining in colonies at the end of the experiment; d) the number of new queens remaining in the colonies at the end of the experiment.

Chapter 4

Does commercial bee use mask declines in wild pollinators?

A version of this paper is available as a working paper of the same name by the authors A. Kleczkowski, C. Ellis, F. De Vries, N. Hanley and D. Goulson. The abstract, introduction and discussion of the working paper were written by C. Ellis and the original analysis was carried out by A. Kleczkowski. This version includes a new model and analysis developed by C. Ellis in light of reviewer comments on the working paper and has been written by C. Ellis.

4.1 Abstract

Production of insect-pollinated crops relies on both pesticide use and pollination leading to a conflict between these two inputs. In this paper we combine ecological modelling with economic analysis of a single farm output to show that increases in pesticide use can lead to declines in wild bee populations around the farm. A decline can lead to a local extinction if commercial bees are used as they mask the decrease in pollination services which would otherwise incentivise conserving the pollinator population. Thus we demonstrate the importance of combining ecological modelling with economics to study the provision of ecosystem services and to inform sustainable management of ecosystem service providers.

4.2 Introduction

Globally, 35% of food crops are at least partly dependent on insect pollination (Klein et al., 2007). Ensuring sufficient pollination of these crops will be challenging in the future. The fraction of agriculture made up by insect-pollinated crops is increasing (Aizen & Harder, 2009), while wild pollinator populations are threatened by both habitat loss (Winfree et al., 2009) and agricultural intensification; thought to be the main causes of reported declines in diversity in the EU and range in the USA (Biesmeijer et al., 2006, Cameron et al., 2011).

Honeybees are used to supplement or substitute wild pollinators, along with other commercial pollinators such as laboratory breed bumblebees (Velthuis & Van Doorn, 2006). While commercial pollinators are often assumed to be adequate substitutes for wild pollinators (though see Brittain et al., 2013a; Hoehn et al., 2008), the use of commercial pollinators is itself not without risk. Honeybees have suffered losses in recent years due to the abandonment of hives (Colony Collapse Disorder) and the *Varroa* mite (Cox-Foster et al., 2007). If losses of honeybees occur over a wide area, there can be an impact on the supply of these insects for pollination services, which can lead to price rises. Relying on commercial pollinators such as honeybees puts farmers at risk from these supply shocks, with consequent implications for farm profits over time.

Given the risks associated with reliance on commercial pollination sources, maintaining viable wild pollinator populations is likely to be crucial for sustaining the production of insect-pollinated crops into the future (Winfree et al., 2007). The potential costs of the loss of local pollination services is illustrated by the need for pollination by farm workers in Sichuan, China, following the loss of insect populations in this area (Partap et al., 2001). Whilst hand pollination was a viable option when wages were cheap, a 10--fold rise in wages over the last 10 years has led to the abandonment of apple production as pollination is no longer affordable (Partap & Tang, 2012). One of the factors implicated in the reduction of pollinators in this area and in declines elsewhere, is the use of pesticides, or specifically, insecticides. There is growing evidence of negative effects of realistic levels of commonly used insecticides on population determining traits such as reproductive rates, foraging rates and navigation in bees (Mommaerts et al., 2010; Henry et al., 2012; Whitehorn et al., 2012; Goulson, 2013). Awareness of this evidence has led to the temporary banning of a widely used group of insecticides -- neonicotinoids -- within the European Union. Farmers of insect pollinated crops therefore face a dilemma as one essential input (pesticides) is potentially dangerous to another (pollinators). As abstaining from the use of particular pesticides is not usually possible without sacrificing yields dramatically, farmers must either attempt to reduce the impact of pesticides on flying pollinators, or increase the use of commercial pollinators, as these can in some cases be replenished year after year. If the latter strategy is taken, wild bees may decline without any immediate commercial consequences, which removes the option of using wild pollinators in the future as well as potentially reducing the resilience of the wider pollinator population.

Wild pollinators require habitat either off-farm or within the farm area. Although pollinating insects can forage for large distances, in intensive agricultural landscapes there is a decay in visitation of flowers by pollinators with increasing distance from the nearest habitat patch (Ricketts et al., 2008). To offset this, farmers can encourage wild bees to nest within foraging distance of flowers by providing nesting habitat and providing alternative foraging resources on the farm for when the crop is not in flower. The effect of such interventions has been found to be strongest in intensively farmed areas, whereas in areas of more diffuse farmland bees may already have opportunities for nesting and alternative forage (Carvell et al., 2011). Hence local or field-scale management practices may offset the negative impacts of intensive monoculture agriculture on pollination services to some extent (Kennedy et al., 2013). That said, habitat provision must be of a sufficient size to support pollinators and therefore may be at the expense of planting for agriculture to be successful.

Other authors have investigated the optimal amount and positioning of habitat patches within farmland incorporating a trade-off between land-use for crops and land-use for habitat. Brosi et al. (2008) focused on the relationship between dispersal distance and reproductive dispersal by modelling optimal nesting site placement on linear farms and found that patches had to be of a particular size to sustain a local population, though optimal habitat configuration depended on the specific parameters used. Keitt (2009) also used a spatially explicit model to relate patterns of habitat to persistence of wild pollinators but included stochastic parameters for nest growth and pollination. It was found that there were critical levels of habitat required to prevent local extinction of pollinators, and that the cusp at which extinction occurred was difficult to predict (Keitt, 2009). These models lack realism in a number of areas not least as farmers could not use commercial pollinators, thus over emphasising the importance of wild bees to private production, particularly when pesticides are also used. We also consider a variably converted farm area, though in this case we investigate the outcomes in terms of profits and wild bee populations when pesticides are used and there is the option to use commercial bees. The option to use commercial bees reduces the incentive to provide natural habitat and as we show, can mask declines in wild bees.

We use an ecological-economic model to investigate the relations between two essential inputs, pollination and pesticides, and two sources of pollinators with different characteristics; commercial pollinators, which can be replaced at a cost, and wild pollinators, which rely on a population being sustained within the farm area. The model is parameterised using farm management data for strawberries, a relatively well-studied crop on which both wild and commercial bees are used, as well as the neonicotinoid pesticide thiacloprid which protects the crop from destructive pests such as capsid bugs. The conclusions, however, are generalizable to other systems where conflict occurs between pesticides, crop area and wild bee persistence. Our model differs from previous modelling attempts which have looked at either habitat considerations (Brosi et al, 2008; Keitt 2009) or pesticide impacts (Bryden et al, 2013) in isolation by combining these in a realistically parameterised model.

We find that the use of commercial bees does mask wild bumblebee declines due to pesticides, and this causes yields to drop after years of stable yields if commercial bees are also sensitive to pesticides. This relationship changes the optimal habitat management from as little on-farm habitat as possible, to moderate levels of on-farm habitat. While the specific trade-offs will be particular to various crop systems, the lack of predictability of such effects should lead to prudent management approaches and may require incentives or other structures to ensure outcomes which are optimal in the long-run.

4.3 Model description

4.3.1 Overview

The results are based on a simulation model which updates the number of wild bees foraging (wB) each year and combines this with the number of commercial bees (cB) each year to calculate soft fruit yield (Y) and hence farm profits (P). Honeybees and commercially reared bumblebees are both used in fruit production. For simplicity we consider all commercial pollinators to have the characteristics of commercially reared bumblebees (in terms of nest size and pollinating efficiency) and we generate results for both the scenario where commercial pollinators are affected by pesticides, and the scenario where wild bees are affected but not commercial ones. The actual situation may be that commercial pollinators are affected, but to a slightly lesser extent than wild bees; efforts can be made to minimise chemical exposure to commercial nests such as shutting the bees inside the boxes before spraying, or only spraying before the placement of nest boxes. Wild nests, on the other hand, may be exposed to multiple sprays of insecticides and though both wild and commercial bumblebee nests are vulnerable to disease, wild nests are more likely to have infestations of parasites at the time spraying occurs (commercial bee boxes *should* arrive at the farms free from disease and therefore only pick up infections and parasites from that point onwards) putting them at increased risk of any interactive effects between parasites and pesticides (Alaux et al., 2010).

4.3.2 Initialisation

Before the simulation begins the total farm area (A) is set to 100 ha. Of the total size, the percentage assigned to bee habitat (v) is simulated to be between 0% and 70%. Crop size is taken to be 1 – vA. Commercial bumblebee use (C) is set to 1 or 0.

4.3.3 Wild bee dynamics

Numbers of wild bee nests (N) on the farm in each year (t) are calculated using an equation which allows nest density to increase by a factor of R (the reproductive rate) up to a maximum K (carrying capacity) (equations 1 and 2). Number of dead nests each year (D) is driven by a stochastic process, with the probability of death related to the number of foragers within the nests in a given year (equation 3).

Equation 1: $N_{[t]} = \min((N_{[t-1]} - D_{[t-1]}) \times R, K)$

K is calculated from the likely on-farm nesting densities of wild bumblebees. Nest densities will depend on the landscape type; around 11 to 15 nests per ha were found in non-linear countryside in a large scale survey in UK habitats, with higher densities in gardens and around linear features (Osborne et al., 2008). While actual densities will vary between locations, we assume that densities of 15 nests per ha can be found in on-farm habitat and assume that no nesting can occur within the cropped area, total carrying capacity is therefore calculated simply as:

Equation 2: $K = 15 \times vA$

Not all bumblebee nests will produce queens in a given year, and the likelihood of reproduction will depend in part on nest size. Pesticides can indirectly impact the likelihood of a nest reproducing by impairing the performance of foragers or increasing worker mortality and thus decreasing a nests ability to gather and process resources. These impacts can lead to increased colony failure either through early colony death or by limiting the number of new queens produced (Gill et al, 2012; Whitehorn et al., 2012). Nest success after exposure to pesticides has been found to fit a stochastic model of colony death; nests treated with imidacloprid were found to develop as predicted by a model where the probability of nest death was inversely proportion to number of foragers adjusted for pesticide impairments (Bryden et al., 2013). In our model nests fail according to the same equation (equation 3) with $\mu = 55$ and $\Phi = 40$. It is estimated that in each nest there will be 100 foragers ($F = 100$). And 20% of workers will be actively foraging at any moment ($W = 0.2$). The number foraging are reduced by impairment (I) through equation 4. I differs for wild bees and commercial bees (the factors are designated wI and cI respectively) and overall numbers of commercial bees cB depends on the crop area and the stocking density (cS). The number of nests dying each year $D_{[t]}$ is generated through a stochastic process with the probability of nest failure $d_{[t]}$.

Equation 3: $d_{[t]} = \mu/(\mathrm{Forageswbt} + \Phi)$

Equation 4: $wB_{[t]} = N_{[t]} \text{ x } F \text{ x } wI \text{ x } W$

$cB = C \text{ x } (1 - vA) \text{ x } cS \text{ x } F \text{ x } cI \text{ x } W$

Pesticides can impact both commercial bees as well as wild bees by impairing forager performance; pesticides have been found to affect the navigation of honeybees reducing the number of foragers which successfully return to the nest (Henry et al., 2012). While these effects will impact overall nest or hive death rates, it is not assumed to affect the ability of the farmer to hire or purchase commercial bees in the subsequent years. However there is some evidence that decreased supply due to disease outbreaks over years may affect the hiring price of honeybees over time (Burgett et al., 2010).

4.3.4 Model flow

The model runs through the following seasonal cycle:

1) Nest reproduction

Wild bee nest numbers change each year according to the equation 1.

2) Forager number calculation

Total forager numbers are calculated for wild bees and commercial bees and adjusted for impairment by pesticides by equation 4. The total pollinators per farm area are calculated by totally the forager numbers across the wild and commercial nests; $B_{[t]} = (wB_{[t]} + cB) \div A$.

3) Pollination

The number of foragers per ha at each time period ($B_{[t]}$) is then used to calculate the yield through equation 5. Equation 5 assumes that without pollinators there is a set but low proportion of potential total yield (minY), and that forager number has an incremental effect on overall yield within an area up to a limit, above which additional pollinators have no further impact. The equation is parameterised approximately using the maximum proportion of good quality fruits found in the experiments in Chapter 2 ($\S = 0.9$), the proportion of good quality fruits without bees ($\alpha = 0.35$) and the incremental effect of bee visitation ($\beta = 0.0024$). Y_{Max} is taken as the yield per ha for strawberries reported in the Farm Business Survey 2011 (Nix, 2014).

Equation 5: $Y_{[t]} = Y_{Max} \times \min(\S, \alpha + \beta \times B_{[t]})$

4) Cost calculation

Total costs for each year (TC[t]) are the sum of variable (yield dependent) costs and fixed costs including costs of seeds, pesticides and commercial bees and other inputs. Costs of seeds, pesticides and bumblebee boxes are taken from a farm survey of 25 soft-fruit farms in Scotland, the survey was undertaken as background research for the field study in Chapter 2. The cost of sowing a wild flower area is taken to be £100 per ha, and costs of pesticide per ha are taken to be £10. Bumblebee boxes are assumed to cost £30. Other production costs and prices per ha (p) are taken from farm management data from the Farm Business Survey 2011 (Nix, 2014). Fixed costs are split between those attributable to the crop area, and those attributable to the whole farm. Harvesting and packaging costs are assumed to be variable and calculated per tonne. Commission (cm) is applied at 9% of the total sales (Nix, 2014).

5) Profit calculation

Profit is then calculated via equation 6.

Equation 6: $$P[t] = Y[t] \text{ x } (1 - vA) \text{ x } p \text{ x } (1\text{-}cm) - CT[t]$$

6) Nest death

At the end of each year, nests death occurs with the probability calculated in equation 3. Finally overall yield, nest number and profits are calculated.

4.3.5 Summary of model runs

The model was run first with no commercial bee use and no impact of pesticide use (run 1) then different impacts of pesticide use on wild bees were investigated (wI = 0.6 to 1) (run 2). In run 3 commercial bees were used at industry recommended densities (6 per ha in fruit-growing area) and a pesticide impact (wI) of 0.67 was applied. In run 4 commercial bees were again used and this time commercial bees were affected to the same extent as wild bees (wI = cI = 0.67).

