Journal of Applied Ecology

British Ecological Society

Journal of Applied Ecology 2016 doi: 10.1111/1365-2664.12718

Providing foraging resources for solitary bees on farmland: current schemes for pollinators benefit a limited suite of species

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Summary

1. Changes in agricultural practice across Europe and North America have been associated with range contractions and a decline in the abundance of wild bees. Concerns at these declines have led to the development of flower-rich agri-environment schemes as a way to enhance bee diversity and abundance. Whilst the effect of these schemes on bumblebee species (*Bombus* spp.) has been well studied, their impact on the wider bee community is poorly understood.

2. We used direct observations of foraging bees and pollen load analysis to quantify the relative contribution that sown flowers (i.e. those included in agri-environment scheme seed mixes) make to the pollen diets of wild solitary bees on Higher Level Stewardship farms (HLS) implementing pollinator-focused schemes and on Entry Level Stewardship farms (ELS) without such schemes in southern England, UK.

3. HLS management significantly increased floral abundance, and as the abundance of sown flowers increased, these sown plants were utilized for pollen by a greater proportion of the solitary bee species present. However, the overall proportion of pollen collected from sown plants was low for both direct observations (27·0%) and pollen load analysis (23·3%).

4. At most only 25 of the 72 observed species of solitary bee (34·7%) were recorded utilizing sown plants to a meaningful degree. The majority of solitary bee species did not collect pollen from flower species sown for pollinators.

5. Total bee species richness was significantly associated with plant species richness, but there was no difference in the total species richness of either bee or flowering plant species between HLS and ELS farms.

6. *Synthesis and applications*. Our results show that the majority of solitary bee species present on farmland in the south-east of England collect most of their pollen from plants that persist unaided in the wider environment, and not from those included in agri-environment schemes focused on pollinators. If diverse bee communities are to be maintained on farmland, existing schemes should contain an increased number of flowering plant species and additional schemes that increase the diversity of flowering plants in complementary habitats should be studied and trialled.

Key-words: agri-environment, agroecosystems, Apoidea, bee conservation, biodiversity, farmland, habitat quality, pollen diet, pollinator schemes, wild bees

Introduction

Wild bees, in common with many other taxa, have experienced declines in richness and abundance across Europe and North America (Biesmeijer *et al.* 2006; Williams & Osborne 2009; Bartomeus *et al.* 2013; Goulson *et al.* 2015). This is of concern as pollinating insects, of which bees are the dominant group, provide a highly valuable pollination service to both crops and wild plants (Ollerton, Winfree & Tarrant 2011; Garibaldi *et al.* 2013). With the demand for increased agricultural yields growing

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across the world, potential pollination deficits have increased the pressure to develop effective management techniques to conserve and maintain bee populations on agricultural land.

There is an increasing consensus behind the idea that food resources are the most important limiting factor for bee populations on farmland (Roulston & Goodell 2011) and that loss of flowering resources resulting from agricultural intensification is the major cause behind the declines in bee populations seen in the 20th century (Carvalheiro *et al.* 2013; Ollerton *et al.* 2014; Scheper *et al.* 2014). Moreover, a reduction in the diversity of pollen sources can have negative impacts on bee fitness through reduced development and immunocompetence (Alaux *et al.* 2010). As a result, the creation of flower-rich habitat through agri-environment schemes has been advocated and trialled as the primary means of conserving and enhancing bee abundance and diversity on farmland (Carvell *et al.* 2007; Winfree 2010). In the United Kingdom, much of the early work on agri-environment schemes focused on bumblebees (*Bombus* spp.), due in part to their particularly pronounced declines in agricultural areas (Goulson *et al.* 2005). Schemes were consequently designed with the foraging requirements of bumblebees in mind, specifically including a large Fabaceae component comprised of plants such as *Trifolium pratense*, *T. hybridum* and *Lotus corniculatus* (Edwards 2003; Carvell *et al.* 2007). Research has shown that these sown resources are attractive to a wide variety of common and threatened bumblebees (Carvell *et al.* 2006, 2007), and that when present in sufficient quantities, they can significantly increase the population size of common bumblebee species (Wood, Holland & Goulson 2015a). However, much less work has been carried out on the impact of agri-environment schemes on the wider bee community.

In temperate areas such as Britain, bumblebees make up only a small part of the overall bee community, representing around 10% of the total species list (25 out of c. 250 species), and in the larger continental faunas of Europe and North America, they represent an even smaller proportion. The wider bee community consists of predominantly solitary species (and their associated kleptoparasites) that collect pollen to provision their own offspring. The fauna contains a number of species within the Halictidae that show variably developed and expressed eusocial behaviour (Plateaux-Quénu 2008). Whilst not technically correct, the term ‘solitary bees’ is generally used as an all-encompassing term to include the eusocial species of the Halictidae with all non-parasitic, non-corbiculate (non-*Apis* and non-*Bombus*) bees found in temperate regions, with this synthetic group the focus of this study.

In order to assess the benefit of an agri-environment scheme, field trials have often compared target areas with control areas and have recorded an increase in bee species richness and abundance (e.g. Knop *et al.* 2006; Kohler *et al.* 2007; Pywell *et al.* 2011) or an increase in important behaviours, such as bumblebee queen nest site searching (Lye *et al.* 2009). Ideally, measures should be assessed by comparing bee trends on sown flower strips before and after implementation of the schemes (Kleijn *et al.* 2006), with such studies finding a positive impact on bee species richness and abundance (Holland *et al.* 2015; Scheper *et al.* 2015). However, whilst these studies show that enhanced areas provide resources for a greater variety of bee species than before, it is not clear that the overall bee community has become richer as a result of the intervention, as some bees that were already present in the landscape may simply have been attracted to enhanced areas. Moreover, the relative contribution of pollen from sown plants to the diet of different solitary bee species is poorly known, and whilst they may be attracted to sown flowers, these resources may not make up a significant proportion of their overall diet. Data on *Bombus* species, other than presence, were not collected due to the extensive previous work conducted on this group on farmland and their response to agri-environment schemes (Carvell *et al.* 2006, 2007).

In this study, we conducted extensive surveys across a range of farms in southern England and quantified the pollen diets of wild solitary bees using direct observations and pollen load analysis to address the following objectives: (i) to compare the contribution that plants sown as part of agri-environment schemes make to the pollen diet of solitary bees relative to that provided by wild plants. We predict that as sown resources increase in relative abundance, they will increase in relative utilization by solitary bees; (ii) to quantify the proportion of solitary bee species using sown resources. We predict that as sown resources increase in relative abundance, they will be utilized by a relatively greater proportion of solitary bee species; (iii) to identify solitary bee species most likely to be benefiting from currently sown resources; and (iv) to identify potential temporal resource gaps in current agri-environment scheme design, or key wild flowering plant species not currently included in seed mixes. This study will provide valuable information to scientists, governments and land managers in designing more effective measures to conserve the broader wild bee community on agricultural land.

