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Research

Quantifying the production of plant pollen at the farm scale

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Summary

- Plant pollen is rich in protein, sterols and lipids, providing crucial nutrition for many pollinators. However, we know very little about the quantity, quality and timing of pollen availability in real landscapes, limiting our ability to improve food supply for pollinators.
- We quantify the floral longevity and pollen production of a whole plant community for the first time, enabling us to calculate daily pollen availability. We combine these data with floral abundance and nectar measures from UK farmland to quantify pollen and nectar production at the landscape scale throughout the year.
- Pollen and nectar production were significantly correlated at the floral unit, and landscape level. The species providing the highest quantity of pollen on farmland were *Salix* spp. (38%), *Filipendula ulmaria* (14%), *Rubus fruticosus* (10%) and *Taraxacum officinale* (9%). Hedgerows were the most pollen-rich habitats, but permanent pasture provided the majority of pollen at the landscape scale, because of its large area. Pollen and nectar were closely associated in their phenology, with both peaking in late April, before declining steeply in June and remaining low throughout the year.
- Our data provide a starting point for including pollen in floral resource assessments and ensuring the nutritional requirements of pollinators are met in farmland landscapes.

Introduction

Floral resources (pollen and nectar) are the primary food source for most pollinators and thus a major factor limiting their populations (Roulston & Goodell, 2011; Woodard & Jha, 2017). Decades of agricultural intensification have led to a decline in the quantity, diversity and temporal continuity of floral resources (Baude *et al.*, 2016; Hemberger *et al.*, 2023), likely contributing to parallel rates of decline in many pollinator taxa (Biesmeijer *et al.*, 2006; Powney *et al.*, 2019). Reversing pollinator declines requires us to understand more about where floral resources are located – both in time and in space – and how pollinators are using them so that we can manage landscapes to increase the quantity, quality and seasonal continuity of food for pollinators (Sponsler *et al.*, 2023).

Farmland covers approximately half of the world's habitable land area and > 70% in some countries such as the UK (FAO, 2018). Agricultural expansion and intensification is thought to be the leading driver of pollinator declines (Potts *et al.*, 2010; Goulson *et al.*, 2015; Powney *et al.*, 2019), and yet, it is in our agricultural landscapes that we rely most directly on pollinators, through the services they provide to crop pollination (Klein *et al.*, 2007). Improving agricultural landscapes for pollinators is therefore a high priority and has the potential to deliver simultaneous benefits for biodiversity and food production. Most pollinator conservation schemes, including those in the UK, focus on increasing the number of flowers in farmland landscapes, often incentivising farmers through payments schemes (Carvell *et al.*, 2007; Natural England, 2009). However, without knowing the existing quantities of pollen and nectar provided by farmland through the year, or the species and habitats that provide these resources, it is difficult to design targeted management interventions that meet the food requirements of pollinators throughout the year (Ogilvie & Forrest, 2017; Timberlake *et al.*, 2019; Sponsler *et al.*, 2023). This may lead to seasonal gaps in their annual forage needs (Timberlake *et al.*, 2019, 2021; Guezen & Forrest, 2021; Jachuła *et al.*, 2021), or potential shortfalls in some of the specific nutrients they require (Vaudo *et al.*, 2015; Filipiak, 2019; Jones & Rader, 2022).

Broadly speaking, pollinators require two types of food from flowers: nectar and pollen. Nectar primarily consists of sugars, which provide much of the energy required by pollinators for flight and thermoregulation, though a range of other important compounds are also found in trace amounts (Willmer, 2011). Pollen, however, is a much more complicated mixture of proteins, lipids, vitamins and minerals (Vaudo *et al.*, 2015). The proteins found in pollen are essential for the growth and development of bee larvae (Ruedenauer *et al.*, 2016; Moerman *et al*., 2017), while lipids are required in the formation of phospholipid bilayers, which are important structural features of all cells (Furse *et al*., 2023a). If either of these essential nutrients are in low supply during development, this can lead to negative effects on adult bee physiology and offspring performance (Kämper *et al*., 2016; Bukovinszky *et al*., 2017; Rotheray *et al*., 2017; Woodard & Jha, 2017). Proteins and lipids comprise a large proportion of pollen mass, but their relative concentration differs considerably amongst plant species (Buchman, 1986; Roulston & Cane, 2000; Donkersley *et al*., 2014; Vaudo *et al*., 2020; Furse *et al*., 2023b). This variation in the protein: lipid ratio of pollen is thought to be a major driver of foraging behaviour in bees (Vaudo *et al*., 2020, 2024). Despite the well-established role of pollen in supporting pollinator nutrition and driving foraging behaviour in bees, we still know very little about the quantity and phenology of pollen availability in real landscapes, greatly limiting our ability to improve its supply for pollinators.