Table 4.1 Summary of model runs

Run number	*Commercial bees used?*	*Wild bees affected by pesticides?*	*Impairment (wild bees)*	*C. bees affected by pesticides?*	*Impairment (C. bees)*
1	No	No	NA	No	NA
2	No	Yes	Range 0.6 to 1	No	NA
3	Yes	Yes	0.67	No	NA
4	Yes	Yes	0.67	Yes	0.67

4.4 Results

When no commercial bees are used, profits are negative without on-farm habitat, and peak at low-moderate levels of on-farm habitat

In runs where no commercial bees were used, pollination was provided by wild bees only. If pesticides had no impact (run 1), profits were stable over time and peaked when on-farm habitat proportion was 20% (fig. 4.1). Profits were negative when there was no area of the farm used for habitat and peaked when habitat took up 20% of farm area (fig. 4.1). Profits depend on revenues made from the crop area balanced against those lost through providing habitat rather than growing crops on the remaining area.

When no commercial bees are used and bumblebees are impacted by pesticides, profits are lower and peak profits occur at higher level of on-farm habitat

Profits declined over time when wild bees were affected by pesticides (wI = 0.67) (fig. 4.2a) as the number of foraging bees declined over time (fig. 4.2b). Overall profits were lower than in the situation without pesticide impacts (fig. 4.2a). The optimal percentage of on-farm habitat was 50% in this scenario, higher than when there was no impact of pesticides on wild bees, as more nests (and therefore more habitat) are required to make up for the impairment of foragers. The optimal amount of on-farm habitat required also changed over time as nest numbers declined; by ~20 years into the projection, 60% on-farm habitat provided the highest yield (fig. 4.2a).

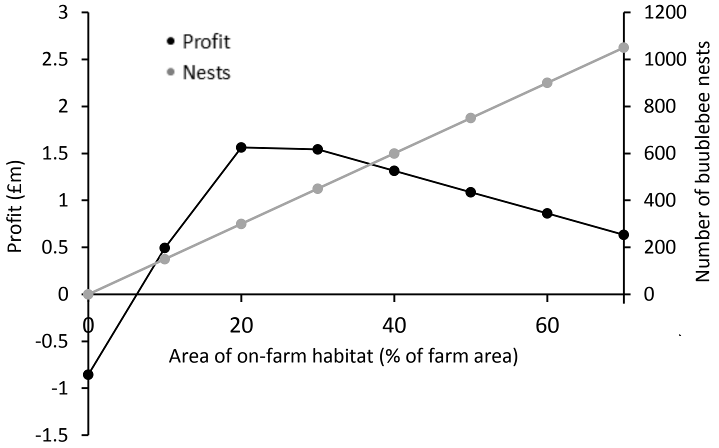

Figure 4.1. Expected profits and the number of bumblebee nests when wild bees alone are used and pesticides have no effect on bees. The number of wild bumblebee nests increases with increasing proportion of on-farm habitat but where stable throughout the projection period. When no on-farm habitat is provided yields are limited by the lack of pollination and farms make a loss. Profits peak when 20% of farm area is used as habitat. At this point the benefits of having the bees around to pollinate outweighs the cost of seeds and income lost from no using that area for growing fruit.

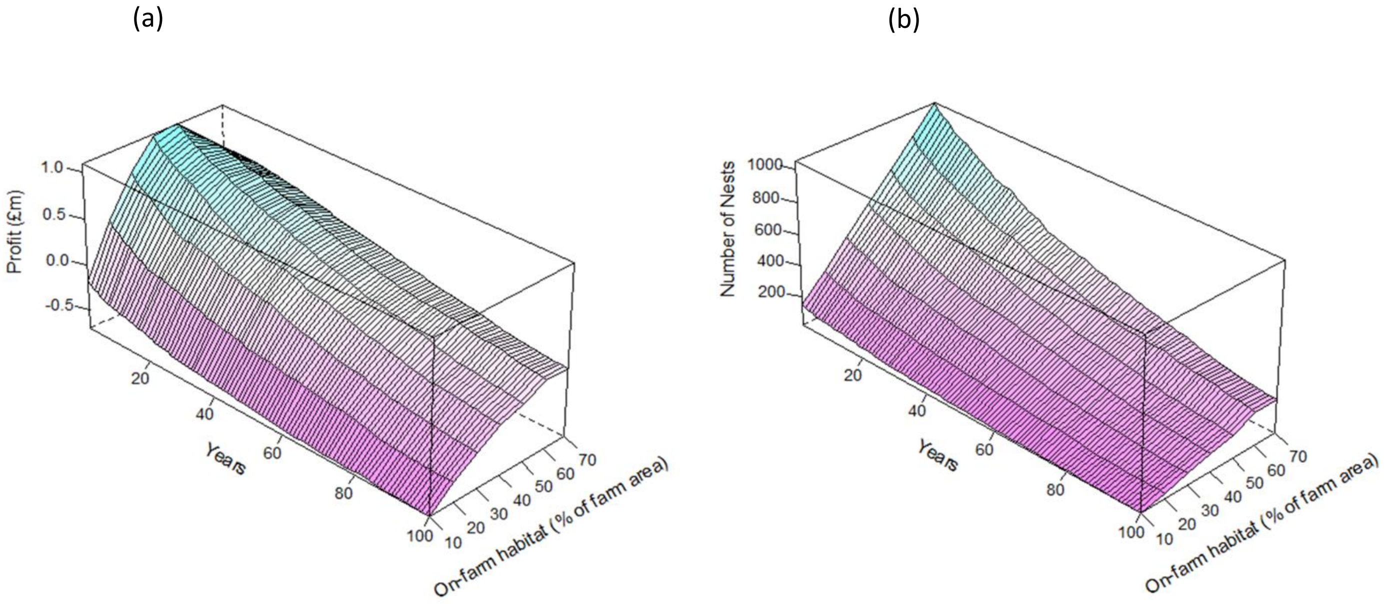

Figure 4.2. (a) Expected profits and (b) nest numbers when wild bees alone are used and wild bees are affected by pesticides. The numbers of bumblebee nests and profits both decrease over time at all levels of on-farm habitat. Profits are lower overall than when wild bees were unaffected by pesticides and higher levels of on-farm habitat are required for maximum profits.

The speed at which wild bumblebees decline depends on the balance of nest death relative to nest reproduction

When wild bees are used alone, the likelihood of wild bumblebee decline depended on the relationship between the impairment of foragers (and hence nest survival) and the reproductive capacity of the surviving nests each year (fig. 4.3). We have used a parameter of R = 4 as the maximum number of new nests founded by an old nest. With an impairment factor of 0.7, the probability of nest death was 79%, leaving 21% of nests on average, to reproduce. At this level nest reproductive on average is not high enough to replace the nests lost, and so wild bee nest numbers declined within 100 years.

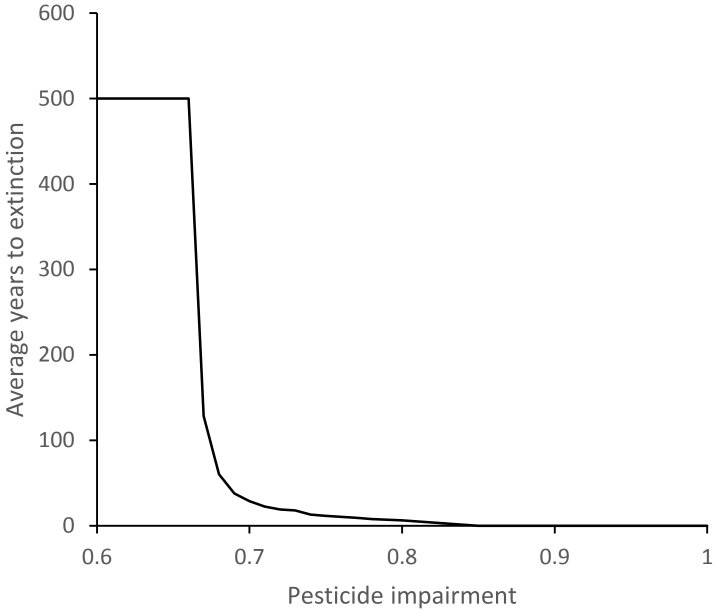

Figure 4.3. The transition from persistence to extinction occurs over a very small range of values, numbers of nest decline when the impairment factor is above 0.66 as above this number the probability of nest death > 0.75 (the threshold at which a birth rate of (R) 4 allows replacement of lost nests. By 0.7 the probability of nest death is 0.79 and the average number of years to extinction is just 29.

When commercial bees are used (and unaffected by pesticides), profits remain stable despite declines in wild bees, and are highest when on-farm habitat is low

Profits are higher when commercial bees are used at the same time as wild bees than when wild bees are used on their own. Profits remained stable throughout the projection period. Profits were stable whether wild bee nests declined or not (fig. 4.4a and b), with highest yields when no farm area is set aside for habitat.

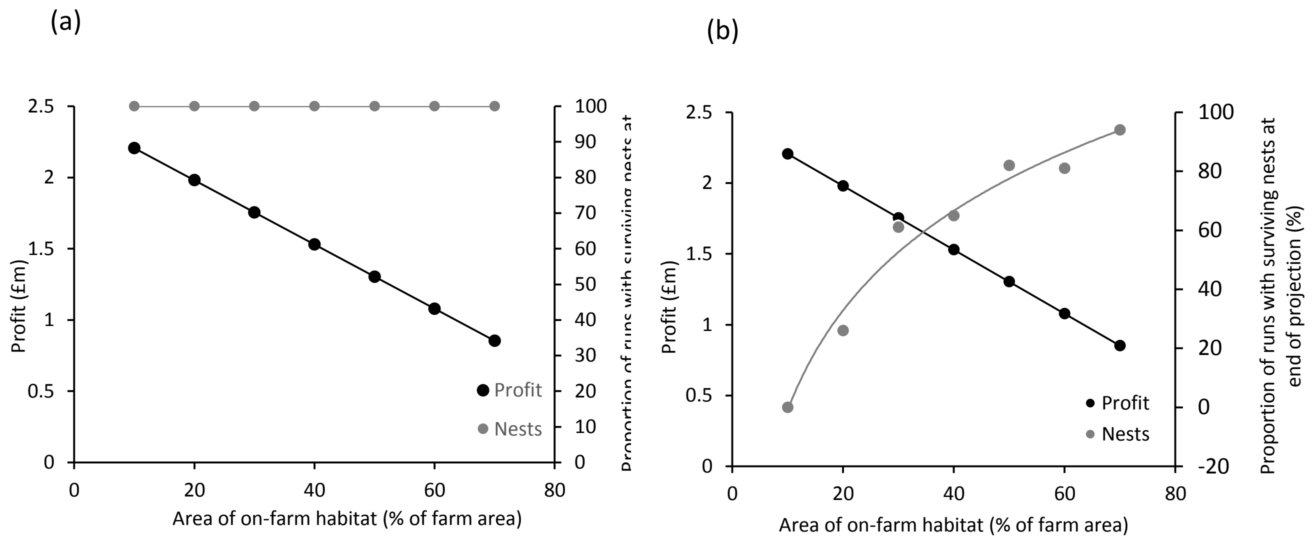

Figure 4.4. Profit and number of wild bumblebee nests by the percentage of on-farm habitat when commercial bumblebees are used. The impact of pesticides on wild bees was set to: a). wI = 0.60, b). wI = 0.67, with no effect on commercial bees. In both cases profit is identical despite wild bee numbers declining in (b). The loss of wild bumblebees has no effect on profits, therefore the optimal economic strategy when commercial bees are not affected by pesticides is to have as little on-farm habitat as possible (b).

When commercial bees are used and both these and wild bees are affected by pesticides, profits decline over time, however when the level of on-farm habitat is high, declines are not observable until after a time lag.

When both commercial foragers and wild foragers were impaired by pesticides (run 4), profits were lower than in when wild bees only were affected (run 3) and declined throughout the projection period. As in run 3, profits were highest when on-farm habitat percentages were low as crops could be pollinated without wild bees in the presence of commercial bees. Profits did however, decline throughout the projection period as the reduced number of commercial bee foragers could not provide the entire pollination service, leaving crops vulnerable to pollinator decline. Interestingly, at percentages of on-farm habitat higher than 30%, no (or very little) reduction in profit was observation before around year 20, but profits had dropped by the end of the projection period (fig. 4.5a). With higher levels of on-farm habitat, there were more wild bees per area of crop, and so there is a period where farms are over supplied with pollinators. This continues until the wild bee population drops to a level at which pollination services are limited, at which point profits begin to drop (fig. 4.5b).

The mean period of time before the decline in bees is observable varies with areas of on-farm habitat, as is as highest when habitat percentage was highest (mean time before a decline in profit = 43 years at 70% habitat, table 4.2).

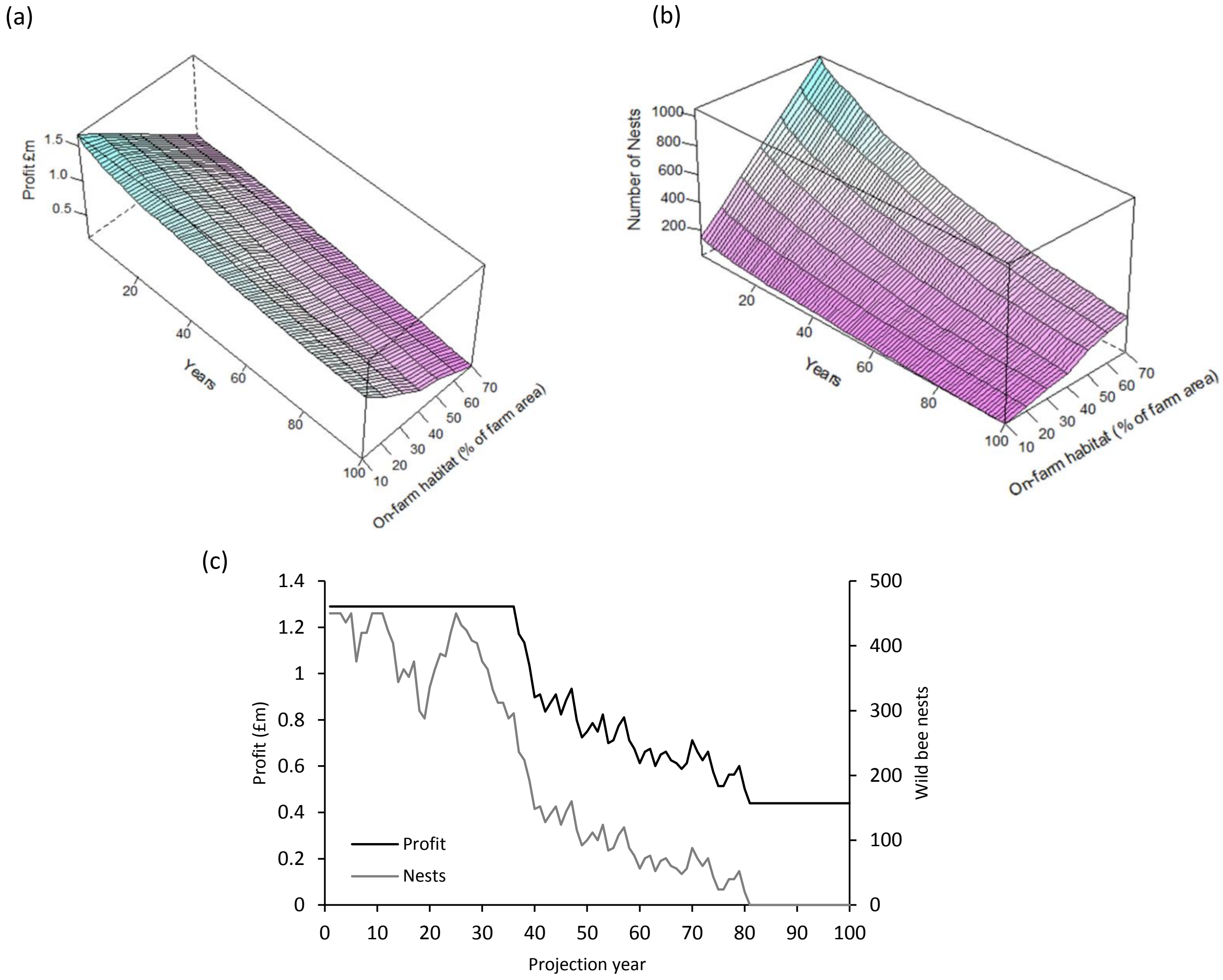

Figure 4.5. If commercial bees are used and both wild bees and commercial bees are affected by pesticides, profits are higher at lower setaside proportions, but there is a decline over time. (a) At higher levels of on farm habitat, profits are maintained over the shorter term (~20 years) and then decline, while the decline in wild bumblebee nests occurs even in the short term (b). Therefore the decline in profit is not evident until the number of wild bumblebees has already fallen. (c) shows one run from run 4; profits are maintained in the short term while bumblebee nest numbers fall. This is compared to other management options in figure 4.6.