Materials and methods

STUDY AREA

Nine HLS and ten ELS farms were selected in Hampshire and West Sussex, UK. The selected HLS farms had been implementing an average of 5·56 ± 0·13 ha of pollinator-focused flower-rich schemes representing 2·17 ± 0·05% of the farm area by ownership for a minimum of 3 years. As 70% of farms in England were at the time in some form of environmental stewardship (Elliot 2013), ELS farms were chosen as the control group for this study. Flower-rich schemes were available under ELS, but these schemes had a low uptake so only basic ELS farms without such management were selected for this comparison. Pollinator-focused flower-rich schemes were typically established with a seed mix containing c. 15–30 flowering forb species (Carvell *et al.* 2007; Pywell *et al.* 2011). Additional plant species such as *Hypochaeris radicata* and *Trifolium repens* are sometimes included in experimental mixes (i.e. Scheper *et al.* 2015), but this did not represent the situation in our study area and so these species were not characterized as sown. Whilst there were no such flower-rich areas on ELS farms, most of the species included in these seed mixes can be found growing in a wild state on these farms. Consequently, in order to allow a comparison of pollen choice preferences and relative rates of utilization across farm types, plant species included in pollinator-friendly agri-environment schemes were characterized as 'sown' even when found growing wild as part of the wider plant community. For a full list of the plant species characterized as being sown as part of pollinator-focused management, see Appendix S1 in Supporting Information. Farms were predominantly arable, or mixed arable/dairy with wheat, barley, oilseed rape and permanent/silage grassland as the major crops.

BEE AND FLORISTIC SURVEYS

In 2013 and 2014, a standardized 3-km transect was designed for each farm, passing through all major habitat types present. For HLS farms, this included pollinator-focused flower-rich schemes (HE10 floristically enhanced grass margins, HK7 species-rich grassland restoration, HF4 pollen and nectar mixes), non-agricultural grass margins and hedgerow and woodland edge habitats. For ELS farms, only non-agricultural grass margins and hedgerow and woodland edge habitats were surveyed, as no pollinator-focused schemes were present. Crops and areas of agricultural grassland were not surveyed. Each transect was subdivided into discrete sections, with each section covering a distinct habitat type. Transects on HLS farms were designed to survey as many pollinator-focused schemes as possible whilst remaining contiguous and passed through an average of 1496 ± 148 m of flower-rich habitat in an average of 3·77 ± 0·24 discrete habitat patches per farm.

Bee activity was recorded along the transect following standard bee walk methodology (Carvell *et al.* 2007), with all bees within 2 m of the recorder identified to species level. Individuals that could not be identified in the field were netted for later identification. The first flowering plant species visited, and the purpose of the visit, for either pollen or nectar, was recorded. *Hylaeus* species, which lack scopal hairs on their body, instead ingesting pollen and regurgitating it in the nest, cannot reliably be determined to be foraging for pollen and so all plant visits were recorded simply as visits. On each transect, the number of species of flowering plants and the number of flowering units of each plant species within 2 m of the recorder was estimated within each discrete transect section. Grasses, sedges and rushes were not recorded as these plant species are not attractive to bees in the study region. This assessment followed Carvell *et al.* (2007) with one flower cluster (e.g. an umbel, a head, a capitulum) counted as a single unit. Sixteen farms (eight HLS, eight ELS) were surveyed in 2013. Transects were walked three times through the season, between 25th May–5th June, 26th June–15th July and 3rd–11th August. Seventeen farms (eight HLS, nine ELS) were surveyed in 2014. Transects were walked three times through the season, between 17th–27th May, 21st June–9th July and 3rd–15th August. These discrete sampling blocks are henceforth referred to as 'sampling rounds'.

In 2015, farms were surveyed for a fixed period of time rather than using distance based transects. ELS farms were surveyed for 3 h with 1·5 h spent on non-agricultural grass habitats and 1·5 h on woody hedgerow/woodland edge habitats. HLS farms were surveyed for 3 h with 1 hr on pollinator-focused flower-rich schemes, 1 hr on non-agricultural grass habitats and 1 hr on woody hedgerow/woodland edge habitats. The survey followed standard bee walk methodology as described above, but at a reduced pace to ensure thorough sampling. All bees within 2 m of the recorder were identified to species level. The first flowering plant species visited, and the purpose of the visit, for either pollen or nectar, was recorded. Solitary bees with clearly visible pollen on their body were collected, placed in individual Eppendorf tubes and frozen. The collection of pollen loads from foraging bees may overestimate pollen use of more easily observable flowers. Ideally, pollen would be sampled from bees as they return to their nest, but this method was not chosen for this study as is often time-consuming and may lead to low sample sizes for species with difficult to locate nests. All flowering plant species present on the transects were recorded, but their abundance was not quantified. Pollen samples from insect visited flowering plant species present were collected to form a pollen reference library. Pollen reference slides were prepared by transferring pollen-laden anthers to a drop of water on a microscope slide. The slide was gently heated to allow grains to absorb water and achieve their maximum size and to evaporate excess water. The remains of the anthers were removed, molten glycerine jelly stained with fuchsin was added and the slide was sealed with a coverslip. For a full list of sampled flowering plant species, see Appendix S2. Fourteen farms (7 HLS, 7 ELS) were surveyed in 2015. Transects were walked four times throughout the season, between 22nd April–13th May, 26th May–17th June, 25th June–4th July and 29th July–10th August. All bee surveys were conducted between 0930 and 1700 h when the temperature was above 13 °C with at least 60% clear sky, or above 17 °C with any level of cloud. No surveys were conducted when it was raining. All bee and floristic surveys were conducted by the same individual (TJW) to minimize recorder bias.

POLLEN IDENTIFICATION

The scopal pollen load of foraging solitary bees collected in 2015 was analysed by light microscopy using the method outlined by Westrich & Schmidt (1986). Before removing pollen from the scopae, the total load was estimated relative to a full load for that species, ranging from 8/8 (full load) to 1/8 (one-eighth load). The pollen grains were removed from the scopae using an entomological pin and transferred to a drop of water on a microscope slide. Pollen that was not clearly held in the scopae was not sampled as this may have become attached to other parts of the body during nectar visits to non-host plant flowers. The slide was gently heated to allow grains to absorb water and achieve their maximum size and to evaporate excess water. Molten glycerine jelly stained with fuchsin was then added, and the slide was sealed with a coverslip. The proportion of the load comprised of different plant species was estimated along three randomly selected lines across the cover slip at a magnification of ×400. The proportion of the load by volume was estimated by the relative area of the slide occupied by each plant species, rather than the absolute number of grains, in order to better reflect the total volume of pollen collected, an important correction in mixed loads where pollen grains of different plant species often differ widely in size (Cane & Sipes 2006). Species representing less than 1% of the load were excluded from further analysis as their presence may have arisen from contamination (Westrich & Schmidt 1986).

The proportions of pollen collected were corrected according to the overall size of each load to give a final weight, for example a full load (8/8) comprised of 50% *Centaurea nigra* and 50% *Leucanthemum vulgare* would receive a final *C. nigra* weight of 50 and a final *L. vulgare* weight of 50, whereas a quarter load (2/8) comprised of 100% *Hypochaeris radicata* would receive a final *H. radicata* weight of 25. The pollen grains were identified to species using Sawyer (1981), and the reference collection assembled during the project. The majority of samples were identified to species level, but where this was not possible, pollen was identified to genus, for example in *Brassica*, *Plantago* and *Geranium*. For a full list of taxa and the level of identification, to either species or genus, see Appendix S3.

STATISTICAL ANALYSIS

Generalized linear mixed-effect models (GLMMs) were used to test for the impact of management type on bee and plant species abundance and diversity and the impact of plant species richness on bee species diversity and diet breadth. Models were fit using the maximum likelihood (Laplace Approximation) method. All data analyses were conducted in R version 3.1.1 (R Development Core Team, Vienna, Austria) using the lme4 package for the GLMMs (Bates *et al.* 2014). All models were fitted with Poisson and negative binomial error distributions and were tested for overdispersion. In all cases, negative binomial error structures were the most appropriate and final models were not overdispersed. Final models were compared by ANOVA with a null model containing the same random factor to test for significance.