While there are a small number of studies on landscape-level nectar supplies (e.g. Baude *et al*., 2016; Hicks *et al*., 2016; Timberlake *et al*., 2019; Langlois *et al*., 2020; Tew *et al*., 2021; Barnsley *et al*., 2022), equivalent studies on landscape-level pollen supply are lacking (but see Jachuła *et al*., 2022 for a landscape-level pollen assessment in Poland). This is largely due to the fact that pollen is much harder to measure than nectar. Nectar is a relatively simple sugar solution secreted over time to ensure the replenishment of flowers, so measurements of nectar productivity can be standardised by recording the production of sugar per 24 h, providing a simple common currency for measuring this resource (e.g. Baude *et al*., 2016). In comparison with nectar, pollen production is much more challenging to measure for two primary reasons. First, it is a solid rather than a liquid, so cannot be easily extracted and quantified. Second, unlike nectar, it is not replenished by flowers but is a finite resource produced only once by each flower and irreversibly depleted when pollinators collect it. This means that in order to quantify daily pollen productivity and avoid double-counting the same pollen from 1 d to the next, it is necessary to measure both the amount of pollen produced by a flower and the number of days the flower remains open (i.e. its floral longevity). Only then can you calculate landscape-level pollen availability per unit time and express it in a way that is relevant to pollinators.

By combining pollen production data and floral longevity measurements with floral abundance estimates from replicate farms, our study aimed to quantify farmland pollen production at the species level, the habitat level and the landscape level throughout an entire flowering season and compare this with equivalent values for nectar availability. There were three specific objectives to our work: (1) measure pollen production values of farmland plant species and compare these with values for nectar production; (2) identify the species and habitats that provide the greatest proportion of farmland pollen throughout the year and compare these with equivalent values for nectar; and (3) quantify the phenology of pollen supply at the landscape level and compare this with the phenology of nectar supply.

Materials and Methods

The primary goal of our fieldwork was to quantify pollen production at the species level, the habitat level and the landscape level, throughout an entire flowering season. To achieve this, we first quantified the volume of pollen produced by individual flowers of a range of common farmland plant species. We then recorded the floral longevity of each of these plant species to establish how long the pollen from each flower remains available to pollinators so that pollen values could be expressed per unit time. We combined these species-level pollen values with floral abundance data from different farmland habitats on replicate UK farms to calculate pollen availability at the habitat level. Finally, we scaled up to the landscape level to quantify the phenology of pollen availability throughout the year at a whole-farm scale.

Study sites and species

There were two sets of field sites used in this study: one set for collecting data on species-level pollen production and floral longevity, and another set for measuring the phenology of floral abundance in different farmland habitats throughout the year. The data on species-level pollen production and floral longevity were collected in various phases from 2011 to 2022 at 24 field sites located within an 8 km radius of Bristol, UK. These sites were chosen as they provided a wide range of habitats including pasture, field margins, hedgerows, arable fields, woodlands, public green space and private gardens, and therefore a wide range of plant species. The pollen production and floral longevity of a plant's flowers are less variable traits than a plant's floral abundance or phenology, which are highly influenced by the location and the time of year; thus, pollen and floral longevity measurements did not need to be made at the same time or location as the floral abundance measurements. The floral abundance data were collected in 2017 on three medium-sized (140–280 ha) mixed (dairy, sheep and arable) farms in Somerset, all located within a 30 km radius of Bristol, UK. The three farms had slightly different habitat compositions, but the dominant habitat types were pasture and arable crops, with hedgerows separating the fields. Two of the farms contained woodland and two contained field margins, but all other habitat elements (pasture, hedgerows and arable fields) were present on all three farms (Supporting Information Table S1). Further details of the three farms can be found in Timberlake *et al*., 2019, and the floral resource supply of these sites was found to be broadly representative of the wider region, falling within the interquartile range of floral resource supply on 12 farms across the west of England (Timberlake *et al*., 2021).