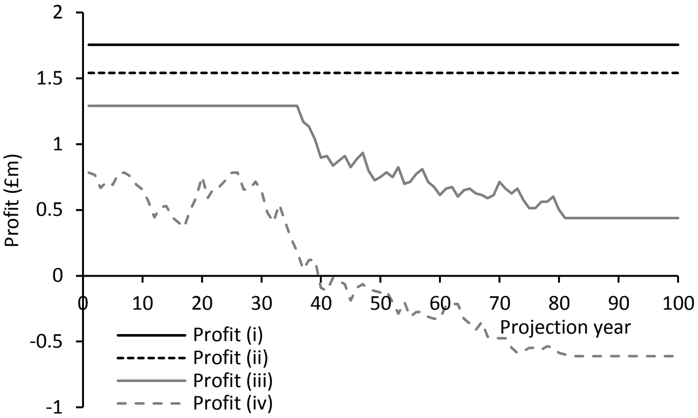

Figure 4.6. Shows profit changes over the projection period for (i) commercial bees used and wild bees with an impact on wild bees ii) commercial bees not used and no effect on wild bees iii) commercial bees used and wild bees with an impact on both iv) wild bees used alone with pesticide impacts. This illustrates the difference in certainty offered by the various management options, in case iii) profits may be high for a number of years before falling when the number of overall bees declined to the point where yield is affected.

Table 4.2: Average number of years of stable profits before a decline is noticeable increases with the amount of on-farm habitat provided.

Percentage on-farm habitat (%)	*Average point of decline in profit years ± s.d.*
10	1.8 ± 1.2
20	10.8 ± 6.9
30	20.8 ± 12.1
40	30.4 ± 18.2
50	34.5 ± 20.8
60	39.1 ± 20.8
70	43.2 ± 22.0

If commercial bees are unaffected by pesticides, prices would have to rise dramatically before threatening future business, while if commercial bees are affected by pesticides more modest price rises could lead to business failure

Commercial bee costs make up a small proportion of crop production costs per ha. Profits are high at all level of on-farm habitat in run 3, where commercial bumblebees are used and are not affected by pesticides. Table 4.3 shows what the costs of commercial bees would have to be (per box) for profits to fall to 0. When commercial bees are use and there are no impacts of pesticides production is not vulnerable to price rises.

When commercial bees were affected by pesticides (run 4) profits were lower and the cost of bees necessary for profits to be 0 decreased relative to run 3 though they were still very high (table 4.3).

Table 4.3: Profits under the scenario when commercial bees are not impacted by pesticides, and under the scenario where they are showing profits after year 1, and year 60*. The limit to the cost of commercial bees is shown, this is the price at which profits would become negative. As costs are currently ~£30, dramatic price rises would be required for the cost of bees to limit production.

		Cost which bees would have to be for profits to be 0.		
On-farm habitat (%)	Nests	C.bees not impacted	C.bees impacted (start of run)	C.bees impacted (end of run*)
10	540	£3,647	£3,035	£2,183
20	480	£3,638	£3,056	£2,127
30	420	£3,626	£3,042	£2,036
40	360	£3,612	£3,022	£1,985
50	300	£3,592	£2,994	£2,053
60	240	£3,564	£2,953	£2,051
70	180	£3,523	£2,884	£1,923

4.5 Discussion

Commercial bee use effectively masks declines in wild bees reducing the private value of wild bee conservation on farms. If commercial bees are unaffected by pesticides, the small cost relative to other inputs means that profits are highest when commercial bees are used and little farm area is converted to on-farm habitat for wild bees. If wild bee numbers decline under pesticide pressure, profits remain high as commercial bee numbers can deliver the required pollination level for maximum yields. This is in contrast to the situation when wild bees alone are used and when there is no option to use commercial bees. In this case there is an optimal percentage of habitat conversion at moderate levels in accordance with other modelling studies (Brosi et al., 2008; Keitt, 2009).

The outcome changes when commercial bees are impaired by pesticides along with wild bees. In this case, yields are stable and high for a number of years and then fall suddenly as wild pollinators decline past a particular point. High yields are maintained when there is an over-supply of pollinators $(C + w) > x$, but fall after wild pollinators numbers had declined to a level where overall pollinator numbers limit yields. The point at which wild bee numbers began to limit yield is highly variable and therefore difficult to predict, though the average year of transition increases with the percentage of on-farm habitat. Once wild bees number begin to limit yields, farmers then have the option to increase the number of commercial bees to make up the shortfall, this increases the amount spent on commercial bees relative to revenue leaving production more vulnerable to subsequent price increases.

While price rises in the future are uncertain, there have been large price rises in the past; prices for honeybee hire for use on almond farm doubled between 2006 and 2008 in the US (Pettis & Delaphane 2010). This is a far lower increase than that required to end production in the results shown here, though if farmers have to increase the number of nests at the same time as price rises occur than this differential decreases. Price rises in honeybees have been linked to supply issues in America due to a combination of factors including pesticides, mites and disease. Honeybees support themselves over the winter on honey collected through a short-period in the summer, and both sprayed pesticides and systemic pesticide applied through seed-coating have been found in high concentrations in stored honey and bee bread within nests (reviewed in Sanchez-Bayo & Goka, 2014). While the link between pesticide residues and over-wintering losses is not straightforward, pesticide residues on crops are likely to impact the condition of the nest from year to year and so could impact the supply of honeybees over time. On the other hand, there is no such precedent for price rises in commercially reared bumblebees; these bees are bred in laboratories each year, and so can be replaced from a different stock that the one supplying the previous year. However the market is relatively young (Velthuis & Van Doorn, 2006) and therefore unpredictable price changes may occur due to other factors such as increased regulation.

Foragers of both laboratory bred bees and honeybees are likely to be affected by pesticide use. The relative impact of pesticides on commercial and wild bees will depend on the farm practices used. Farmers can reduce the impact on commercial bees by shutting the hives or boxes when spraying takes place, though systemic pesticides, by design, are likely to persist within the plant for weeks after application so bees will still be exposed through the ingestion and transport of contaminated nectar and pollen. Wild pollinators cannot be shut inside nests while spraying takes place and so are potentially left more vulnerable, though some action can still be taken to avoid direct impact on wild pollinators such as spraying when wild bees are not active.

In the analysis here we present results including those of zero and negative profits. In reality, after successive years of negative profits farmers are likely to stop producing. If pollinators become difficult to come by it may be profitable to move towards crops which do not depend on pollinators even before profits have declined completely. Non-pollinator dependent crops may deliver higher profits than pollinator-dependent crops if there is a pollinator shortage. Non-pollinator dependent crops are often of lower value, and have lower nutritional value than pollinator dependent crops (Eilers et al., 2011). Consumers of pollinator dependent crops would also have to potentially pay more for fruits imported from overseas, leading to a welfare loss for both consumers and producers.

Although pesticide pressures can in theory be eased, and wild bee populations allowed to recover after a decline, pesticides are an essential input to production and so restoration of wild pollinators is unlikely while pesticide use at damaging levels continues. Under a scenario of pollinator loss, without a functioning market for commercial bees farmers will ultimately to a shift to non-pollinated crops. Such a shift has already occurred in the apple growing region of Sichuan, China, where human pollinators were used as substitutes, allowing a high pesticide, low habitat strategy to continue. When human pollination became too expensive, the only option for farmers was to leave the market altogether, and discontinue apple production. When declines in wild capital such as wild pollinators are irreversible, and there is uncertainty over whether natural capital or other sources of capital will be most beneficial in the future, there is a value to maintaining the natural capital for future use (Arrow & Fisher, 1974; Kassar & Lasserre, 2004). This `option' value is an incentive for conserving wild pollinators, even when there are commercial pollinators (or human-substitutes) available and will be positive even if there are no immediate advantages of supporting wild pollinators. This value, however, will depend on the time-horizon and risk-aversion of the farmer, as farm profits may be stable for years before declines are evident. If farmers are risk-prone and have short-time horizons then there may be little private benefit to conserving wild pollinators for crop production, implying that interventions may be required if wild pollinator populations (or the sustained production of pollinated crops) are regarded as socially valuable.

In our model, all pollinators came from either nesting within the farm area or commercial boxes within the farm area. This represents an extreme example where farms are isolated within a hostile matrix, and the on-farm habitat provides an island of habitat within that. In reality, bumblebees and honeybees can forage up to 1- 2 km (though they tend to forage more locally if there are abundance resources around) and so pollinators can be drawn in from the surrounding areas for pollination on the farm (Hagen et al., 2011). However the ability of farms to draw in wild pollinators within an intensely farmed area reduces with distance to natural habitat (Ricketts et al., 2008); farms not within flight distance of supportive habitat will need to rely on on-farm resources.

In our model, all colonisation of the nesting area occurred from the population within the farm area, therefore there was little chance of recovery if the local wild population is failing to reproduce. On real farms, bees from other areas may fly in and recolonize areas, as reproductive flight can be longer than typical foraging flights. The eventual success or failure of the on-farm population would depend on the interplay between recolonisation probability and pesticide impacts. Models have been used to predict pollinator visitation on farmland through applying nesting and foraging suitability scores across real landscapes (Lonsdorf et al., 2009). Such approaches would ideally be combined with functional models of pesticide use and effects on bee populations to predict likely long-term farm outcomes.

The wild bee population modelled here will often be made up of multiple populations of bee and non-bee pollinators (such as hover-flies). The presence of multiple pollinator groups could buffer the system from extinction; the relative tolerance of pollinator networks to extinction has been shown in modelling studies (Memmott et al., 2004; Kaiser-Bunbury et al., 2010). However these studies do not assume that threats to the different populations are correlated. While different pollinators groups may respond in slightly different ways to external pressure such as pesticide use, the effects are likely to be negative on all groups, and may be stronger on non-bee pollinators as these are smaller (Goulson, 2013). The model discussed in this paper is unique in its inclusion of a chronic threat to pollinators (pesticide use), which is likely to affect all pollinator groups. The benefit of maintaining multiple groups of ecosystem service providers as insurance against a fluctuating environmental was discussed by (Baumgaertner, 2007), who also considered the role of commercial bees in providing “financial insurance” against wild bee declines. The problem considered here differs as we consider a threat which is likely to be detrimental on the whole pollinator community, means that holding diverse pollinators will not be beneficial.

For simplicity we have assumed that all factors other than nest death (or reproductive failure) are deterministic. Thus profits are constant and high for a particular overall number of pollinators. In reality the pollination process itself will be stochastic, and there will be an overall higher likelihood of successful pollination if more pollinators are around. We assume that all nests which reproduce produce a set number of queens which survive until the next year, this simplifies the actual process which will rely on perhaps a larger number of queens being produced by successful colonies, who then may or may not mate, survive until the next year and establish a nest themselves. Each of these stages will involve some risk, and there is very little research on mating or overwintering success in bees, probably as hibernation is difficult to observe, and only the nests that successfully establish will be available in the subsequent year. There is also little research on the "normal" proportion of nest failure, though one study has found a nest failure rate of around 30% (Müller & Schmid-Hempel, 1992). The overall success is likely to depend on other factors such as weather conditions and the level of disturbance, so normal failure rate will vary substantially between years. Clearly large studies across multiple bumblebee species and multiple years are required to gain a real idea of the distribution of outcomes. Experimental work by Bryden et al. (2013) (on bumblebees) supports the assertion that impairment of foragers leads to increased likelihood of nest failure as does Müller & Schmid-Hempel's (1992) study linking forager number to overall likelihood of reproduction. There are few laboratory studies and semi-field experiments on the level of forager impairment due to pesticides and those that have measured this report a range of values depending on the experimental design and dosage (Gill et al, 2012; Bryden et al, 2013; Feltham et al, 2014). The level of impairment by pesticides in natural settings may be different again as there is also evidence that pesticides can interact synergistically with diseases, poor nutrition and other chemicals which may increase the likelihood of impairment in natural settings above those seen in experimental settings (Iwasa et al, 2004; Alaux et al, 2010; Laurino et al, 2011).

We have based the calculations and parameters on strawberries, a high value crop grown of which 1.3 million tonnes is harvested per year in Europe 1.4 million tonnes in the USA (2012 data from FAO). As Keitt (2009) concluded, the actual form of the relationship is likely to be idiosyncratic, depending on the yield response to both pesticides and bees, and the landscape in which the farmers are working. However the general conclusions will be valid for crops with similar or higher dependency on bees which also require pesticides and are grown within intensive agricultural environments, including other soft-fruits and nuts such as almonds. We show that pesticide use is not only an externality, affecting wild bees in the vicinity of the farm, but part of a trade-off for farmers of insect-dependent crops. In the presence of commercial bees, farmers have little incentive to support bees around farms; while bees might be important to crop yields the availability of cheap substitutes means that high profits can be maintained in the short-term, this is despite a longer term risk of declining profits which can threaten the ability of farmers to maintain production. Safeguarding farmland pollinators may therefore require incentives, to encourage the creation of on-farm habitat not least so that future pollination options are not reduced.