Differences in the total number of bee and plant species and total floral abundance recorded between different farm types were analysed using GLMMs with management type as a fixed factor. Sampling year was included as a random factor to take account of the temporal data structure and differences in sampling methods. The abundance analysis used the 2013–2014 data, and the species richness analysis used the 2013–2015 data. The impact of plant species richness on bee species richness (including *Apis*, *Bombus* and kleptoparastic bee species) and oligolectic solitary bee species richness was analysed using GLMMs with plant species richness as a fixed factor and sampling year as a random factor. This analysis used the 2013–2015 species richness data.

The impact of plant species richness on the number of pollen species detected in bee pollen loads was analysed using a GLMM with plant species richness as a fixed factor and sampling round (April/May, May/June, June/July and July/August) as a random factor. The number of pollen species detected in bee pollen loads was also calculated for the seven most common polylectic bee species for which a total of 30 pollen loads had been collected from each species, representing the majority of the pollen load data (759 of 1054 samples, *Andrena chrysosceles*, *A. flavipes*, *A. haemorrhoa*, *A. semilaevis*, *Lasioglossum calceatum*, *L. malachurum* and *L. pauxillum*). The number of species detected in pollen loads was summed over the year for each species to reduce temporal variation. Farms where no samples of a species were taken were excluded from that species' analysis, as the species may have been absent from the sample for reasons other than floristic composition, for example nesting site availability and low detection rate. The relationship between plant species richness and the number of pollen species collected by polylectic bee species was analysed using a GLMM with plant species richness as a fixed factor and bee species as a random factor. Both these analyses used the 2015 microscopic pollen load analysis data.

The proportion of sown flowers relative to total flowers was calculated for each farm over the 2013–2014 period. The proportion of observed solitary bee pollen visits to sown flowers and the proportion of solitary bee species visiting sown flowers for pollen was also calculated over the 2013–2014 period. The impact of the proportion of sown flowers on the proportion of observed solitary bee pollen visits and the proportion of solitary bee species visiting sown flowers was analysed using Spearman's rank correlation tests, as in each case the response variable could not be transformed to normality.

Differences in the proportion of pollen collected from different plant types were analysed using binomial tests. For the observational data, the proportion of pollen visits to sown and wild plants was calculated for each sampling round across all years for both farm types. For the pollen load data, a third category of crop plant data was included. A number of pollen loads contained *Brassica* type pollen, most of which is highly likely to have come from the crop plant oilseed rape *Brassica napus*. No wild *Brassica* species such as *B. nigra* were recorded during floristic surveys with the only other source being small areas of *B. rapa* that is sometimes sown as part of conservation management for birds. As a result, we are confident that the majority of the *Brassica* type pollen originated from crop plants and so this was excluded from the comparison between sown and wild plant pollen use. As the pollen load data are non-integer (with variably full pollen loads with mixed species composition), the proportion of each pollen type was used to calculate an appropriate value from the number of collected samples, that is where 173 bees were collected with pollen loads in total comprised of 9·7% pollen from sown plants and 90·3% pollen from wild plants by volume this was calculated as 17 samples from sown plants and 156 samples from wild plants. These calculated values were used in the binomial tests.

Results

A total of 105 species of bee was recorded over the survey period. This comprised the honeybee *Apis mellifera*, 15 species of bumblebee *Bombus* (including five parasitic *Psithyrus* spp.), 72 species of solitary bee and 17 species of parasitic bee (see Appendix S4). There was no difference in the total number of bee species recorded on each farm type in each year (mean HLS 23·2 ± 2·4, mean ELS 21·5 ± 2·1, $\chi^2 = 0{\cdot}6$, $P = 0{\cdot}418$). A total of 9·69 million flowering units were recorded on the transects in 2013–2014. Floral abundance was significantly greater on HLS farms than on ELS farms in each year (mean HLS 501 758 ± 74 397 flowering units, mean ELS 97 530 ± 22 703 flowering units, $\chi^2 = 32{\cdot}6$, $P < 0{\cdot}001$). A total of 6·24 million flowering units of plant species characterized as sown were recorded on the transects in 2013–2014. Sown floral abundance was more than ten times higher on HLS farms than on ELS farms in each year (mean HLS 354 271 ± 71 761, mean ELS

33 579 ± 12 739, $\chi^2 = 23{\cdot}0$, $P < 0{\cdot}001$, see Appendix S1). A total of 291 species of flowering plants were recorded over the survey period. There was no difference in the total number of plant species recorded on each farm type in each year (mean HLS 75·2 ± 4·2, mean ELS 68·8 ± 3·1, $\chi^2 = 1{\cdot}9$, $P = 0{\cdot}171$).

Fifty-six species of solitary bee were observed making 1416 pollen foraging trips. Across all farms, as the proportion of sown plants increased, so the proportion of observed pollen foraging visits to sown plants increased as well (Spearman's rho = 0·920, $P < 0{\cdot}001$, Fig. 1). However, the proportion of pollen collected by solitary bees from sown plants varied greatly throughout the year and between farm types. In late April/early May, no pollen visits to sown plants were observed on either farm type (Fig. 2a,b). In late May/early June, the proportion of observed pollen visits to sown plants was similarly low on both ELS and HLS farms (HLS 13·1%, ELS 9·4%, $\chi^2 = 0{\cdot}83$, $P = 0{\cdot}364$, Fig. 2a,b). In late June/early July, the proportion of observed pollen visits to sown plants increased to 60·1% of visits on HLS farms compared to 18·5% of visits on ELS farms, a significantly higher proportion ($\chi^2 = 113{\cdot}92$, $P < 0{\cdot}001$, Fig. 2a,b). In late July/early August, the proportion of pollen visits to sown plants decreased on both farm types, though it was still significantly greater on HLS farms (HLS 21·1%, ELS 10·1%, $\chi^2 = 4{\cdot}5$, $P = 0{\cdot}033$, Fig. 2a,b).

A similar trend was observed in the analysis of collected pollen samples. One thousand and fifty-four individual bees with pollen loads from 47 bee species were collected for microscopic pollen analysis. Excluding oilseed rape type (*Brassica* type) pollen from the analysis, no pollen was collected from sown plants in late April/early May. In late May/early June, the proportion of pollen collected from sown plants was similarly low (ELS 15·4%, HLS 10·6%, $\chi^2 = 1{\cdot}2$, $P = 0{\cdot}283$, Fig. 2c,d). In late June/early July, the proportion of pollen collected from sown plants increased to 47·4% on HLS farms compared to 16·5% on ELS farms, a significantly higher proportion ($\chi^2 = 46{\cdot}2$, $P < 0{\cdot}001$, Fig. 2c,d). In late July/early August, the proportion of pollen collected from sown plants decreased to a similar level on both HLS and ELS farms (ELS 18·3, HLS, 21·1, $\chi^2 = 0{\cdot}1$, $P = 0{\cdot}824$, Fig. 2c,d).