Quantifying the pollen production and floral longevity of plant species

The plant species for which we measured pollen production and floral longevity were selected from the list of species recorded on the three floral abundance farms in Somerset. To keep the workload manageable, we selected the species that contributed 98% of all floral units across the three farms, resulting in a list of 73 plant species to sample (Table S2). This captured all of the common species while avoiding the labour-intensive sampling of scarce species, which contribute very little to farm-scale floral abundance. One species of 73 (*Fallopia japonica* Houttuyn) was dropped as only female plants are found in the UK, therefore producing no pollen (this species contributed 1% of all floral units across the three farms). For the remaining 72 plant species (comprising 97% of all floral units), we measured the pollen production and floral longevity of each species at multiple sites across the 24 sampling sites.

Measuring species-level pollen production For the 72 common farmland plant species selected in our study, we recorded the total volume of pollen produced by each individual floral unit. This was done by collecting at least 10 stems of unopened flowers in the field, transferring them to a beaker of water in the laboratory to allow them to open in a sterile environment, and then harvesting 25–150 pollen-laden anthers (depending on anther size) from a range of newly opened flowers. For each species, we calculated the mean number of anthers per floral unit, the mean number of pollen grains per anther and calculated the volume of each pollen grain. We then multiplied up these values to calculate the total volume of pollen produced by each floral unit. Although we measure only the volume of each pollen grain, and not the mass, values of pollen volume could theoretically be converted to approximate values of pollen mass using a typical density value for pollen. We define a 'floral unit' as one or multiple flowers that can be visited by insects without flying (Carvalheiro *et al.*, 2008); for example, a composite flower head of daisy, *Bellis perennis* L. See Notes S1 for full details of the pollen sampling methodology.

Measuring species-level floral longevity For each of the 72 plant species, we recorded the floral longevity of 10–20 individual flowers in two different field sites (though in a few cases, only one site was possible). Flowers were identified while in bud and tagged before opening. If the flower was a composite head containing many individual flowers (e.g. a daisy), individual flowers on multiple flower heads were marked using a permanent marker pen. After marking the flowers, return visits were made to the flower 5 d a week (Monday–Wednesday and Friday–Saturday) to measure their lifespan. Each flower was inspected to determine whether the anthers had dehisced (i.e. when pollen becomes available) and then checked daily to identify the point at which the flower died or dropped its anthers (pollen no longer available). Floral longevity was calculated as the number of days from the anthers dehiscing to the point at which the flower died, or the anthers dropped off – this corresponds to the number of days over which the flower's pollen is available to pollinators.

Quantifying daily pollen production Daily pollen production is defined as the volume of pollen that is available to a pollinator over a 24-h period. This was calculated by dividing the total volume of pollen produced by a floral unit by the mean floral longevity of the species (measured in days). This provides a *per unit time* measure for pollen, which is comparable to the daily nectar production values listed in Baude *et al.* (2016), Timberlake *et al.* (2019). These daily pollen or nectar values can be multiplied up by daily estimates of floral abundance to calculate the total supply of pollen or nectar at a landscape level.

Recording landscape-level floral abundance

From March to October 2017, each of the three floral abundance farms was visited once per week to record the number of open floral units in each type of semi-natural habitat (permanent pasture, semi-natural woodland, hedgerows and field margins). On each sampling occasion, six 50-m transects were randomly placed in each semi-natural habitat type (e.g. 24 transects in total, for a farm with four habitat types). Ten quadrats of 1 m^2 were distributed along the transect length at 5-m intervals and the number of open floral units of each flowering plant species within or directly above each quadrat was recorded. For trees and shrubs, all floral units in a 5-m vertical column above the quadrat were counted. Above this, the tree's height within the vertical column was estimated with a clinometer and the floral abundance values were multiplied up accordingly (Baude *et al.*, 2016). Floral abundance values per metre squared were multiplied by the area of each habitat within the sampling sites to provide an estimate of each species' floral abundance at a landscape level. For each plant species, a generalised additive model (GAM) in the R package MGCV (Wood, 2010), was used to model a smooth, nonlinear trend in floral abundance over time, allowing floral abundance values to be estimated for all species on any day of the year. A thin-plate regression spline was used to model day of the year, with the degree of smoothing selected using the default generalised cross-validation method (Wood, 2010). These daily floral abundance estimates were then multiplied by the daily pollen production values for each species to calculate the total volume of pollen produced by each plant species over time at the habitat or landscape level.