Chapter 5

Natural Capital Asset Check: Pollinator Case Study

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This work was published as part of the follow on phase of the National Ecosystem Assessment. The framework was developed by EFTEC (an economic consultancy) in association with a committee of ecologists and economists. This case study was one of 7 included in the final report. C. Ellis researched and wrote the case study. All co-authors commented on drafts.

5.1 Abstract

The Natural Capital Asset Check was composed as part of the UK National Ecosystem Assessment follow on project. While the National Ecosystem Assessment aimed to quantify the role of natural assets in the production of ecosystem services, this follow-on work was to focus on the maintenance of natural assets. The framework was devised by EFTEC, an environmental economics consultancy with input from the UK National Capital Committee which included economists and ecologists. The framework was intended to allow for an assessment of the ability and potential for natural assets to meet critical functional roles in the future and to be broad enough to be applied to varied natural assets. Other case studies included estuarine habitats, urban green space and arable soils. This case study (pollinators) evaluated the ability of wild and domesticated pollinators in the UK to meet crop production needs both now and in the future. A literature review was conducted on past trends in pollinator numbers and likely factors which could alter the extent or condition of pollinators in the future. Publically available data on insect pollinated crops was combined with published bumblebee nest densities to assess the relative vulnerability of crops to pollinator loss.

5.2 Natural capital asset

Question	Guidance on Answer
A. Define Natural Capital asset being checked	*Configuration of living and/or non-living processes and functions over space and time, which produce through their existence and/or some combination of their functions, a positive economic or social capital.* The natural capital in question is the natural capital that makes up the pollination service provided by insects to crop plants across the UK. The natural capital asset is made up of both managed pollinators (honeybees) and wild pollinators (mainly bumblebees, solitary bees and hoverflies) and the habitat, ecological processes and human capital that support them. The best indication of the functioning of the natural capital asset is likely to be the insect populations themselves; however the ability of these populations to provide ecosystem services going forward will also depend on the extent and condition of supportive habitat both on farms and in the wider countryside. Habitat areas should provide both nesting sites and foraging resources for wild pollinators and should be linked to maintain healthy pollinator networks. Honeybees are managed within nests but still require that forage plants are available in the surrounding area. Other factors exert negative pressure on wild pollinator populations by increasing mortality or reducing reproductive rates and thus lowering the population size. Such neg-

	ative factors include pesticides, which can cause acute mortality if incorrectly applied, and may reduce foraging and reproductive success in populations of bees near to farms. Pesticide use may affect populations at a local level, but widespread pesticide use over a large area and over a long period of time could have a cumulative impact. Populations of wild pollinators and honeybees are also subject to biotic threats such as diseases, predators and parasites. Otherwise healthy populations should be able to withstand acute threats of this kind, but there is evidence that negative factors can act in combination with a greater impact; for example pesticide exposure can exacerbate the effect of some diseases (Alaux et al., 2010). A diverse assemblage of wild pollinators supported by a network of habitats along with a stable honeybee supply may be the best defence against the impacts of these multiple threats. As well as honeybees, farmers will use other commercial pollinators the most common of which are commercial bumblebees, which are factory reared. For the purpose of the asset check, honeybees are considered as natural capital while commercial bumblebees are not. Honeybees are managed in hives which can persist continuously for years, and are therefore affected by some of the same pressures as wild pollinators, including changes in climate, pesticide use and the threats of pests and diseases. Commercial bumblebees on the other hand, are bred in laboratories and are supplied in boxes which are disposed of at the end of the year; therefore the supply and health of commercial bumblebees are not dependent on the same drivers as other pollinators. Commercial bumblebees are considered as one substitute for wild pollinators in section U of this

report.   Honeybees can be owned and the placement of hives can be controlled, whereas wild populations of pollinators cannot be owned and can only be managed to some extent. Therefore we are considering an asset that is made up of a mix of a conventional asset which can be controlled and owned, and non-conventional assets made up of wild populations which are not. The services from wild populations are provided for free, and may be undervalued by land users.

While a healthy functioning capital asset would contribute to pollination requirements of UK crops, it will not provide all of the pollination requirements of UK crops. Some crops are grown in vast areas and require pollinator densities above that of wild populations, and/or require pollination at times when honeybees are not active (for example strawberries). For these crops farmers will always need to supplement the wild population and honeybees with other commercial pollinators. It would therefore be inappropriate to suggest that the level of ecosystem service provision from a healthy functioning natural asset would be to supply all of the pollination needs of all crops in the UK, as the total needs will be provided by a mix of the natural asset (honeybees and wild bees) and commercial pollinators. Wild pollinators and honeybees are however, very important and are likely to meet a great proportion of UK pollination requirements. Moreover, there is evidence accumulating that a diverse mix of pollinator species can provide superior pollination services to relying on one species, both because species provide complementary functions and as the can be differences in adaptation to environmental conditions (Hoehn et al., 2008, Brittain et al., 2013a). Therefore the complete substitution of the natural asset would not be advisable. The direct impact of a reduction in wild pollinators or a reduced supply of honeybees would be a likely rise in costs to farmers as alternative pollinators would be

	required in greater numbers or honeybees would be more expensive to obtain or hire. The impact on farmers of increased costs from pollinator loss will depend on a number of factors which are discussed further in section three.
B. What is the spatial scale for which the asset check is being conducted	Across the UK, with a focus on farmland.
C. Define the timescale for the asset check.	The asset check focuses on potential changes post 1990. However longer timescales are also considered to observe long-term trends.
D. What are the main ecosystem services the asset provides?	Hoverflies, wild bees and honeybees provide pollination services to the UK. Pollination was categorised as a regulating service in the 2010 National Ecosystem Assessment which valued the services from pollination of crops at £430m per year (Smith et al., 2011). Pollinators also provide pollination services to wild plants, maintaining floral diversity, and contributing towards other ecosystem services such as providing seed and berries for bird populations (Jacobs et al., 2009) and supporting natural vegetation for recreational use. Pollinators also have existence values outside of their use values so people may be willing to pay to conserve bees and other pollinators even if pollination services do not directly benefit them. Honeybees also provide both recreational value and provisioning services through honey production.

5.3 Integrity of natural capital asset

Question	**Guidance on Answer**	**Trends**			
		Past trend	**Current trend**	**Future Trend**	**Summary of Trends** **(see key*)**
E. What is the extent of the natural capital asset?	Wild bees, including bumblebees and solitary bees, and hoverflies are found throughout the UK. The populations of pollinating species fluctuate from year to year and are not monitored systematically making evaluations of number or density of wild pollinators difficult. There is a particular challenge to monitoring mobile organisms as activity patterns will depend on weather and surrounding resources as well as the underlying extent of the population. Monitoring social	In an analysis of 10 x10 km grid squares from the BWARs dataset, bee and hoverfly species numbers where compared from observations before and after 1980; bee diversity was found to be reduced in the majority of grid squares (Biesmeijer et al., 2006). The largest declines were in species with narrow habitat	Carvalheiro and colleagues have used data at different scales from 10 km upwards to detect changes post 1990 (Carvalheiro et al., 2013). Although bumblebee species richness has continued to decline in Great Britain between the 1970 to 1989 dataset and the 1990 onwards data, the species richness decline has been less	The slowing of the rate of species richness decline in bumblebees and flowering plants, and the apparent recovery of solitary bees detected by Carvalheiro et al is encouraging. However this slowing may be due to the fact	*Insert symbol* *Solitary bees* ↔ *Bumblebees* ↓ *Hoverflies*

	species such as bumblebees is made more difficult as many individual workers observed foraging are collectively representative of only one reproductive unit, or nest. One way of dealing with this issue is estimate nest density, rather than abundance of individuals. Using data collected by volunteers for the National Bumblebee Survey 2004, Osborne and colleagues found that nests of bumblebees where at higher densities in gardens and around countryside linear features such as hedgerows and edges of woodland (Osborne et al., 2008). Other studies have used molecular methods to calculate nest numbers by analysing sibling relationships between bees caught across areas of land. In one such study which compared nest densities of common bumblebee species, it was found that nest densities per ha fell between 0.26 and 1.17 depending on the species (M.	requirements. There were no directional changes in hoverfly diversity over the same time period. Bee pollinated plant diversity also declined between datasets, whereas the diversity of other plants did not. Carvell and colleagues also found a decline in “bee-friendly” plants between pre-1980 and post 1980 (Carvell et al., 2006). They found declines in ranges as measured by changes in occupancy of 10 km grid	dramatic that that observed between 1950-1969 and 1970-1989. Solitary bee species appear to have recovered somewhat, species richness increases were detectable in recent years. Rates of wild flower species decline have also slowed. Despite the general downwards trend observable before 1993 it is likely that honey bee colonies numbers are now increasing. This is due to the increased public interest in bees and	the most vulnerable species have already been lost. Social bees are more susceptible to habitat losses and pesticides than solitary bees (Williams & Osborne, 2009) which may explain the recovery in solitary bees relative to bumblebees. The current public interest in bees will continue to pull people towards beekeeping. However many new beekeepers may only stay with the	↔ *Honeybees* ↑

	Knight et al., 2005), summing to 2.4 nests per ha over the 6 most common species. Similarly Darvill et al. (2004) found nest densities of 0.13 and 1.93 nests per ha for two species of bumblebee. These estimates were lower than the estimate from the volunteer collected data, which estimated bumblebee nest densities at around 7 per ha for the same study area as M. Knight et al, 2005 (Osborne et al, 2008). There have been no similar studies on solitary bee or hoverfly population density at a landscape scale. The Bee, Wasps and Ants Recording Society (BWARS) holds observation records for bees and hoverflies dating back to the 1800s. While these data are not standardised in a way that would allow abundance data to be elucidated they do	squares (from New Atlas of British and Irish Flora),and changes in frequency in randomised fixed 1km plots from Countryside Survey datasets from 1979 and 1998. Post 1980 changes in nectar plant diversity were detected in the Countryside Survey Integrated Assessment in 2007 (Smart et al, 2010). In this case changes where categorised by land use, and were significant (and negative) between	beekeeping. There is a general perception that bee starter colonies are hard to come by (Peterson et al., 2012a; Peterson et al., 2012b) and new beekeeper courses have been over-subscribed. BBKA has seen rises in membership in recent years providing positive indications of the increase in honeybee colonies overall.	activity for a few years, making little impact on pollination services going forward. Disease risks and increased monitoring are likely to increase costs for commercial beekeepers. Unless pollination and honey prices can cover these costs, commercial beekeepers may leave the market.	

	give an indication of species range across the UK, and relative species richness. Relative species richness increases towards the South and West of the Country. The relationship between species richness and abundance is unlikely to be linear as the increased species richness in the South and West of the UK is likely to be made up of rare species which may contribute little to pollination on farmlands. The BWARs dataset can, however, be used to monitor species losses over time. Honeybees The number of honeybee colonies in the UK has been estimated at 274,000 (European Commission 2010) Commission Regulation (EU) No	1990 and 2007 in small habitat parcels within arable and horticultural area, improved and neutral grassland, broadleaved and mixed woodland. Numbers of beehives and beekeepers declined between 1983 and 1993, and are lower currently than levels in the 1950s. In 2001 figures from a government commissioned survey estimated colony numbers at 230,000, and beekeeper numbers at 33,000. This			

	726/2010. While there has been a downward trend detectable in the number of hives based on data up to 1992 (Potts et al., 2010) there has also been a surge in amateur interest in beekeeping in recent years which has boosted the number of hives. Most amateur beekeepers keep only one hive, whereas commercial bee farmers keep around 400 each. Commercial bee farmers consequently own around 40% of the hives, despite being far fewer in number (around 300 as opposed to 33,000 amateur beekeepers). The majority of amateur beekeepers do not move their hives to take advantage of different flowering seasons and so only contribute to pollination services in the area around where the hive is kept. The hives owned by bee-farmers are therefore	represented a substantial increase from the last official figure of 130,000 in 1993. Most recent official figures put the total colony number at 274,000 in 2010. (European Commission, 2010) Commission Regulation (EU) No 726/2010			

	likely to contribute disproportionately to pollination services to crops.				
F. What is the condition of the natural capital asset?	Honeybee overwintering rates in the USA have caused concern, particularly due to the sudden disappearance of honeybees from a colony, or Colony Collapse Disorder. Honeybee overwintering rates have been recorded for the COLOSS network in Scotland and England and Wales. Overwintering losses have been around 20% in Scotland since 2007, and peaked in 2010 at 27% (Peterson & Gray, 2010; Peterson et al., 2012b). In England and Wales the colony losses where highest in 2008 at 30% but have been lower since and were 14% in 2011 (BBKA, 2012). Although varia-	*Describe/ quantify trend* Colony Collapse Disorder or the sudden disappearance of colonies has been cited as a cause for overwintering losses in the UK (Peterson et al., 2012b). *Varroa* mites and starvation are other common causes of overwintering losses. Beekeepers are vigilant to such losses,	*Describe/ quantify trend* The rise in new beekeepers will increase the extent of the natural asset, however new beekeepers suffer higher overwintering losses suggesting that husbandry practices require attention (Van Der Zee et al., 2012). That being said, there is an increased awareness of disease and the sharing of best	*Describe expected future trend* There are emerging threats to both honeybees and wild pollinators through alien pests such as the small hive beetle which feeds on young bee larvae and is endemic to the USA. While this pest cannot be eradicated, good monitoring and husbandry can prevent catastrophic effects	*Insert symbol* *Wild bees and hoverflies* **O** *Honeybees* ↔

	ble between location and years, there is no evidence for an upward trend in overwintering losses in the UK in recent years (see table S5.1). While the cases of colony collapse disorder are likely to be multi-faceted, a combination of *Varroa* mites, pesticides and viruses (particularly Deformed Wing Virus) have been implicated (Cox-Foster et al., 2007). The vast majority of beekeepers in the UK treat and inspect their hives for *Varroa* and other pests. While pesticides have been long known to adversely affect bees and other pollinating insects, particular attention is now paid to neonico-	and can to some extent mitigate them by propagating new colonies. Overwintering losses reached 30% in England in 2008, but are currently lower. Neonicotinoid pesticides are thought to have an effect on both wild pollinators and managed bees and have increased in use over the past 9 years. While much neonicotinoid use is on crops which are not pollinated by bees, the neonicotinoids clothianidin, imidacloprid	husbandry practice should allow new beekeepers to manage hives in a healthy way. There is no indication that the peak of overwintering losses in 2008 in England is part of an increasing trend. The policy concerning pesticides is evolving at the current time with a two year moratorium on neonicotinoid pesticide use across the EU coming into place in	and minimise spread. Other emerging diseases include *Nosema ceranae*, originally from Asia but now widespread in both managed honeybees and wild bumblebees. The future condition of wild pollinators and honeybees will depend to an extent on land use and pesticide policies adopted.	