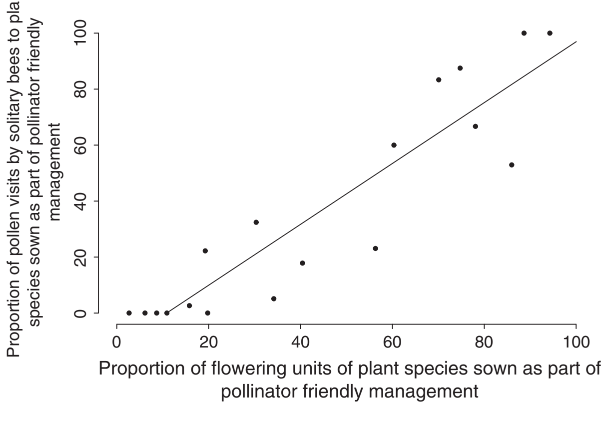

Fig. 1. Relationship between availability of flowering units of plant species sown as part of pollinator-friendly management and their observed utilization for pollen by solitary bees on surveyed farms.

Across all farms, as the proportion of sown plants increased the proportion of solitary bee species present observed making pollen foraging trips to sown plants increased as well (Spearman's rho = 0·743, $P < 0{\cdot}001$, Fig. 3). However, at best only 46·2% of solitary bee species were observed visiting sown plants for pollen. Over the whole survey period, bee species richness was significantly associated with plant species richness ($\chi^2 = 33{\cdot}7$, $P < 0{\cdot}001$, Fig. 4). A total of 16 oligolectic bee species were recorded following Westrich (1989), and oligolectic bee species richness was also significantly associated with plant species richness ($\chi^2 = 10{\cdot}0$, $P = 0{\cdot}002$). The number of species of pollen detected in pollen loads on each farm was significantly associated with the number of flowering plants recorded on the transects, with this effect consistent over the survey period ($\chi^2 = 16{\cdot}8$, $P < 0{\cdot}001$, Fig. 5). However, for the seven most common polylectic bee species representing the bulk of the pollen load data (759 out of 1054 samples), there was no significant relationship between diet breadth and observed plant species richness ($\chi^2 = 0{\cdot}7$, $P = 0{\cdot}416$), suggesting that the relationship is instead driven by the addition of more specialized bees to the community in floristically richer environments that collect pollen from a different suite of host plants.

Over the whole survey period, pollen collected from sown plants by solitary bees represented only 27·0% of pollen visitation observations and 23·3% of pollen collected by volume. The most popular sown plants were *Leucanthemum vulgare*, *Centaurea nigra* and *Daucus carota* (Table 1). Of the 72 species of solitary bee only 31 species had five analysed pollen loads or five observed pollen visits. Of these, 14 species collected at least 10% of their pollen from sown plants (Table 2) with 17 species collecting a lower proportion than this. Of the 41 species with fewer than five analysed loads or five observed visits, 11 were observed visiting, or their pollen loads contained pollen from, sown plants (*Andrena wilkella*, *Hylaeus brevicornis*, *H. cornutus*, *H. dilatatus*, *Lasioglossum albipes*, *L. smeathmenellum*, *Megachile centuncularis*, *M. versicolor*, *M. willughbiella*, *Osmia leaiana* and *O. spinulosa*). This list includes *Hylaeus* species which lack scopal hairs on their body, making accurate determination of pollen visits impossible in the field. However, all British species with the exception of *Hylaeus signatus* are known to be polylectic (Westrich 1989), and so any observed visits to sown plants were included in this list, but not included in the main pollen visitation analysis. Five species were only recorded in the male sex and there was no evidence that females of the final 25 species visited sown plants for pollen. This most liberal estimate of 25 out of 72 solitary bee species (34·7%) likely to be using sown plants to a greater

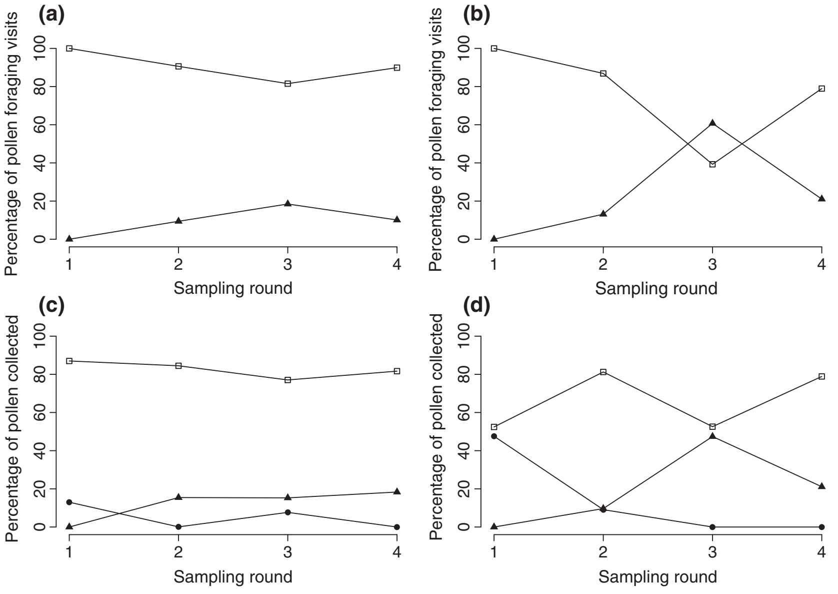

Fig. 2. Proportion of pollen collected by solitary bees from (a) observed pollen foraging trips on ELS farms, (b) observed pollen foraging trips on HLS farms, (c) pollen load analysis from ELS farms and (d) pollen load analysis from HLS farms. Triangles = plant species sown as part of agri-environment management, squares = wild plant species and circles = crop plant species (*Brassica* spp). Sampling round one, late April/early May; sampling round two, late May/early June; sampling round three, late June/early July; sampling round four, late July/early August.

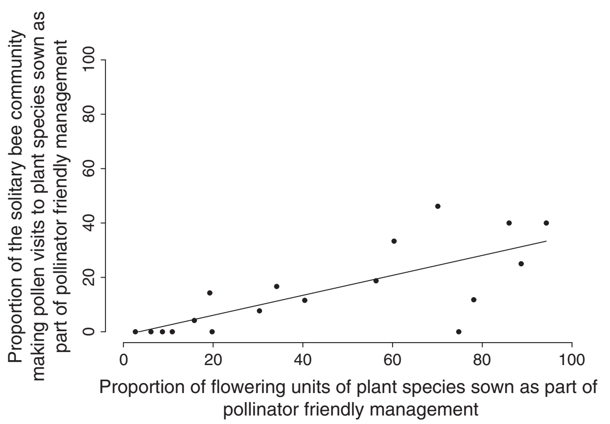

Fig. 3. Relationship between availability of sown floral resources and the proportion of solitary bee species utilizing them for pollen on surveyed farms.

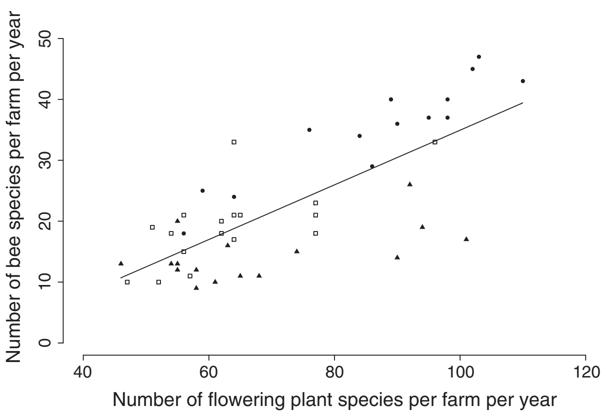

Fig. 4. Relationship between plant species richness and bee species richness on surveyed farms. Squares = 2013, triangles = 2014, circles = 2015.

or lesser extent is similar to the overall observed proportion of pollen collected from sown plants.