Addressing the three objectives

Objective 1: Measure pollen production values of farmland plant species and compare these with values for nectar production To evaluate the relationship between per-floral-unit nectar and pollen production of the 72 farmland plant species, we regressed daily nectar values (from Baude *et al.*, 2016; Timberlake *et al.*, 2019) against the daily pollen values calculated in this study. A general linear model was used to test for a relationship between the two floral resources and assess the extent to which pollen production can be predicted from nectar production (or vice versa).

Objective 2: Identify the species and habitats that provide the greatest proportion of farmland pollen throughout the year and compare these with equivalent values for nectar For each plant species in each habitat, we multiplied their daily pollen production value by their daily floral abundance value to calculate the total volume of pollen produced. These values were then summed across the whole year and across all habitats on the farm to calculate the total annual pollen production of each species at the farm scale. For each species, we calculated its percentage contribution to total farm-scale pollen production, enabling us to identify the most important species at the landscape level. We repeated this analysis using nectar production values to compare the sets of species, which are most important for the provisioning of each resource. Finally, to compare the resource value of different farmland habitats through the year, we summed the habitat-level pollen production values across all species within a habitat to provide an estimate of the total volume of pollen produced by the plant community of that habitat at a given point in time. Again, this analysis was repeated for nectar data as well, to compare the two resources.

Objective 3: Quantify the phenology of pollen supply at the landscape level and compare this with the phenology of nectar supply To quantify the phenology of pollen supply at the landscape level throughout the year, we summed the pollen production values from all habitats on each farm to give an estimate of total landscape-level pollen supply at each sampling time point. Combining values from all three farms, a GAM in the R package MGCV (Wood, 2010), was used to model a smooth, nonlinear trend in pollen supply over time. A thin-plate regression spline was used to model day of the year, with the degree of smoothing selected using the default generalised cross-validation method (Wood, 2010). To compare the phenological pattern of pollen and nectar supply at the landscape level, we repeated this analysis using the nectar production values of each plant species. For comparison, we also modelled the phenology of floral abundance alone. The phenological pattern of these three different measures of floral resources (pollen supply, nectar supply and floral abundance) was visually compared to assess their degree of similarity. All analyses were carried out in R, v.3.5.1 (R Core Team, 2022).

Results

A total of 1316 measurements of floral longevity were recorded from 72 species across the 24 sites. The species recorded were from 23 different families, with Asteraceae making up the largest proportion of these (n = 13). Mean floral longevity values of each species ranged from 1 to 8 d, but the flowers of most species remained open for just 1–4 d and only five species had a mean floral longevity of >5 d; the mean and median values were 2.6 ± 1.4 SD and 2.3 d, respectively (Fig. 1). We collected pollen data from these same 72 species and combined the two data sets to calculate their daily pollen production values; all values are provided in Table S2. Across the three floral abundance farms, we recorded a total of 235 322 floral units from 125 flowering plant species and 97% of these floral units were from our 72 target species. The pollen production data and floral abundance measurements were combined to address the three objectives.

Objective 1: Measure pollen production of individual farmland plant species and compare them with nectar production values

The mean daily pollen production of the 72 plant species was 16.2 mm^3 FU^{-1} d^{-1}; however, this varied amongst species by five orders of magnitude, with a standard error of 15.4. The species that produced the highest volume of pollen per floral unit (FU) per day were *Salix* spp. at 1110 mm^3 FU^{-1} d^{-1}, *Heracleum sphondylium* L. (8.6 mm^3 FU^{-1} d^{-1}), and *Cirsium vulgare* L. (6.4 mm^3 FU^{-1} d^{-1}) (Table 1). See Table S2 for a full list of pollen production values. At a floral unit level, there was a significant positive association between the daily pollen and nectar production values of the 72 farmland plant species for which both pollen and nectar data were available (linear model, $F_{1,71}$ = 35.33, P < 0.001, adjusted R^2 = 0.326; Fig. 2). This indicates that on average, species that produce large quantities of nectar also produce large quantities of pollen, likely because both resources are broadly correlated with flower size, that is large flowers will produce large amounts of both pollen and nectar. While there is a general positive relationship between pollen and nectar production, there are nevertheless some notable exceptions. For example, *Salix* spp. produced far more pollen than expected based on its nectar production, while *Myosotis arvensis* L. and *Allium ursinum* L. produced far less pollen than expected based on their nectar values. Three species produced no nectar, but still produced pollen: *Filipendula ulmaria* L., *Corylus avellana* L. and *Tripleurospermum inodorum* L.