	tinoids, which are systemic pesticides usually applied to the seed coat and then move up through all parts of the plant, including pollen and nectar. Pesticide incidence monitoring in England showed a peak in pesticide incidents in 2009 and 2010 (defined as significant mortality caused by one pesticide use event) (Alix et al., 2013), but the numbers are still relatively low. This acute statistic however, will not detect the effects of chronic exposure to neonicotinoids which is more difficult to monitor. While the disease status of honeybees is well documented, the disease status of wild pollinators is not. Bumblebee colonies also have varia-	and thiamethoxam are used on oil seed-rape as well as thiacloprid (which is used a foliar spray). While imidacloprid use on oil seed rape has reduced over recent years, the use of thiamethoxam has increased dramatically. Thiacloprid is used on soft-fruit and orchard fruit. Acetamiprid is used at a low level on orchard fruit.	December 2013 for the three neonicotinoids which are most widely used in the UK (clothianidin, imidacloprid and thiamethoxam).		

	ble survival rates which are not well studied making it is difficult to predict populations from year to year.				
	Together, extent and condition reflect the integrity of the stock of natural capital, which produces flows of ecosystem services. *Use of historical data must be relevant to the environmental and/or ecosystem services changes from the natural capital asset.*				
Uncertainties	There is evidence both from bee numbers and the plants that support them that wild bee diversity is decreasing. Well established. Although some sources state that honeybee numbers are declining, no evidence of this was found; sources imply that numbers are increasing (though most new beekeepers are amateurs rather than professional). Established but incomplete evidence. No evidence was found of increased overwintering rates in the time span for which data is available (since 2006). Well established. *Give level of uncertainty in analysis* for D, E and F, and reasons for this.* ** Use Uncertainty scale described in introduction.*				

Key for trends	↑	increasing	↓	decreasing
	↔	evidence shows no trend	O	no evidence

🟪	↑↓	both increasing and decreasing	(this could reflect ambiguous evidence and/or spatially differing trends)

G. Drivers of changes in Extent and Condition	List policy drivers	*Policy drivers* Wild pollinators around farmland are supported under agricultural stewardship schemes in England and Wales. The Entry Level Stewardship scheme encourages the creation, restoration and maintenance of low input permanent grassland and hedgerow management, both of these will be of benefit to pollinator populations (Natural England, 2013a). There are drivers to reduce the “hungry gap” so that pollinators are supported throughout the year rather than only during the time of mass flowering. To achieve this swards of native flowering plants including clovers, hogweed and cow parsley are encouraged. The Higher Level Stewardship scheme builds from this providing further support for maintenance of species rich grasslands and pollen and nectar mixes (Natural England, 2013b). However, uptake of these schemes in HLS is low. Many of the habitats covered by the UK Biodiversity Action Plan are beneficial to pollinators: improvements to field margins and boundaries and linear features in agricultural landscapes will be of benefit to pollinators around farmland, while improvements in lowland meadows, calcareous grasslands and heathlands will benefit the wider wild pollinator networks. Current agri-environment schemes in England, Wales and Scotland will end in 2013. This will coincide with a review of the European Union Common Agricultural Policy (CAP). Current proposals suggest that an increase in support of agri-environment schemes is likely with new payments for the support of Ecological Focus Areas and permanent grassland. Ecological Focus

		Areas are areas of in-field and field-side features such as fallow, buffer strips and beetle banks which will make up 5-10% of farmed area. Such a move would likely be positive for pollinators; it would serve to link up populations across landscapes, provide habitat and alternative forage for pollinators and bring pollinators closer to the crop. Nine species of solitary bee and seven bumblebee species were treated as priority species under UK Biodiversity Action Plans and have therefore been incorporated into NERC S41 and equivalent legislation in Scotland and Wales. These species are regarded as conservation priorities but are not individually supported to same level as they were under UKBAPs. This represents a move towards a more holistic approach to conservation, based on ecosystem integrity rather than individual species. While rare pollinators may currently provide little in the way of pollination services to crop lands, their maintenance is important for the conservation of diverse wild flower species. Policies to improve the health of honeybees are evident in all regions of the UK (DEFRA, 2009; Scottish Government, 2010; DARDNI, 2011) with the purpose of “achieving a sustainable and healthy population of honeybees for pollination and honey production”. These strategies all emphasize improved communication between stakeholders, surveillance and monitoring of pests and disease, competency development, and improving the evidence base. In England and Wales, a prevalence reporting network has been developed (BeeBase) to encourage vigilance against diseases and pests, and monitor spread. The

		Balai direction (92/65/EEC) names American foulbrood, Small Hive Beetle and *Tropilaelaps* mites as notifiable across the EU (European Commission, 1992). While the honeybee health plans make brief mention of habitat and foraging plant requirements with respect to honeybee needs, the nutritional needs of wild pollinators are not addressed. The Welsh Government has an “Action Plan for Pollinators” currently under consultation, recognising the contribution of wild pollinators and their expected requirements (Welsh Government, 2013). The action plan currently states the intention to provide linked, conducive habitats on a local and landscape scale, supporting native flora in protected areas, and encouraging pollinator friendly gardening and land use in urban areas. Plans for monitoring of populations, effects of pesticides and diseases and stakeholder engagement are also included. There is a UK national action plan on the sustainable use of pesticides (DEFRA 2012b). The EU has imposed a two-year moratorium on neonicotinoid use based on evidence from both honeybees and wild bees. Most pesticide policy particularly refers to the effect of pesticides on honeybees despite the significant impact that commonly used pollinators can have on solitary bees (Gradish et al., 2012) and bumblebees (Scott-Dupree et al., 2009). Neonicotinoid pesticides have been used on oilseed rape seeds and are known to have long half-lives in soil so may continue to affect populations despite the moratorium (half-lives reviewed in Goulson, 2013).

		The area of oil seed rape has increased in the UK over the last 10 years (DEFRA 2012a) and prices have risen in the same period reflecting the demand for biodiesel across the EU (Department of Transport 2012). While mass-flowering crops provide a food source and can increase the growth of bumblebee colonies (Westphal et al., 2009), they can also act as a sink pulling pollinators from native plants (Blitzer et al., 2012) and disrupt community composition by favouring short-tongued bumblebees (Diekoetter et al., 2010).
	List biophysical drivers	*Biophysical Drivers* Neonicotinoid pesticides are known to cause a reduction in reproduction of bumblebee nests (Whitehorn et al., 2012) and to impair navigation behaviour in honeybees (Henry et al., 2012) and pollen collection in bumblebees (Gill et al., 2012). The effect of exposure to neonicotinoids can act in synergy with the effect of other pesticides and fungicides leading to higher than expected levels of toxicity (Iwasa et al., 2004) and diseases such as Nosema (Alaux et al., 2010) therefore any on-going effects of neonicotinoids may make disease management more difficult, potentially leading to increasing overwintering losses in honeybees and reduced population sizes in wild pollinators. Healthy pollinator populations require adequate habitat including foraging resources and nesting sites. Pollinators are sensitive to habitat loss (Winfree et al., 2009), and tend to decrease in abundance further from areas of semi-natural habitat

		(Ricketts et al., 2008). Though this trend was not observed in areas of heterogeneous farmland with fine scale floral resources (Winfree et al., 2008) suggesting that both areas of habitat and diffuse habitat within agricultural lands can support pollinators. Declines in pollinator diversity are thought to be due in part to post war losses of unimproved grasslands and decline in hedgerows (Goulson et al., 2008). Areas of important habitat for wild bees in the UK have been stable or increasing in recent years, though in some cases condition of these habitats is poor (Breeze et al., 2012). Pollinators are supported within conservation areas: Natura network grasslands and calcareous grasslands have high pollinator species richness, while bumblebees are in high abundance in dry heath (Murray et al., 2012). Within farmlands agri-environment schemes, including unmowed field margins and sown flower strips can boost bee diversity and abundance around farms (Pywell et al., 2006; Carvell et al., 2007) and “green veins” such as hedgerows and verges can also boost pollinator populations (Schweiger et al., 2005). Increases in urban areas are unlikely to be a problem for generalist species, as gardens provide rich foraging areas and support dense populations of some wild bee species (Goulson et al., 2010), but may reduce specialist species which rely on wild flowers. Nest sites availability can also limit bumblebees and solitary bees. Bumblebees nest in grassy tussocks or underground cavities whereas solitary bees and hoverflies use a variety of substrates including bare soil and tree stumps. There is evidence from Scotland that agri-environment prescriptions such as field margins can promote nesting and foraging at the same time in bumblebees (Lye et al., 2009). Few management prescriptions target increasing nesting sites in other pollinator groups.

		Climate change will affect the pollinator network. Any directional change in temperature will cause bees to shift their ranges northwards, possibly decoupling local food webs (Memmott et al., 2007). Climate change can also cause phonological shifts causing some species to emerge earlier, or to have multiple reproductive cycles in a season. Longer pollinator seasons may be of benefit to producers of insect pollinated crops in Scotland, who currently use managed bumblebee colonies to pollinate soft-fruits in the early parts of the year (predominately April to May, though on some crops managed bumblebees are used throughout the year). Overall the impact of climate change on pollinator populations and crop pollination is highly uncertain.
	List socio-economic & other drivers	*Socio-economic & other drivers* The number of honeybee farmers supplying pollination will be affected by the honey market as well as expenses for disease prevention. While disease prevention costs may be expected to rise, honey prices have also risen over the last 10 years (FAOSTAT, 2013). A positive economic outlook for honey producers could have knock-on effects increasing pollination services. Increasing awareness of pollination requirements of crops may lead to more beekeepers moving to supply pollination around farms.

		Likewise the extent of wild pollinators may be dependent on the increasing awareness that they provide important services. In response to concerns about pollinator sustainability, most of the major supermarkets have implemented "bee-friendly" farming guidelines which suppliers must adhere to. There is also pressure from consumer, who can chose to buy conservation grade fruit and vegetables which require farmers to support pollinator populations around farmland.
H. What are the asset's main ecosystem functions?		*List important ecosystem functions (or supporting and intermediate ecosystem services) that support the main final services from the asset. Supporting and intermediate services are defined in the UKNEA.* *Note that supporting and intermediate services may originate from other assets that co-produce final services.* Providing regulating service of pollination to both wild and crop plants. Provisioning services through honey production. Recreation services through honeybee keeping. Non-use values.
I. **Integrity Test**: Is the ability of the asset to support ecosystem services being maintained?		*Give details for different services (if relevant), consider the trends under questions E and F and the services from question D.* Although honeybee numbers are increasing, this may not lead to increased pollination services, as the increase in number of colonies is made up of those kept by amateur beekeepers, mainly in suburban areas. Also some crops and many wildflowers are not well pollinated by honeybees.

	While honeybees may not provide all pollination services, the condition of the honeybee stock is well monitored and new policies in place will further safeguard honeybees. Wild bee diversity has declined and insect pollinated wild plant species richness continues to decline in some habitats. Monitoring efforts have so far detected losses of rare species; there are no systematic schemes for monitoring the abundance of common species so the trends in these are not clear. Pollination services to wild plants are at risk, particularly for specialised plant species, as the diversity of these have declined in parallel with pollinators with narrower niche breadth. Whether the asset as a whole is able to support crop pollination depends on the specific requirements of crops which are discussed in the next section.

5.4 Performance of natural capital asset

In this context ‘performance’ is fitness to carry out the role which is required of a capital asset. This is regarded as useful because defining the target performance of natural capital assets captures both the current and future quantity and quality of an asset. Human ‘requirements’ include basic human needs, but also reflect infinite wants, so the definition of performance is usually subjective.

Question	Guidance on Answer
J. Is there a measure of the current output of services from the asset?	*Either a direct measure of levels of services (see question D), or an indication of this based on the amount of the asset (stock) and its ability to provide the service (condition) (see question I)* The output of the services from the asset is the yield increase in insect-pollinated agricultural commodities which can be attributed to pollinators. Given the variability in agricultural yields due to inputs other than pollinators, it is not feasible to use yield data to monitor the performance of the asset. Breeze et al. (2011) took the approach that the required stocking density of honeybee hives on pollinator dependent crops could be used as a proxy. By assessing the number of hives demanded by the area of insect dependent commodities in production, we can get an idea of the number of honeybee hives which would be needed to maximise production. Assuming that all hives in the UK are moved three times per year, Breeze et al then used the number of honeybee hives to calculate the capacity of the current level of hives to meet this demand. They found that the capacity of honeybees to fulfil pollination requirements has declined in the UK, mainly due to the increase in the areas of oil-seed rape and field beans, which require insect pollination. The capacity of honeybees to meet demand for pollination services fell to 30% in 2007, down from 71% in 1984. These figures are likely to over-estimate the ability of

UK honeybees to meet demand for pollinators; the calculations assume that all honeybee hives are moved multiple times per year, given that most hobby beekeepers (who look after 60% of the colonies) do not move their hives it is unlikely that the current stock could meet as much as 30% of crop production needs.

Wild pollinators are important for the supply of pollination services. Wild pollinators can also pollinate a wider range of crops than honeybees. Honeybees are short-tongued and so (along with short-tongued bumblebees) tend to nectar rob from flowers with long corollas by biting holes at the base of the flower (Free 1962, Free 1968). Common long-tongued bumblebee species *Bombus pascuorum* and *Bombus hortorum* are more suitable pollinators of field/broad beans for this reason. Apples and other orchard fruit trees flower earlier than most honeybees are active, and so are usually pollinated by solitary bees, whose emergence patterns are a better match. Bumblebees are the main pollinators of soft-fruit, as not only are they tolerant to indoor or semi-indoor fruit production characteristic of soft-fruit growing, but they can transfer more pollen and visit more flowers per unit of time than honeybees (Willmer et al., 1994). Oil seed rape can be pollinated by honeybees or wild pollinators, including hoverflies. Hoverflies are likely be able to pollinate similar crops to honeybees and solitary bees, although higher densities are required to reach the same level of pollination as they tend to move less between flowers and also carry less pollen (Jauker et al., 2012).