Discussion

Our results show that, as expected, increasing resource availability through the creation of flower-rich habitat increased both the utilization rates of sown plants for pollen by solitary bees and the proportion of solitary bee species utilizing sown plants for pollen. These findings are in line with studies that have found that sown resources can provide improved resources for wild bees in enhanced areas (Knop *et al.* 2006; Kohler *et al.* 2007; Pywell *et al.* 2011; Scheper *et al.* 2015). However, whilst utilization rates of sown flowers were higher in areas in which they were abundant, the proportion of solitary bee species utilizing sown plants for pollen was always a minority, even in areas where sown resources represented the vast majority of available forage. It is important to note that this study was conducted in a study region in which the landscape is composed of 21–22% semi-natural habitat (Wood, Holland & Goulson 2015b). This is considerably more than areas of conventional farmland in many developed European countries which often contain between 5% and 10% semi-natural habitat (e.g. Westphal, Steffan-Dewenter & Tscharntke 2003; Herrmann *et al.* 2007). As such, the relatively high bee diversity and low sown resource utilization may reflect the less intensified nature of this area, and more studies of a similar nature should be conducted in more intensified landscapes.

The most important sown plants for solitary bees were *Leucanthemum vulgare*, *Centaurea nigra* and *Daucus carota*. The former two were widely used by polylectic *Lasioglossum* species with *D. carota* an important pollen source for scarce late summer species such as *Andrena alfkenella* and *A. minutuloides*. Plants from the family Fabaceae are often a major component of pollinator-focused agri-environment schemes, since many schemes were

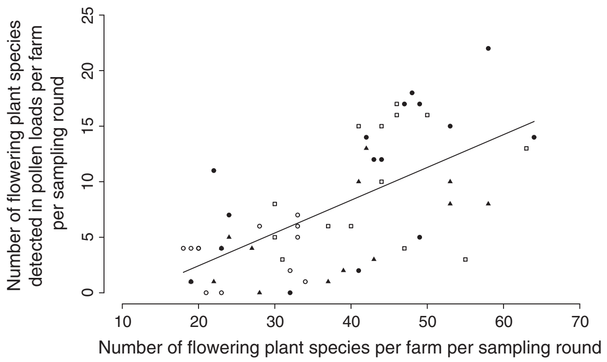

Fig. 5. Relationship between plant species richness and the species richness of pollens detected in bee pollen loads on surveyed farms across the season. Open circles = late April/early May; open squares = late May/early June; closed circles = late June/early July; closed triangles = late July/early August.

designed primarily to provide resources for threatened bumblebees that show close association with members of the Fabaceae (Edwards 2003; Goulson *et al.* 2005). These schemes can have significantly positive effects on the size of bumblebee populations on farmland (Carvell *et al.* 2015; Wood, Holland & Goulson 2015a), and whilst some threatened solitary bee species are dependent on Fabaceae (i.e. *Eucera longicornis*, Westrich 1989, not recorded in this study), overall use of Fabaceae as a pollen source by solitary bees was very low at 2·3% of pollen visitation observations and 3·0% of pollen collected by volume.

In contrast, an important pollen source for solitary bees in the spring was the genus *Brassica*. This predominantly comprises oilseed rape (*Brassica napus*), a major crop in England. *Brassica* species are also sometimes included in wild bird focused agri-environment schemes to provide winter seeds, but the area under this form of management is dwarfed by the area cropped with oilseed rape. *Brassica* type pollen was collected by 12 species of *Andrena*, in particular *A. scotica* (40·2% of total pollen collected by volume), *A. haemorrhoa* (23·1%), *A. minutula* (20·2%), *A. nitida* (19·1%), *A. cineraria* (15·7%) and *A. subopaca* (14·2%). Mass flowering crops, in particular oilseed rape, have been associated with higher densities of foraging bumblebees, larger bumblebee colonies and larger numbers of bumblebee colonies in agricultural environments, due to increased resources availability during early colony development (Westphal, Steffan-Dewenter & Tscharntke 2003; Herrmann *et al.* 2007; Wood, Holland & Goulson 2015b). However, oilseed rape is widely treated with pesticides including neonicotinoids that have been linked to bee declines around the world (see Goulson *et al.* 2015). There are few field studies of impacts on solitary bees, but one study found reduced numbers of solitary bees foraging on neonicotinoid-treated oilseed rape and neighbouring field margins compared to controls, and also reduced occupancy of nest holes by *Osmia bicornis* (Rundlöf *et al.* 2015), so the net benefits of this mass flowering crop for solitary bees may depend upon its wider agricultural management.

The area of land cropped with oilseed rape in the UK has increased markedly in the past 30 years, from 269 000 ha in 1984 to a peak of 756 000 ha in 2012, driven mainly by rising commodity prices and demand for biofuels (Defra 2015). This increased availability of pollen and nectar resources during the period before agri-environment schemes begin to flower may partly explain positive trends in some spring *Andrena* species in the UK. Widespread in the north and the west of the UK, *A. cineraria* had been scarce in the south of England until the 1990s when it markedly expanded its range (Baldock 2008). In addition, a number of scarce and threatened parasitic insects use spring flying mining bees such as *A. cineraria* as a host, specifically the oil beetle *Meloe proscarabaeus*, the bee fly *Bombylius discolor* (Nationally Scarce), the parasitic bee *Nomada lathburiana* (Red Data Book 3) and the conopid fly *Myopa pellucida* (Red Data Book 3). National recording efforts and county atlases show that these species have all increased in range and frequency since the 1990s, particularly in the south-east of England (M. Edwards *pers. comm.*, Baldock 2008; Baldock & Early 2015), with the latter three species being recorded during this study.

Oilseed rape is an increasingly widely grown crop across much of the world and is the most important insect pollinated crop in arable areas of England. Whilst it can be wind pollinated, insect pollination increases seed yield, quality and market value (Bommarco, Marini & Vaissière 2012). Solitary bees from the genera *Andrena*, *Osmia* and *Lasioglossum* are more efficient pollinators of oilseed rape than bumblebees and honeybees in Britain (Woodcock *et al.* 2013). However, current pollinator-focused schemes are dominated by herbaceous grassland plants which produce their peak flower abundance in July and August. These options provide low to non-existent resources in the spring, with none of the univoltine spring flying *Andrena* collecting more than 10% of their pollen from sown plants. Instead, visits to plants associated with woodland, hedgerow, grassland and arable weed habitats predominated. However, increasing floral abundance in the late summer is important, as pollen demand for larval rearing by social bumblebees is at its highest at this point (Dicks *et al.* 2015). Identifying bee species that are resource limited on farmland is an important part of targeted agri-environmental management, and it has been argued that current agricultural landscapes are particularly flower poor in the summer (Holland *et al.* 2015), with availability of suitable forage decreasing through the season (Scheper *et al.* 2014). The creation of 2% of predominantly summer flowering flower-rich habitat by farm area is sufficient to consistently supply a suite of common farmland bumblebee species with enough pollen to raise their larvae throughout the season (Dicks *et al.* 2015).

Current seed mixes biased towards summer flowering plants may consequently be an appropriate focus, but a change in composition to include more attractive species that flower in May and early June would support a

Table 1. Most important pollen forage plants for solitary bees at different times of the year from field observations and pollen analysis. Plant species sown as part of agri-environment management are marked in bold. Sampling round one, late April/early May; sampling round two, late May/early June; sampling round three, late June/early July; sampling round four, late July/early August

Observations (2013–2015)

Round one	% of visits	Round two	% of visits	Round three	% of visits	Round four	% of visits
Taraxacum agg.	66·89	*Chaerophyllum temulum*	19·37	*Tripleurospermum inodorum*	26·67	*Pulicaria dysenterica*	17·36
Sinapis arvensis	11·49	*Heracelum sphondylium*	14·25	***Centaurea nigra***	**23·26**	*Senecio jacobea*	12·81
Brassica rapa	10·14	*Crataegus monogyna*	9·69	***Leucanthemum vulgare***	**16·15**	*Odontites vernus*	11·98
Crataegus monogyna	4·05	***Leucanthemum vulgare***	**7·69**	*Heracelum sphondylium*	7·26	***Daucus carota***	**11·16**
Anthriscus sylvestris	2·70	*Tripleurospermum inodorum*	7·41	*Hypochaeris radicata*	5·19	*Heracleum sphondylium*	9·92
Alliaria petiolata	2·03	*Hypochaeris radicata*	7·12	*Bryonia dioica*	3·85	*Rubus fruticosus agg.*	9·09
Bellis perennis	0·68	*Sisymbrium officinale*	4·84	*Crepis capillaris*	3·70	*Tripleurospermum inodorum*	8·26
Hyacinthoides non-scripta	0·68	*Ranunculus repens*	4·56	*Chaerophyllum temulum*	1·63	*Picris hieracioides*	5·79
Lamium album	0·68	*Oenanthe crocata*	3·99	***Achillea millefolium***	**1·48**	*Hypochaeris radicata*	1·65
Prunus spinosa	0·68	*Crepis vesicaria*	2·85	*Trifolium repens*	1·04	***Centaurea nigra***	**1·65**

Pollen analysis (2015 only)

Round one	% of pollen	Round two	% of pollen	Round three	% of pollen	Round four	% of pollen
Brassica spp.	31·22	*Heracleum sphondylium*	11·17	*Tripleurospermum inodorum*	27·52	*Senecio jacobea*	21·66
Taraxacum agg.	29·84	*Chaerophyllum temulum*	9·66	***Leucanthemum vulgare***	**14·62**	*Rubus fruticosus agg.*	17·52
Alliaria petiolata	13·41	*Sisymbrium officinale*	8·04	***Centaurea nigra***	**12·53**	***Daucus carota***	**12·55**
Sinapis arvensis	9·78	*Crataegus monogyna*	8·00	*Rubus fruticosus agg.*	4·50	*Pulicaria dysenterica*	11·58
Bellis perennis	3·48	*Tripleurospermum inodorum*	7·90	*Heracleum sphondylium*	4·43	*Heracleum sphondylium*	7·43
Acer campestre	3·07	***Leucanthemum vulgare***	**6·06**	*Sisymbrium officinale*	3·17	*Tripleurospermum inodorum*	6·03
Hyacinthoides non-scripta	1·79	*Hypochaeris radicata*	5·88	*Brassica* spp.	3·10	***Centaurea nigra***	**4·11**
Lamium album	1·36	*Brassica* spp.	5·19	***Sonchus arvensis***	**3·06**	*Odontites vernus*	3·74
Glechoma hederacea	1·28	*Oenanthe crocata*	4·35	*Bryonia dioica*	2·23	***Trifolium hybridum***	**2·21**
Crataegus monogyna	1·19	*Crepis vesicaria*	3·60	*Ranunculus repens*	2·18	*Trifolium repens*	2·07

greater variety of bee species, including important crop pollinators. Conservation management that takes land out of production can both benefit biodiversity and increase agricultural yields, essentially making the intervention economically neutral (Pywell *et al.* 2015). However, as the majority of pollination is carried out by the most abundant bee species in any location, usually representing a small fraction of the total number of species present, a purely economic argument is insufficient to justify conserving bee diversity in general (Kleijn *et al.* 2015). In addition to bees being a valid conservation target in their own right, it has been argued that maintaining pollinator species diversity is crucial for providing ecosystem resilience in the face of future environmental change (Senapathi *et al.* 2015). Bee communities are strongly structured by, and associated with, plant species diversity (Tscharntke, Gathmann & Steffan-Dewenter 1998; Potts *et al.* 2003; Batáry *et al.* 2010), and so management that does not increase plant species diversity at the farm level is unlikely to increase bee diversity either, no matter the total increase in resource availability. Increasing the diversity of plants species included in wild seed mixes is likely to increase their efficacy (Scheper *et al.* 2015), and the inclusion of grassland species such as *Taraxacum* agg., *Hypochaeris radicata* and *Ranunculus repens* would provide resources for a wider variety of species. However, hedgerow plants such as *Heracleum sphondylium*, *Chaerophyllum temulum* and *Alliaria petiolata* and arable plants such as *Sinapis arvensis*, *Sisymbrium officinale* and *Tripleurospermum inodorum* are also popular, and their management relies on wider farmland management such as herbicide and hedge cutting regimes. Agri-environment schemes promoting improved hedgerow management and various uncropped or unharvested headlands for arable plants currently exist, but their ability to increase the abundance and diversity of pollen sources for solitary

Table 2. Solitary bee species potentially benefiting from plant species sown as part of agri-environment schemes. Selected species had a minimum of five analysed pollen loads or five observed pollen foraging visits and collected a minimum of 10% of their pollen from sown plant species in either category. *n* p, total number of pollen loads; *n* obs, total number of pollen foraging observations