The stocking densities of honeybees required for adequate pollination has been estimated for crops, the most important of which in the UK are summarised in table S5.2, and the middle of the stocking density range given in Breeze et al is noted. As mentioned above, honeybees may not be the sole or main provider of services to these crops, some crops can be pollinated by both honeybees and wild pollinators, and others can only be pollinated by a particular subset of wild pollinators; such special requirements are also noted in the table. The density requirement of bumblebees, solitary bees or hoverflies required is less frequently evaluated. There are recommended densities of bumblebee colonies from the providers of commercially reared colonies, usually around 6 to 9 colonies per ha for soft-fruit. However higher densities are likely to be required on some fruits than others due to differing attractiveness to bumblebees, and different dependency on pollination.

Drummond (2012) provides a direct comparison of stocking density requirements of honeybees and bumblebees for highbush blueberries, and find that 10 bumblebee colonies per ha provided the same pollination as 7.5 to 10 honeybee hives. Using the ratio implies that 1.33 bumblebee nests per ha would be required for each honeybee hive. Bumblebees are known to be better pollinators of blueberries than honeybees, so this ratio may be low for crops that are well pollinated by both types of bee. Table S5.2 shows the required bumblebee nest density using this ratio. It should also be noted that bumblebee nests vary greatly in size through the season, being very small in spring. Orchard crops flower early in the season, and at this time bumblebee nests will be small and adequate pollination by bumblebees is less unlikely. Table S5.2 provides a qualitative assessment of how vulnerable various crops are to pollinator shortages, given the timing of flowering and the requirements for specific pollinators.

K. What goods and benefits do these services support?	Wild and managed pollinators support the production of insect dependent crops in the UK. Globally, 35% of food crops are at least partly dependent on insect pollination, as are some energy crops such as oil-seed rape. Insect pollinated crops have higher value added than non-pollinated crops, therefore representing a high proportion of goods by market value. Insect pollinated crops also contain higher vitamin and micronutrient concentrations per kg than non-insect (mainly wind) pollinated crops (Eilers et al., 2011). The ability of UK-produced volumes of goods to meet home demand ranges from 5% for broad beans and 70% for strawberries and raspberries (See table S5.3). The loss of insect pollination would cause imports of insect mediated crops to rise, weakening UK food security. The wider pollinator network also supports flowering plant reproduction. It has been estimated that the proportion of wild plant species in temperate regions requiring insect pollination at 78% (Ollerton et al., 2011). The insect pollinated plants provide other ecosystem services including forage for birds and animals, and recreational value to humans. There are also non-use values associated with wild flowers and particularly rare flowers such as orchids which are protected. Amateur beekeepers often do so while making a loss, suggesting that bees also provide recreational value. Other pollinating insects also have non-use or existence values as signified in the high sign up to societies such as the Bumblebee Conservation Trust and Buglife.

L. What is the target performance from the asset?	Insect pollination boosts the yield of crops, increasing the market value and allowing farmers to stay in production. The target performance varies from crop to crop (see table S5.2), as different crops require different stocking densities so that pollination does not limit production. In addition to the performance in relation to the producers, the pollinator assets should also sustain wild flower and plant pollination.
Uncertainties	*Give level of uncertainty* in answer to L and reasons for this.* ** Use Uncertainty scale described in introduction.* Established but incomplete evidence. Stocking densities for honeybees are taken from the scientific literature but these are not collected by standardised means and are not always from studies in the UK or other temperate regions. Numbers of wild bumblebees required are based on an assumption that the equivalency of honeybees and wild bumblebees that exists for blueberries can be extended to other crops. Data on density of solitary bees and hoverflies across the UK is not known. The spatial distribution of honeybee hives is not known, it may be that many honeybee hives are located in cities and are not moved to provide crop pollination. The performance measures provided are therefore qualitative in nature and give an indication of how well the needs of different crops are met by the available natural pollinator assets.

Defining performance: Answering these questions can help define performance, but not all questions can be answered for all assets	What policy targets are there for the asset?	*(e.g. maximum sustainable yield for fish stocks, global concentrations of GHG)* The UK government has a target to manage honeybees for sustainable pollination services. Such a target has been referred to in honeybee policy, rather than policy concerning the total pollinator asset.
	What is the trend in the main services the asset provides?	*See question d for services, and UKNEA synthesis report Figure 5 for trends.* Although honeybee numbers are increasing, the location of hives is based on the owner rather than the pollination needs of the country and so many are in urban areas which already support a high proportion of wild pollinators. Most crop plants require pollination by short-tongued generalists, including 4 of the 6 common species of bumblebee, honeybee and solitary bee species. While there are multiple species to provide these services, crops differ in the level of vulnerability to pollinator decline based on the pos-

		sibilities for substitution given the phenology of flowering and pollinator preference. With increasing area requirements for insect pollinated crops, the maintenance of pollination services into the future is uncertain.
	What types of goods are supported by the asset?	*(e.g. food, drinking water, pollution control) See UKNEA synthesis report Figure 10 for terminology* Provisioning goods, recreation, regulating services.
	Who benefits from the goods?	*Identify the number and location of beneficiaries* Consumers of insect-pollinated food benefit both in the UK and abroad. Farmers of such goods benefit from lower costs of pollination services, if needs are met by wild bees, and from the choice of whether or not to farm insect-pollinated food or not. The UK is also an exporter of oil seed rape; pollinators increase the yield of oil seed rape to the benefit of producers and consumers.

	What wellbeing results from the goods?	UK consumers benefit from a greater supply of insect-pollinated food. There is not only an economic benefit but also a non-tangible benefit that some derive from eating local food. Insect-pollinated crops contain more vitamins and so society benefits as a whole if more consumers can access these goods cheaply (Eilers et al., 2011). Wild flowers add to recreational and aesthetic value of the UK countryside, and insect pollinated wild plants such as brambles and hedgerows provide food for animals and birds, thus increasing the biodiversity value further.
M. Are any future changes in target performance expected?	*How is target performance expected to change? Consider exogenous factors like those associated with the drivers under question F, and the asset's role in climate change adaptation.* The target performance is expected to increase if area of oil-seed rape continues to increase.	
N. Can future target performance be defined?	*What is the target level of future performance of the asset?* *What are the drivers of this (see question G).* Future target performance could be defined if areas of expected insect pollinated crops in the future are known.	

5.5 Natural capital asset criticalities

Question	Guidance on Answer
O. What is the trajectory of change for the asset?	*Specify if any linear or non-linear changes are known or anticipated (see trends from questions E and F)* The loss of specialised pollinators since post-war agricultural intensification may not be surprising given changing land use. However floral diversity has also declined since 1990 in small habitat patches within larger areas (Smart et al, 2010). It is possible that continued declines in wild flower diversity affect pollinator diversity further or vice-versa. The positive feedback between these two declining assets is cause for concern. Generalist pollinators have not shown declines to the same extent and are relatively adaptable to modified landscapes. Hoverflies also have not suffered to the same extent. Honeybee numbers have declined but seem now to be increasing in the UK. Whether this trend will be reflected in greater pollination services depends on whether the new beekeepers are placing their hives in agricultural areas, or whether the increase is more due to the growth in beekeeping in urban areas. If the increase is evenly distributed then we could expect an increase in services provided by honeybees.

	Emerging diseases and pests threaten both wild pollinators and honeybees. The relative importance previously placed on honeybees could leave the asset potentially vulnerable if honeybees do suffer from problems such as CCD in the future. Overwintering rates in honeybees are already variable, and liable to cause supply problems if caused by a disease or weather event which affects many beekeepers at once. It is prudent therefore that while honeybee husbandry and disease surveillance is treated with high priority, equivalent efforts are also made to boost the diverse assemblage of wild pollinators which may be more resilient to such changes.
P. Are there any standards or agreed limits of change to the asset?	*Specify if there are any relevant standards or limits for the condition of the asset (e.g. adult spawning stock biomass for fish) or the services from it (e.g. fish landing quota).* There are no agreed limits of change to the honeybee asset, although honeybee plans are now in place for “sustainable” pollination suggesting that resilience of the honeybee stock is a priority. There are no agreed limits of change to wild pollinators.
Q. Are there likely to be any threshold effects?	*State knowledge of any thresholds – thresholds can include where the integrity of an asset declines in a non-linear way, where the influence of feedbacks on an asset change, or where the ability of an asset to recover declines.* A diverse mix of wild pollinators and honeybees will reduce the probability of collapse of pollinator services. That being said, a poorly managed epidemic affecting either honeybees or *Bombus* spp would be likely to cause significant reductions in services

	available that year. Honeybees are the most vulnerable to such a shock as diseases can spread quickly between colonies. Crops which depend on long-tongued species of bumblebees are also somewhat vulnerable, as there are fewer species to replace this service if lost. There is some evidence that mass-flowering crops support short-tongued species at the expense of long-tongued bumblebees (Diekoetter et al., 2010). The integrity of the asset could decline in a non-linear way if there is a positive feedback between wild flower diversity loss and pollinator diversity.
R. What is the reversibility of changes to the asset?	*Can changes to the asset be reversed? (e.g. can the asset, and its functions, be restored or recreated?)* Most pollinator species in the UK complete one or more generations per year, and can be expected to undergo stochastic fluctuations due to weather or other perturbations. Many “bad” years in succession or a chronic threat to bees will ultimately have an impact on populations which will not be avoided until the threat is removed. Should such a threat cause a population to go locally extinct, the area is likely to be recolonised once the environment is conducive again. However if the threat is widespread then local recolonisation may not be an option. It is extremely difficult, though not impossible to reintroduce lost pollinator

	species. Attempts are being made to reintroduce *Bombus subterraneous* to the UK with limited success so far. Even after a successful reintroduction it would take years for an introduced species to spread to the extent required to make a difference to pollination services, during which time any wild plants dependent on that pollinator may have already been lost. Changes in honeybees are also difficult to reverse, as once a disease or pest becomes endemic, the high density of hives allows easy spread. Prevention and early detection of such problems can mitigate against this.
S. What is the cumulative effect of impacts on the asset?	*What patterns of impacts result from past, current and future trends and drivers (see questions D, E and F)?* The increasing proportion of oil seed rape could further exacerbate the trend towards generalist, short tongued pollinators at the expense of specialists and short-tongued species. AES schemes in England to fill the "hungry gap" and to increase areas of grassland will to some extent mitigate the losses by encouraging a diversity of wild flowers but it is unknown whether the areas over which these schemes will be implemented will be sufficient to offset any loss.

	Neonicotinoid use and increasing amateur beekeeper number may act in synergy to increasing overwintering losses in honeybees and increase the vulnerability to disease. Without intervention to support disease treatment and surveillance, costs may rise causing professional beekeepers to leave the industry.
T. What risks are associated with current trends in the asset integrity?	*Identify risks of significant detrimental impacts: see answers to questions N, and relate this to answers to questions P – S.* Most industries will currently rely on a mix of wild pollinators and honeybees or other substitutes, but any loss in wild pollinators would increase the cost of pollination (as more honeybees or substitutes are required), as would threats to honeybees such as a disease or pest outbreak. If the costs of providing pollination services are low compared to the gross value of production, farmers are likely to be able to accept this cost increase. If costs are high compared to the gross value of production, then farmers will either pass on the costs to consumers, or leave the market. Table S5.3 compares the price of pollination by honeybees, with the Gross Value of Production (GVP). For most crops the cost of pollination relative to GVP is quite low (less than 4%), though for businesses operating on the margin any increases in costs will be significant. Firms will only be able to pass price rises onto consumers if imports for the crop are not easily available. The current “self-sufficiency” of the crop has been calculated as the UK consumption of these crops, over the UK production. Consumers of crops such as strawberries, with a relatively high cost of pollination to GVP ratio, and a high self-sufficiency, are more likely to be affected by rises in the cost of pollination.

U. What substitutes exist for the main ecosystem services from the asset?	*For the services identified in G, are substitutes available? If so what supplies are available or potentially available?* ***Substitutes for crop pollination*** There are substitutes available for crop pollination; there is a large industry for commercial bumblebees, which were developed for use in greenhouses but can be used in polythene tunnels and in open fields. There are increased efforts to domesticate solitary bees such as *Osmia rufa* in man-made nests which can be placed throughout orchards and fields. Honeybees themselves, are a substitute for wild pollinators, but have been treated as natural capital in this evaluation for the reasons outline in section A. Further research and development may increase the availability of non-bee pollinators such as hoverflies. The difficulty with substituting wild pollinators entirely is that such substitutions are costly, and substitution may not be perfect; one commercial species is unlikely to provide the breadth of functional provided by a natural community (Hoehn, Tscharntke et al. 2008). Commercial solutions also tend to focus on single-species (for example *Bombus terrestris* is the main commercialised pollinator used in Europe), this can increase the vulnerability of the system to disease threats and environmental changes, as such threats will no longer be buffered by a diverse range of species. Substitutes are however, useful for increasing the abundance of pollinators in a location at a particular time. ***Substitutes for wild plant pollination***

	While honeybees do spillover and pollinate wild flowers (Tuell et al., 2008), and bee farmers focused on honey production will move nests to utilise wild flower resources (i.e. heather), honeybees are not able to pollinate all wild flowers both due to morphological and phonological limitations. Even if they were able to pollinate all wild plants which require insect pollination, it would require a redistribution of the honeybee stock to woodland, grassland and riparian habitats, and away from urban areas, which would be infeasible from a cost and management perspective. Wild plant pollination is therefore much more difficult to substitute and therefore more vulnerable to loss of pollinators than crop pollination.
Uncertainties	*Give level of uncertainty* in analysis and reasons for this.* Established but incomplete evidence. Though there will be thresholds below which wild pollinator populations will be threatened, the lack of systematic abundance monitoring makes it very difficult to tell where these thresholds are. Current monitoring networks can detect changes in species richness over time, but only detect species losses after they have occurred. The economic risks of pollinator decline depend not only on the extent of wild pollinators but on the price and availability of substitutes. Assessments of vulnerability of consumers to such changes can only be made crudely.