Species	*n* p	*n* obs	Utilization of sown plants		Important sown pollen sources (pollen analysis)	Important sown pollen sources (observations)
			% of pollen collected	% of observed pollen visits		
*Andrena alfkenella**	6	10	78·6	90·0	*Daucus carota* (78·6)	*Daucus carota* (90·0)
Andrena flavipes	45	70	17·7	17·1	*Centaurea nigra* (8·9), *Trifolium hybridum* (5·2), *Leucanthemum vulgare* (3·4)	*Leucanthemum vulgare* (7·1), *Centaurea nigra* (4·3), *Trifolium hybridum* (2·9), *Trifolium pratense* (2·9)
Andrena minutula	15	30	19·8	26·7	*Daucus carota* (19·8)	*Daucus carota* (20·0), *Centaurea nigra* (3·3), *Sonchus arvensis* (3·3)
*Andrena minutuloides**	8	10	85·0	70·0	*Daucus carota* (85·0)	*Daucus carota* (70·0)
Colletes daviesanus	2	5	100·0	40·0	*Achillea millefolium* (100·0)	*Achillea millefolium* (40·0)
Halictus tumulorum	21	23	46·5	34·8	*Ranunculus acris* (20·2), *Leucanthemum vulgare* (10·8), *Trifolium pratense* (6·2), *Medicago lupulina* (3·7), *Centaurea nigra* (3·7), *Silene dioica* (1·9)	*Leucanthemum vulgare* (17·4), *Ranunculus acris* (4·3), *Centaurea nigra* (4·3), *Medicago lupulina* (4·3), *Trifolium pratense* (4·3)
Lasioglossum calceatum	38	70	13·2	21·4	*Leucanthemum vulgare* (7·7), *Centaurea scabiosa* (3·0), *Phacelia tanacetifolia* (1·8), *Knautia arvensis* (0·6)	*Leucanthemum vulgare* (11·4), *Knautia arvensis* (2·9), *Leontodon hispidus* (2·9), *Centaurea nigra* (1·4), *Centaurea scabiosa* (1·4), *Phacelia tanacetifolia* (1·4)
Lasioglossum leucozonium	21	51	12·8	3·9	*Leontodon hispidus* (8·9), *Centaurea nigra* (4·0)	*Leontodon hispidus* (3·9)
Lasioglossum malachurum	437	553	32·1	47·2	*Leucanthemum vulgare* (14·8), *Centaurea niga* (12·0), *Plantago* spp (1·5), *Phacelia tanacetifolia* (0·9), *Melilotus officinalis* (0·9), *Achillea millefolium* (0·7), others (1·2)	*Centaurea nigra* (26·8), *Leucanthemum vulgare* (17·7), *Achillea millefolium* (1·3), *Phacelia tanacetifolia* (0·5), others (0·9)
Lasioglossum pauxillum	70	93	19·5	15·1	*Leucanthemum vulgare* (14·1), *Centaurea nigra* (2·7), *Daucus carota* (1·1), *Plantago* spp (0·8), other (0·8)	*Leucanthemum vulgare* (11·8), *Centaurea nigra* (1·1), *Leontodon hispidus* (1·1), *Daucus carota* (1·1)
Lasioglossum puncticolle	2	8	100·0	37·5	*Centaurea nigra* (100·0)	*Centaurea nigra* (37·5)
Lasioglossum villosulum	25	32	34·8	21·9	*Leontodon hispidus* (34·8)	*Leontodon hispidus* (18·8), *Sonchus arvensis* (3·1)
Lasioglossum xanthopus	7	8	67·9	100·0	*Leucanthemum vulgare* (67·9)	*Leucanthemum vulgare* (100·0)
Lasioglossum zonulum	4	7	33·4	14·3	*Centaurea nigra* (20·6), *Silene dioica* (12·9)	*Centaurea nigra* (14·3)

*Data only available for summer generation females.

bees is poorly studied. These and similar schemes should be trialled as complementary methods to benefit solitary bee populations on farmland.

CONCLUSIONS

Current pollinator-focused agri-environment management can increase floral abundance and provide pollen resources for a limited suite of farmland bee species. However, in our study the majority of solitary bee species foraged from other plants persisting in the wider farm environment. As a taxa almost entirely dependent upon flowering plants for food, an association between bee species richness and flowering plant richness is to be expected. As the addition of flower-rich schemes as part of pollinator-friendly management did not significantly increase flowering plant richness at the farm scale, it should not be surprising that bee species richness was also not significantly different at this level. Management that increases resource availability is important, but our results suggest that techniques that increase floristic richness at the farm scale are necessary if we wish to conserve a richer bee community on farmland.

Acknowledgements

We would like to thank all of the farmers that allowed us to use their land during the study. We would also like to thank Mike Edwards for help with bee identification and general discussion. This work was funded by the Natural Environment Research Council grant NE/J016802/1 and the Game and Wildlife Conservation Trust.

Data accessibility

All data presented in this manuscript are available from the NERC Environmental Information Data Centre http://doi.org/10.5285/a9d713e8-c8d5-4129-8db0-d771443111cf (Wood, Holland & Goulson 2016).

References

Alaux, C., Ducloz, F., Crauser, D. & Le Conte, Y. (2010) Diet effects on honeybee immunocompetence. *Biology Letters*, **6**, 562–565.

Baldock, D.W. (2008) *Bees of Surrey*. Surrey Wildlife Trust, Pirbright, UK.

Baldock, D.W. & Early, J.P. (2015) *Soldierflies, their Allies and Conopidae of Surrey*. Surrey Wildlife Trust, Pirbright, UK.

Bartomeus, I., Ascher, J.S., Gibbs, J., Danforth, B.N., Wagner, D.L., Hedtke, S.M. & Winfree, R. (2013) Historical changes in northeastern US bee pollinators related to shared ecological traits. *Proceedings of the National Academy of Sciences*, **110**, 4656–4660.

Batáry, P., Báldi, A., Sárospataki, M., Kohler, F., Verhulst, J., Knop, E., Herzog, F. & Kleijn, D. (2010) Effects of conservation management on bees and insect-pollinated grassland plant communities in three European countries. *Agriculture, Ecosystems and Environment*, **136**, 35–39.

Bates, D., Maechler, M., Bolker, B. & Walker, S. (2014) LME4: Linear mixed-effects models using Eigen and S4. R package version 1.1-7 http://CRAN.R-project.org/package = lme4

Biesmeijer, J.C., Roberts, S.P.M., Reemer, M., Ohlemüller, R., Edwards, M. & Peeters, T. *et al.* (2006) Parallel declines in pollinators and insect pollinated plants in Britain and the Netherlands. *Science*, **313**, 351–354.

Bommarco, R., Marini, L. & Vaissière, B. (2012) Insect pollination enhances seed yield, quality, and market value in oilseed rape. *Oecologia*, **169**, 1025–1032.

Cane, J.H. & Sipes, S. (2006) Characterizing floral specializations by bees: analytical methods and a revised lexicon for oligolecty. *Plant Pollinator Interactions from Specialization to Generalization* (eds N.M. Waser & J. Ollerton), pp. 99–122. University of Chicago Press, Chicago, USA.

Carvalheiro, L.G., Kunin, W.E., Keil, P., Aguirre-Gutiérrez, J., Ellis, W.N., Fox, R. *et al.* (2013) Species richness declines and biotic homogenisation have slowed down for NW-European pollinators and plants. *Ecology Letters*, **16**, 870–878.

Carvell, C., Westrich, P., Meek, W.R., Pywell, R. & Nowakowski, M. (2006) Assessing the value of annual and perennial forage mixtures for bumblebees by direct observation and pollen analysis. *Apidologie*, **37**, 326–340.

Carvell, C., Meek, W.R., Pywell, R.F., Goulson, D. & Nowakowski, N. (2007) Comparing the efficacy of agri-environment schemes to enhance bumblebee abundance and diversity on arable field margins. *Journal of Applied Ecology*, **44**, 29–40.

Carvell, C., Bourke, A.F.G., Osborne, J.L. & Heard, M.S. (2015) Effects of an agri-environment scheme on bumblebee reproduction at local and landscape scales. *Basic and Applied Ecology*, **16**, 519–530.

Defra (2015) *Farming Statistics Final Crop Areas, Yields, Livestock Populations and Agricultural Workforce at June 2015 – United Kingdom*. Department of Food and Rural Affairs, London, UK.

Dicks, L.V., Baude, M., Roberts, S.P.M., Phillips, J., Green, M. & Carvell, C. (2015) How much flower-rich habitat is enough for wild pollinators? Answering a key policy question with incomplete knowledge. *Ecological Entomology*, **40**, 22–35.

Edwards, M. (2003) Aculeate conservation group annual report. Unpublished report for the UK BAP bumblebee working group, Midhurst, UK

Elliot, J. (2013) *Rural Development Programme for England 2007–2013*. Hyder Consulting (UK) Ltd., London, UK. http://ec.europa.eu/agriculture/rurdev/countries/uk/mte-rep-uk-england_en.pdf

Garibaldi, L.A., Steffan-Dewenter, I., Winfree, R., Aizen, M.A., Bommarco, R., Cunningham, S.A. *et al.* (2013) Wild pollinators enhance fruit set regardless of honey bee abundance. *Science*, **339**, 1608–1611.

Goulson, D., Hanley, M.E., Darvill, B., Ellis, J.S. & Knight, M.E. (2005) Causes of rarity in bumblebees. *Biological Conservation*, **122**, 1–8.

Goulson, D., Nicholls, B., Botías, C. & Rotheray, E.L. (2015) Bee declines driven by combined stress from parasites, pesticides, and lack of flowers. *Science*, **347**, 1435.

Herrmann, F., Westphal, C., Moritz, R.F.A. & Steffan-Dewenter, I. (2007) Genetic diversity and mass resources promote colony size and forager densities of a social bee (*Bombus pascuorum*) in agricultural landscapes. *Molecular Ecology*, **16**, 1167–1178.

Holland, J.M., Smith, B.S., Storkey, J., Lutman, P.J.W. & Aebischer, N.J. (2015) Managing habitats on English farmland for insect pollinator conservation. *Biological Conservation*, **182**, 215–222.

Kleijn, D., Baquero, R.A., Clough, Y., Dķaz, M., De Esteban, J., Fernindez, F. *et al.* (2006) Mixed biodiversity benefits of agri-environment schemes in five European countries. *Ecology Letters*, **9**, 243–254.

Kleijn, D., Winfree, R., Bartomeus, I., Carvalheiro, L.G., Henry, M., Isaacs, R. *et al.* (2015) Delivery of crop pollination services is an insufficient argument for wild pollinator conservation. *Nature Communications*, **6**, 7414.

Knop, E., Kleijn, D., Herzog, F. & Schmid, B. (2006) Effectiveness of the Swiss agri-environment scheme in promoting biodiversity. *Journal of Applied Ecology*, **43**, 120–127.

Kohler, F., Verhulst, J., Knop, E., Herzog, F. & Kleijn, D. (2007) Indirect effects of grassland extensification schemes in two contrasting European countries. *Biological Conservation*, **135**, 302–307.

Lye, G., Park, K., Osborne, J., Holland, J. & Goulson, D. (2009) Assessing the value of Rural Stewardship schemes for providing foraging resources and nesting habitat for bumblebee queens (Hymenoptera: Apidae). *Biological Conservation*, **142**, 2023–2032.

Ollerton, J., Winfree, R. & Tarrant, S. (2011) How many flowering plants are pollinated by animals? *Oikos*, **120**, 321–326.

Ollerton, J., Erenler, H., Edwards, M. & Crockett, R. (2014) Extinctions of aculeate pollinators in Britain and the role of large-scale agricultural changes. *Science*, **346**, 1360–1362.

Plateaux-Quénu, C. (2008) Subsociality in halictine bees, *Insects Sociaux*, **55**, 335–346.

Potts, S.G., Vulliamy, B., Dafni, A., Ne'eman, G. & Willmer, P. (2003) Linking bees and flowers: how do floral communities structure pollinator communities? *Ecology*, **84**, 2628–2642.

Pywell, R.F., Meek, W.R., Loxton, R.G., Nowakowski, M., Carvell, C. & Woodcock, B.A. (2011) Ecological restoration on farmland can drive beneficial functional responses in plant and invertebrate communities. *Agriculture, Ecosystems and Environment*, **140**, 62–67.

Pywell, R.F., Heard, M.S., Woodcock, B.A., Hinsley, S., Ridding, L., Nowakowski, M. & Bullock, J.M. (2015) Wildlife-friendly farming increases crop yield: evidence for ecological intensification. *Proceedings of the Royal Society B*, **282**, 20151740.

Roulston, T.H. & Goodell, K. (2011) The role of resources and risks in regulating wild bee populations. *Annual Review of Entomology*, **56**, 293–312.

Rundlöf, M., Andersson, G.K.S., Bommarco, R., Fries, I., Hederström, V., Herbertsson, L., *et al.* (2015) Seed coating with neonicotinoid insecticide negatively affects wild bees. *Nature*, **521**, 77–80.

Sawyer, R. (1981) *Pollen Identification for Beekeepers*. University College Press, Cardiff, UK.

Scheper, J., Reemer, M., van Kats, R. Ozinga, W.A., van der Linden, G.T.J., Schaminée, J.H.J., Siepel, H. & Kleijn, D. (2014) Museum specimens reveal loss of pollen host plants as key factor driving wild bee decline in The Netherlands. *Proceedings of the National Academy of Sciences*, **111**, 17552–17557.

Scheper, J., Bommarco, R., Holzschuh, A. Potts, S.G., Riedinger, V., Roberts, S.P.M. *et al.* (2015) Local and landscape-level floral resources explain effects of wildflower strips on wild bees across four European countries. *Journal of Applied Ecology*, **52**, 1165–1175.

Senapathi, D., Biesmeijer, J.C., Breeze, T.D., Kleijn, D., Potts, S.G. & Carvalheiro, L.G. (2015) Pollinator conservation – the difference between managing for pollination services and preserving pollinator diversity. *Current Opinion in Insect Science*, **12**, 93–101.

Tscharntke, T., Gathmann, A. & Steffan-Dewenter, I. (1998) Bioindication using trap-nesting bees and wasps and their natural enemies: community structure and interactions. *Journal of Applied Ecology*, **35**, 708–719.

Westphal, C., Steffan-Dewenter, I. & Tscharntke, T. (2003) Mass flowering crops enhance pollinator densities at a landscape scale. *Ecology Letters*, **6**, 961–965.

Westrich, P. (1989) *Die Wildbienen Baden-Württembergs*. Eugen Ulmer, Stuttgart, Germany.

Westrich, P. & Schmidt, K. (1986) Methoden und Anwendungsgebiete der Pollenanalyse bei Wildbienen (Hymenoptera, Apoidea). *Linzer Biologische Beiträge*, **18**, 341–360.

Williams, P.H. & Osborne, J.L. (2009) Bumblebee vulnerability and conservation world-wide. *Apidologie*, **40**, 367–387.

Winfree, R. (2010) The conservation and restoration of wild bees. *Annals of the New York Academy of Sciences*, **1195**, 169–197.

Wood, T.J., Holland, J.M. & Goulson, D. (2015a) Targeted agri-environment schemes significantly increase the population size of common bumblebee species. *Molecular Ecology*, **24**, 1668–1680.

Wood, T.J., Holland, J.M. & Goulson, D. (2015b) A comparison of techniques for surveying farmland bumblebee populations. *Oecologia*, **177**, 1093–1102.

Wood, T., Holland, J.M. & Goulson, D. (2016). Bee and Flower Abundance and Diversity and bee Pollen Foraging Data from Farms in England. http://doi.org/10.5285/a9d713e8-c8d5-4129-8db0-d771443111cf

Woodcock, B.A., Edwards, M., Redhead, J., Meek, W.R., Nuttall, P., Falk, S., Nowakowski, M. & Pywell, R.F. (2013) Crop flower visitation by honeybee, bumblebees and solitary bees: behavioural differences and diversity responses to landscape. *Agriculture, Ecosystems and Environment*, **171**, 1–8.

Received 21 January 2016; accepted 8 June 2016
Handling Editor: Jacqueline Beggs

Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Flowering plants sown as part of pollinator-focused agri-environment schemes and their average abundance per farm 2013–2014.

Appendix S2. Plant species included in the pollen reference library.

Appendix S3. Plant species identified in pollen analysis and level of taxonomic detail.

Appendix S4. Full list of bee species recorded during the study with species authorities.