5.6 Natural capital asset check

Question	Guidance on Answer
V. Tradeoffs?	*If one or more of the asset’s key ecosystem services (see question D) are increased, does this lead to reductions in other services?* The pollination of mass flowering crops such as oil seed rape has the potential to distort the wild pollinator population by increasing the number of short-tongued bumblebees relative to long-tongued bees (Diekoetter et al., 2010). These short-tongued bees can then spillover to wild flowers and may nectar rob from flowers with long corollas, reducing the food sources available for long-tongued species. Pollination services to crops and to wild plants could trade-off against each other unless efforts are made to provide forage for both short and long tongued species post flowering. During flowering there may also be a trade-off between wild flower pollination and crop pollination as pollinators are drawn away from wild flowers and so flowers with concurrent pollination needs may suffer from pollinator dilution (Holzschuh et al., 2011). Similarly, increasing in honeybees could lead to competition with native pollinators for foraging resources driving down wild pollinator populations (Goulson & Sparrow, 2009), the overall impact of such competition will depend on the number and placement of honeybees but may be more likely to occur after the target crop has stopped flowering, during the “hungry

	gap". Given the importance of both honeybees and wild pollinators, it would be unwise to support honeybees at the expense of wild pollinators, and vice versa.
W. Synergies?	*If one or more of the asset's key ecosystem services (see question D) are increased, does this lead to increases in other services?* The key ecosystem services from the pollinator asset are crop pollination and wild flower pollination. As outlined above there is evidence that wild flower pollination could suffer as a result of increasing pollination to mass flowering crops. However mass flowering crops will also provide a food source to pollinators, increasing colony success if the resource is properly managed. The difference between mass-flowering crops aiding populations and degrading populations will depend on the balance between increased nutrition and post-flowering disadvantages such as increased competition and increased parasite density. The balance between these factors was studied in *Osmia rufa* by Jauker and colleagues (Jauker et al., 2012), who found that the positive effects outweigh the negative post-flowering effects. This is likely due to reasonable synchrony between oil seed rape flowering and *Osmia rufa* lifecycles. Increasing the *Osmia rufa* population should increase the potential for wild plants as well as mass flowering plants to be pollinated in the following year. Mass-flowering crops increase the growth of bumblebee colonies early in the season, but this does not translate in increased reproduction (Westphal et al., 2009), the timings of oilseed rape flowering are therefore not beneficial to bumblebee reproduction despite increasing early colony growth.

	Honeybees do spillover and pollinate wild flowers surrounding arable landscapes (Tuell et al., 2008), however wild bees, although at a similar abundance to honeybees, visited all 43 wild flower species in the area, whereas honeybees were only seen to visit 24 out of 43. Honeybees cannot be relied upon to pollinate all wild flower species. This is unsurprising, as the wild pollinator assemblage is made up of many species with different floral preferences and phenology as opposed to the honeybee population which is composed of only one species. Increasing honeybee numbers will therefore, benefit some wild plant species, but only in areas within flight distance of hives, and only some species. Increasing wild pollinator numbers will be of benefit to wild flower populations if functional diversity of species is preserved.
Uncertainties	*Give level of uncertainty* in analysis and reasons for this.* ** Use Uncertainty scale described in introduction.* Competing explanations.

	There are potential trade-offs between wild plant pollination and crop pollination, however there are also potential synergies. Whether the outcome is positive or negative will depend on the balance of these. There are some management interventions (such as growing plants which will flower just after mass flowering crops) which will assist in creating a positive outcome, but uncertainty around the eventual outcome.
X. Sustainability test: is the asset currently able to give the target performance?	*Compare integrity in question I and performance in question L.* The asset of honeybees is not currently able to pollinate all crops in the UK. There is a trend towards increased honeybee numbers but this will not lead to increased pollination services unless the colonies can be moved around the UK to meet pollination needs. This is unlikely given the amateur nature of new beekeepers, who may not keep with the activity in the long term. Wild pollinators do a large proportion of crop pollination across the UK, but may not be sufficiently abundant to meet increased pollinator needs, particular across large fields associated with increased oil seed rape production.
If yes - will this performance be sustained into the future?	*Relate changes from question O and criticalities from P and Q to future changes identified in questions M and N. Give timescale – from question C.*
If no – state why?	*Is this because target performance is unrealistic, or because integrity of asset is compromised, or both?*

	The pollinator assets of the UK are not being managed with pollination in mind. Honeybees are for the most part, used for recreation and small scale honey production. The large scale bee-farmers do not have sufficient capacity to meet the UK's pollination requirements. The population sizes of common wild pollinators are not known.
Y. Red flags?	*This is a warning if future target performance is at risk, for example because:* *- the asset is underperforming (see question X) and continuing to decline (see Question O), or* *- there is prospect of collapse (a limit or threshold – see questions P and Q) which could be irrecoverable (i.e. being irreversible, see question R, and with no substitute, see question U)* Overwintering rates are a suitable indicator of honeybee stress and should continue to be monitored. Wild pollinator populations would benefit from systematic monitoring allowing populations to be tracked over time. The current monitoring system is better at detecting local population loss, but does not detect declines in populations which could alert land managers to conservation priorities. Incidents of large scale pesticide poisonings have not increased in the UK but any increase in oil seed rape production area will increase the exposure of bees to neonicotinoids. Populations should be monitored for neonicotinoid residues and any impacts of these. Hoverflies are not efficient pollinators but appear resistant to land use changes which affect bees, they may therefore be vital to conserving pollination services into the future and should be monitored for population stress.

	Overwintering rates in honeybees are not currently a cause for concern. The continued loss of wild flower diversity and pollinator diversity however, should be seen as a red flag. The latest data showing a slowing of the decline in wild flower species richness is a positive sign.
Uncertainties	*Give level of uncertainty* in analysis and reasons for this.* *Use Uncertainty scale described in introduction.* There is a possibility that declines in specialised and small bodied species are a relic of post-war agricultural intensification and do not represent a current downward trend. However if there is any positive feedback between wildflower loss and pollinator loss then the trend would be expected to continue, particular as nectar producing plants have also been lost to succession in the last 20 years, which will further stress wild pollinator populations. Established but incomplete evidence.

Table: Summary of natural capital asset check					
Asset	**Trends in natural asset integrity**	**Target performance**	**Criticalities**	**Sustainability of performance**	**Red Flags**
Questions A & B The pollination service provided by insects to crop plants across the UK. The main insect pollinators, bees (including bumblebees, honeybees and solitary bees) and hoverflies are considered. These pollinators are part of	*Question I* Although honeybee numbers are increasing, the increase in number of colonies is made up of those kept by amateur beekeepers, mainly in suburban areas. Some crops and many wildflowers are not well pollinated by honeybees. However the condition of honeybees is well monitored and new policies in place will further safeguard honeybees. Wild bee diversity has declined and insect pollinated wild plant species richness continues to decline in some habitats. Monitoring efforts have so far detected losses of rare	*Question L* Insect pollination boosts the yield of crops, increasing the market value and allowing farmers to stay in production. The target performance varies from crop to crop (see table S5.2), as different crops require different stocking densities so that pollination does not limit production. In addition to the performance in relation to the	*Key issues from part 4, particularly questions P and Q* There are no agreed limits of change to the honeybee asset, although honeybee plans are now in place for “sustainable” pollination suggesting that resilience of the honeybee stock is a priority. There are no agreed limits of change to wild pollinators. A diverse mix of wild pollinators and honeybees will reduce the probability of collapse of pollinator services. Honeybees are vulnerable to	*Question X* The asset of honeybees is not currently able to pollinate all crops in the UK. There is a trend towards increased honeybee numbers but this will not lead to increased pollination services unless the colonies can be moved around the UK to meet pollination needs. This is unlikely given the amateur nature of new beekeepers, who may not keep with the activity in the long term. Wild pollinators do a	*Question Y* Overwintering rates are a suitable indicator of honeybee stress and should continue to be monitored. Overwintering rates in honeybees are not currently a cause for concern. Wild pollinator populations would benefit from systematic monitoring allowing populations to be tracked over time. Incidents of large scale pesticide poisonings have not increased in the UK. Hoverflies

the wider network of pollinators across the UK, which also supports the sexual reproduction of wild plants.	species, there are no systematic schemes for monitoring the abundance of common species so the trends are not clear. Pollination services to wild plants are at risk, particularly for specialised plant species, as the diversity of these have declined in parallel with pollinators with narrower niche breadth. Whether the asset as a whole is able to support crop pollination depends on the specific requirements of crops.	producers, the pollinator assets should also sustain wild flower and plant pollination.	acute shock such as diseases as pathogens can spread quickly between colonies. The integrity of the asset could decline in a non-linear way if there is a positive feedback between wild flower diversity loss and pollinator diversity.	large proportion of crop pollination across the UK, but may not be sufficiently abundant to meet increased pollinator needs, particular across large fields associated with oil seed rape production.	are not efficient pollinators but appear resist to land use changes which affect bees, they may therefore be vital to conserving pollination services into the future and should be monitored for population stress. The continued loss of wild flower diversity and pollinator diversity however, should be seen as a red flag. While short-tongued bumblebees and generalist populations do not seem in peril, those with a narrower habitat niche are in decline. New data showing decreasing

					rate of decline of flowering plant richness is encouraging and should continue to be monitored.
Level of Certainty	*Established*	*Established but incomplete evidence*	*Competing Explanations*	*Established but incomplete evidence*	*Established but incomplete evidence*

5.7 Appendix

Overwinter Losses	Year					
	2006-2007	2007-2008	2008-2009	2009-2010	2010-2011	2011-2012
Scotland[1]	17.5%	21.4%	nd	27.3%	21.8%	nd
England[2]	nd	30.5%	18.7%	17.7%	13.6%	16.2%
USA[3]	31.8%	35.8%	28.6%	34.4%	29.9%	nd
Europe (average)[4]	nd	Nd	12.3%	16.9%	nd	nd

nd = no data

1. Peterson et al (2012a, 2012b, 2010), Gray et al (2007).
2. BBKA (2012)
3. VanEngelsdorf et al (2012, 2011, 2008, 2007)
4. Vanderzee et al 2012

Table S5.1: Table comparing overwintering losses for honeybees in Scotland and England with the USA and European average as comparators.

Crop	Honeybee Stocking density	Bumblebee density	Flowering time	Pollinators	Vulnerability
Oilseed rape	5	7	Mid	All	Mid
Strawberries	10	13	All year	All	High
Dessert apples	7	9	Early	Solitary bees preferred	High
Culinary apples	7	9	Early	Solitary bees preferred	High
Raspberries	1.5	2	Mid	Bumblebees preferred	Low
Blackcurrants	6	8	Mid	Bumblebees preferred	High
Runner beans	1.5	2	Mid	Long-tongued Bumblebees	Mid
Cherries	3	4	Early	Solitary bees preferred	Mid
Broad bean	4	5	Mid	Long-tongued Bumblebees	High
Plums	4	5	Early	Solitary bees preferred	Mid
Pears	3	4	Early	Solitary bees preferred	Mid

Table S5.2: Table to assess the vulnerability of 11 UK grown crops to wild pollinator loss. Equivalent bumblebee stocking densities are calculated using the conversion factor in Drummond (2012) and honeybee stocking densities from Breeze et al, 2011. Vulnerability was assessed from 1 to 5, with 5 being very vulnerable, score increased with importance of wild bee pollinators, and with high pollinator density requirement with low location wild bee factor.

Crop	Cost per ha commercial pollination	GV per ha	Cost pol/GV	Trend in tonnes	HPV £000	Import value £000	% Sufficiency	Consumer Price vulnerability
Strawberries	400	11.92	3.36%	Increase	279,118	119,904	70%	High
Dessert apples	560	12.85	4.36%	Slight increase	64,054	318,331	17%	Mid
Culinary apples	560	11.48	4.88%	Slight increase	41,958	318,331	12%	Mid
Raspberries	120	26.46	0.45%	Increase	117,505	50,716	70%	Low
Blackcurrants	480	32.5	1.48%	Stable	11,185	nd	nd	nd
Runner beans	60*	92.35	0.001%	Decreasing	15,562	28,058	36%	Low
Broad beans	150*	16.97	0.88%	Stable	4,414	80,667	5%	Low
Plums	320	8.9	3.60%	Stable	12,313	64,725	16%	Mid
Pears	240	14.49	1.66%	Stable	14,823	87,956	14%	Mid

Table S5.3. Table to evaluate how important changes in pollinator supply will be to changes in consumer and producer welfare. Costs per ha of honey pollination are based on honeybee densities from table 5.2, and the assumption of a hiring price of £80 per colony. GV per ha is the gross crop value per ha in 2011 (DEFRA, 2013). Trend in tonnes is the overall trajectory of the total volume produced in the UK since 2000. HPV is the total value of the crop in sales. Price vulnerability was deemed to be high for crops with high proportion of home production relative to imports, as for these crops producers may be more able to transfer prices to customers. Crops with low price vulnerability are less likely to be able to pass on higher prices to consumers, so increases in costs will decrease producer welfare and may cause suppliers to leave the market. *Runner beans and broad beans cannot be pollinated by honeybees and so the price of bumblebee substitutes are used, however the most common commercial bumblebee used in the UK is *Bombus terrestris*, a short-tongued bee which may nectar rob from flowers to these crops and therefore provide less pollination than wild bumblebees.

Chapter 6

Overall Discussion

6.1 Are there benefits of preserving wild bees for pollination?

The importance of wild bees for pollination services has been highlighted in recent years not least because the most widespread managed pollinator, the honeybee, has faced multiple threats leading to concern over future pollination services (Cox-Foster 2007). It has been recognised that wild pollinators can play a large part in pollination even in areas that honeybees are used. Wild pollinators increase crop yields of a range of crops from fruit such as melons to global staples such as coffee and oilseeds (Garibaldi et al., 2013). Despite this, the presence of relatively new and convenient substitutes for wild pollinators such as commercially bred bumblebees means that conservation of wild pollinators is not necessarily an economic imperative for farmers. This thesis aimed to look at the potential benefits of supporting an assemblage of wild pollinators to private farmers, and to provide some insight into how pollinators can be managed for ecological and economic aims.

Chapters 2 and 3 include results from field studies undertaken across an 80km^2 area of Scotland, UK, well-known for soft-fruit production. Fruit farmers in this area are reliant on a mixture of commercial bees and wild pollinators the most abundant of which are bumblebees (Lye, 2011). Chapter 2 looked at the relative contribution of wild and commercial pollinators to strawberry and raspberry yields, and at the relationship between functional traits of these pollinators and crop yields. Chapter 3 returned to raspberry farms and asked whether on-farm use of neonicotinoids could affect wild bees foraging on the crop. Chapters 4 and 5 took two different approaches to assessing management of pollinators. Chapter 4 providing a quantitative model of farm-level decision making, using farm business data and an ecological-economic model to investigate the trade-offs between pesticide use, commercial bee use and habitat provision on fruit farms. Chapter 5 instead used a broadly qualitative framework across a national scale to see whether or not the UK is able to support pollinators to a sufficient extent for current and future crop pollination.

6.2 The contribution of wild pollinators and pollinator diversity to crop yields

While there have been studies linking increased diversity of pollinators to increased ecosystem services (Kremen et al., 2002), the actual relationship between pollinator diversity and seed or fruit set will depend on whether different pollinator groups add to the range of flowers pollinated (are complementary) or increase the pollination level provided by another group (are facilitative). The flowers of crop plants are arranged across multiple dimensions; pollinators may be required to pollinate at different heights or at different depths between leaves or boughs of trees. Flowers also need to be visited at different times; crops with long growing seasons may benefit from pollinators with active periods along the season (Bluetghen & Klein, 2011).

Flowers exposed to different weather conditions may be best pollinated by a group of species so that pollination can occur even on days where the conditions are not optimal for the main pollinator.

Hoehn et al (2008) showed that increased diversity in foraging heights of pollinator groups increased seed set in pumpkins by placing pumpkins at different heights using stands. Brittain et al (2013a) looked at visitation and seed set of almonds in a natural setting by wild bees and honeybees, and found that complementarity in the spatial preferences of bees increased seed set in high diversity fields relative to those fields with only one pollinator type. This was particularly important under changing weather conditions where honey bees were displaced to lower areas (Brittain et al., 2013a). The study in chapter 2 also evaluates diversity in a real crop system. Strawberries are grown from April to September in Scotland and thus require pollinators over a long period of time. In addition, a long growing season exposes crops to a variety of weather conditions which may affect the activity of pollinator groups. Chapter 2 found that pollinator groups did pollinate at different times and commercial bees were used to fill in the gap in the first part of the year when no other pollinators were present. Honeybees and bumblebees pollinated under similar weather conditions but flies pollinated in conditions which were unfavourable for bees (Chapter 2).

The study in Chapter 2 used results from a pollen exclusion experiment and from visitation data recorded across the season. The pollen exclusion experiment was only carried out once, therefore yield data over time was simulated using the production function observed during the one-time pollinator exclusion experiment combined with visitation data at multiple time points. Ideally the pollination limitation experiment would have been conducted at times throughout the season.

Chapter 2 found that non-bee pollinators may play a more important role in the pollination of fruits than is perhaps assumed, as they are available to forage later in the year, and can pollinate in conditions which are unfavourable for other pollinators. This finding warrants further study; there are few studies of the influence of non-bee pollinators on crop production. In chapter 2 flies were assumed to require a 5-fold density higher than the more efficient pollinators, bumblebees. The exact relative relationship is not known. Further experiments excluding bees but allowing visitation of hoverflies and other flies would confirm whether flies can be important to commercial scale production.

There was no easy way to detect whether worker bees identified as *Bombus terrestris* were commercial bees or wild *Bombus terrestris/lucorum*. The identity was instead inferred from the numbers of *B. terrestris/lucorum* observed at sites not using commercial bees. It would be possible to test whether this assumption is reasonable by carrying out further visitation surveys. By shutting the commercial bumblebee nests on a subset of farms, we could be sure that the *B. terrestris/lucorum* observed on these farms were from wild nests.

Chapter 2 also added to literature on management and landscape influences on pollinator visitation. In line with findings from Steffan-Dewenter et al (2002) and Winfree et al. (2008), no influence of natural habitat on bumblebees was found. However there were differences in bee visitation rates between farms which were unexplained by the variables recorded from farm visits or from farm surveys. It would be interesting to see if unrecorded management differences such as pesticide spray rates, frequency of mowing near to the crops and floral and nesting resources near to the crop influenced pollinator visitation.

Raspberries were well pollinated at all farms and bumblebee densities observed were high and far greater than those densities seen on strawberries. Clearly attractiveness of the crop is a major factor in whether adequate pollination is achieved and clever management strategies may be needed to attract pollinators to crops such as strawberries. It may be the case that providing nesting sites close to the strawberry crop is necessary to improve bee visitation, whereas more attractive crops (such as raspberries) can draw in pollinators from wider areas.

6.3 The impact of neonicotinoids on nesting bumblebees

Neonicotinoid insecticides are highly toxic and have been shown to impact navigation and foraging of honeybees and bumblebees at levels well below the LD50, or 50% lethal dose. Whitehorn et al. (2012) looked at the impacts of dosing bumblebees in the laboratory with pollen and nectar laced with concentrations of the neonicotinoid imidacloprid (at a level that bees were likely to encounter in the field). Bumblebees were fed this for 2 weeks before they were allowed to forage freely. At the end of the experiment it was found that queen production was dramatically reduced in treatment nests compared to control nests (Whitehorn et al., 2012). Gill et al. (2012) took a similar approach and also included a pyrethroid and combined imidacloprid-pyrethroid treatment. In this case foraging rates and pollen loads were lower when workers had been fed on either the pollen with imidacloprid-pyrethroid or with just imidacloprid (Gill et al., 2012).

The study in chapter 3 provides evidence of effects of neonicotinoid exposure on nests from a field study carried out at working farms. While field level studies have been attempted, it is difficult to find non-neonicotinoid control fields due to the high level of these pesticides in the environment (Mullin et al., 2010; Sanchez-Bayo & Goka, 2014). Well replicated studies of foliar sprays should avoid this issue as it can be assumed that the base level of exposure does not systematically differ between control and treatment fields. One previous study looked at the impact of thiacloprid fed through irrigation systems and found that honeybee activity rates were affected but no hive level differences were observable (Schmuck et al., 2003). Bumblebee nests are smaller and therefore individual level effects are more likely to impact the nest. Laboratory studies of the impact of thiacloprid on bees have found that worker mortality is increased when bees are fed concentrations of thiacloprid below those found in pollen and nectar gathered by honeybees (Mommaerts et al., 2010). The study described in chapter 3 corroborates the findings from Mommaerts and colleagues; worker mortality as measured by the proportion of dead bees left in the nest at the end of the experiment, was higher in nests that had been exposed to thiacloprid than those which had not (Chapter 3). Overall reproductive output of these nests was also lower (chapter 3). An unusually rainy summer meant that the number of queens was very low in all nests and treatments, so it was impossible to tell whether the higher worker mortality would have impacted queen production.

As in chapter 2 the study was carried out at real working farms, which meant that actual farm conditions were replicated. The results can therefore be seen to be representative of what would happen to bee nests within the farm area during spraying. The nests will have been exposed to other stressors which were unmeasured and could have exacerbated the effects of the pesticide. Follow on work measuring other factors such as *Nosema* infestation within nests and other chemical use at these farms would provide further insight. Additional stressors found in the natural environment have been found to synergise the impacts of neonicotinoids, increasing the

LD50 above that from laboratory testing (Iwasa et al., 2004). Interestingly, wax moth infestation was slightly higher in treatment nests, which may suggest that nests are more likely to be infested when weakened by pesticides (Chapter 3).

A limitation of the study was that no pollen analysis was carried out at the farms. Analysis of the residues inside the nest would have strengthened the conclusion as nests were placed at slightly different times after spraying, and spray rates of foliar pesticides are not always uniform so nests were likely to be exposed to thiacloprid at different concentrations. Analyses of residues found within honeybee nests have shown some extremely high concentrations of thiacloprid in Germany and Poland (Genersch et al., 2010; Pohorecka et al., 2012). Quantifying the actual exposure of bumblebees and larvae within the nests to thiacloprid will be important to link exposure to the pesticide to increased mortality rates directly.

6.4 Does the availability of commercial substitutes for pollinators affect farm management decisions?

When farm decision making is modelled, it is usually assumed that substitutes for wild bees are not available and that all bees on the farm come from within the farm landscape. Under these conditions part of the farm area must be set-aside for nesting habitat. The question of how much set-aside and the distribution of habitat areas has been investigated using a simple linear farm and a deterministic model of foraging and reproduction (Brosi et al, 2008), and using a grid-based model and individual bee movements (Keitt, 2009). Keitt's model included stochastic pollination and reproduction (wild flowers in the landscape increased the chance of nest reproduction but did not guarantee it) and the results showed that a critical level of habitat was required to avoid pollinator extinction and low yields. The model in chapter 4, while still including necessary simplifications, included additional features which better reflect actual farm decisions. The model included the option of purchasing commercial bees, and pesticide use was included and assumed to affect both pollination and yield. In addition to these features the model was parameterised using farm business data (chapter 4).

The results show that the ability to purchase commercial pollinators could mask declines in wild bees leading to falls in profits years after the purchasing decisions are made (chapter 4). While economic modelling generally assumes that farmers have perfect foresight, this is unlikely to be the case. Given that yields are variable for a number of factors a decline in wild bee pollination will not be easily spotted. This will be especially true if commercial bees are used as poor fruit quality will not be observed until wild pollinators have decline markedly. The results of chapter 4 show that the private benefits from wild pollinators are only observable under certain conditions, either if no commercial substitutes are used, or if both wild pollinators and commercial pollinators are necessary and wild pollinator declines begin to limit yields. It follows that if wild pollinators are to be supported on farms, then incentives may be required.

Some modelling of nest dynamics has successfully predicted the paths of nests under stressors (Bryden et al 2013), but generally models of nest dynamics are difficult to parameterise, particularly as key processes such as nest reproduction and queen hibernation are virtually unstudied (though see Mueller & Schmid-Hempel, 1992). Modelling of nest growth and reproduction would be greatly improved by research into these processes both in laboratory reared nests and wild nests. A very simple production function was used in chapter 4; this function was reflective of the findings for relationship between strawberries and pollinators from chapter 2. Actual visitation will depend not just on how many pollinators are nesting within the farm area, but also on the relative attractiveness of different plants alternative forage in the landscape and on the populations of pollinators within the wider landscape outside of the farm (Kremen et al., 2007).

An obvious extension of the model would be to include interactions between the farm and pollinators within the wider landscape. These pollinators will be able to move to forage within the farm area, and may also be affected by pesticides within the farm area.

6.5 Natural Capital Asset Check

Chapter 5 presented the Natural Capital Asset Check (NCAC), undertaken as part of the follow on phase of the UK's National Ecosystem Assessment (NEA). The original NEA aimed to provide an overview of the value of the UK's ecosystem services. The conceptual framework for doing so split the UK ecosystem services into different categories of ecosystem services including regulating services such as pollination. The NEA valued the annual pollination services at £430 billion, based on the difference that pollination makes to the value of crop production in the UK (Smith et al, 2011). The Natural Capital Asset Check built on this work with the aim of providing a framework by which to assess if the current and expected extent and quality of natural capital are adequate to provide required levels of ecosystem services.

The NCAC case study for crop pollination is reported in chapter 5. This case study reviewed the evidence regarding the range and abundance of wild pollinators and honeybees across the UK. It was noted that declines in bumblebee diversity were reported to have slowed (Carvalheiro et al., 2013). The data gaps are also notable; data is no longer collected on honeybee numbers at a national level and there is no systematic monitoring of pollinator populations. Evidence of bumblebee declines has been taken from long-term records from which trends in diversity and range can be found but little can be said about bumblebee abundance which might be the more important factor for understanding if the needs or crop pollination are met.

Models such as that presented by Lonsdorf et al can be used to predict relative abundance using landscape information (Lonsdorf et al, 2009). However this model has not performed well in heterogeneous landscapes which may predominate in the UK. Breeze et al. (2011) used predicted honeybee colony numbers and compared these to stocking densities of different crops to establish whether supply could meet the demand for pollination services in the UK. However, this analysis assumed that honeybee nests were moved to areas where pollination was required which is unlikely as the vast majority of beekeepers in the UK are hobbyists. In Chapter 5, published nest data and information on stocking densities for particular crops were used to provide an assessment of the vulnerability of different crops to bumblebee declines (Chapter 5). Nest cover has been evaluated in areas of the UK but not over wide areas, and the densities of bumblebees required for crop pollination were estimates based on stocking densities for honeybees. While this approach to evaluating the performance of pollinators has potential, a proper assessment would require either more widespread surveys of nesting densities in different habitats, including on farms, or abundance data at flowering times for particularly crops. Similarly the NCAC required contributors to answer questions on the likelihood of thresholds being breached, or the likelihood of populations of pollinators being at unsustainably low levels. While it would be useful to have such information such questions are difficult to answer without having long-term monitoring systems in place.

It is not unfeasible to think that in a few years' time ecosystem services will be monitored in a systematic way and we can then start to see if policy interventions are having the intended effects. To get to this point would require substantial funding for monitoring programmes, and also continued investment into maintaining and building the expertise required to undertake research into natural capital thresholds and to use the data appropriately.

6.6 Overall conclusions

The studies in this thesis were limited to the private benefits of wild and commercial pollinators. While I found that wild pollinators are particularly important to attractive fruits such as raspberries (chapter 2), and diversity is important for pollination throughout the season in strawberries (chapter 2), I also found that the private incentives to conserve were low when cheap substitutes are available (chapter 4) and neonicotinoids, while being essential to healthy crop yields, do have detrimental effects on nests near to crops (chapter 3). So while wild pollinators are valuable to farmers, maintaining healthy populations around farms may require incentives for habitat sparing or protection. Chapter 5 highlighted the knowledge gaps surrounding bee populations. Without nationwide systematic monitoring systems in place, we do not know whether the populations of the more common bee species in the UK are increasing or decreasing in size. Similarly, national recording of honeybee colony numbers stopped in 1992.

In chapters 4 and 5, conclusions had to be drawn from data or models involving high levels of uncertainty. Unlike man-made capital, growth and changes to natural capital cannot be easily monitored or costed. Applying techniques from other types of capital to natural capital leaves open the possibility of getting some assumptions entirely wrong. Quantitative modelling such as in Chapter 4 is more useful for understanding the relationships between factors, than for making strict management recommendations.

I focused on the interactions between bees and agriculture; while the benefits of bees to agriculture are not straightforward to calculate, there is a marketable product in the form of fruit or seeds. Other benefits of pollinators are more difficult to value but should not be ignored. These include the pollination of flowering plants and trees and any ecosystem services which stem from these including recreational values of parklands and meadows. These services are valuable not only to humans but to birds and animals which feed on wild fruits and to the integrity of the wider ecosystem. Bees including honeybees are also an essential and charismatic part of the countryside. While these services are difficult to measure excluding them ignores a large part of the value of nature. Broader frameworks which acknowledge the difficulty of measuring ecological services and the uncertainties inherent to complex ecological systems could play an important role in decision making particularly when quantification is difficult or impossible.

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