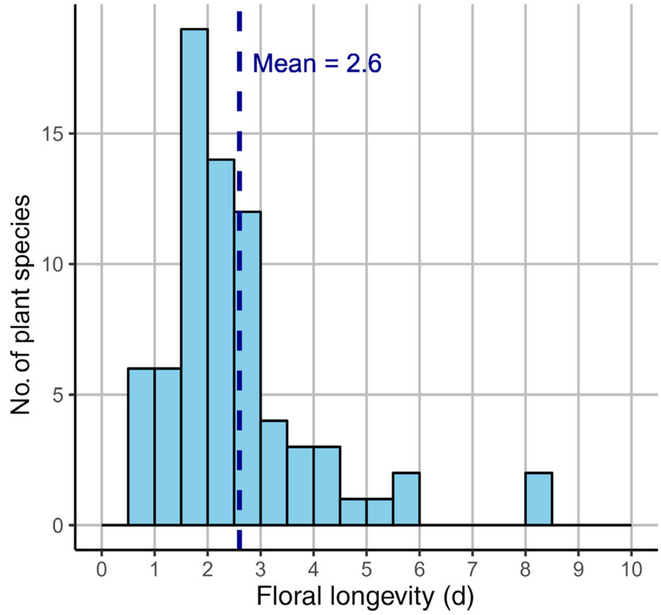

Fig. 1 Floral longevity of most species was between 1 and 3 d, with a mean of 2.6 (vertical dashed line) and only five species with a mean floral longevity value > 5 d. Approximately 10–20 floral longevity records were collected for each species (72 species in total), and a mean value was taken for each species, which is the data summarised in this histogram.

Objective 2: Identify the species and habitats that provide the greatest proportion of farmland pollen throughout the year and compare these with equivalent values for nectar

On the three farms, *Salix* spp. produced a mean of 38.2% (± 32.3% SE) of all farm-scale pollen throughout the year.

Table 1 Daily pollen production per flower and per floral unit (FU) of the top 25 species recorded in the field sites.

Plant taxon	Common name	Pollen per flower d^{-1} mm^{-3}	Flowers FU^{-1}	Pollen FU^{-1} d^{-1} mm^{-3}
Salix spp.	Willow	4.156	267.0	1109.716
Heracleum sphondylium	Hogweed	0.029	295.6	8.577
Cirsium vulgare	Spear thistle	0.048	133.4	6.378
Calystegia sepium	Hedge bindweed	4.484	1.0	4.484
Arctium agg.	Lesser burdock	0.163	27.2	4.436
Sambucus nigra	Elderflower	0.016	224.8	3.518
Centaurea nigra	Common knapweed	0.062	53.8	3.321
Taraxacum officinale	Dandelion	0.014	216.4	3.134
Filipendula ulmaria	Meadowsweet	0.050	57.0	2.828
Rosa canina	Dog rose	2.194	1.0	2.194
Anthriscus sylvestris	Cow parsley	0.016	119.5	1.966
Cirsium palustre	Marsh thistle	0.025	59.6	1.470
Rubus fruticosus	Bramble	1.339	1.0	1.339
Impatiens glandulifera	Himalayan Balsam	1.338	1.0	1.338
Cerastium fontanum	Mouse-ear chickweed	1.284	1.0	1.284
Cirsium arvense	Creeping thistle	0.010	113.4	1.173
Bellis perennis	Daisy	0.012	95.0	1.115
Lonicera periclymenum	Honeysuckle	1.038	1.0	1.038
Hypochaeris radicata	Catsear	0.014	57.8	0.828
Ranunculus ficaria	Lesser celendine	0.743	1.0	0.743
Epilobium hirsutum	Great willowherb	0.611	1.0	0.611
Sonchus oleraceus	Smooth sowthistle	0.005	116.9	0.567
Ranunculus repens	Creeping buttercup	0.552	1.0	0.552
Convolvulus arvensis	Field bindweed	0.354	1.0	0.354
Achillea millefolium	Yarrow	0.001	381.6	0.326

Species are listed in order of highest to lowest daily pollen production per floral unit.

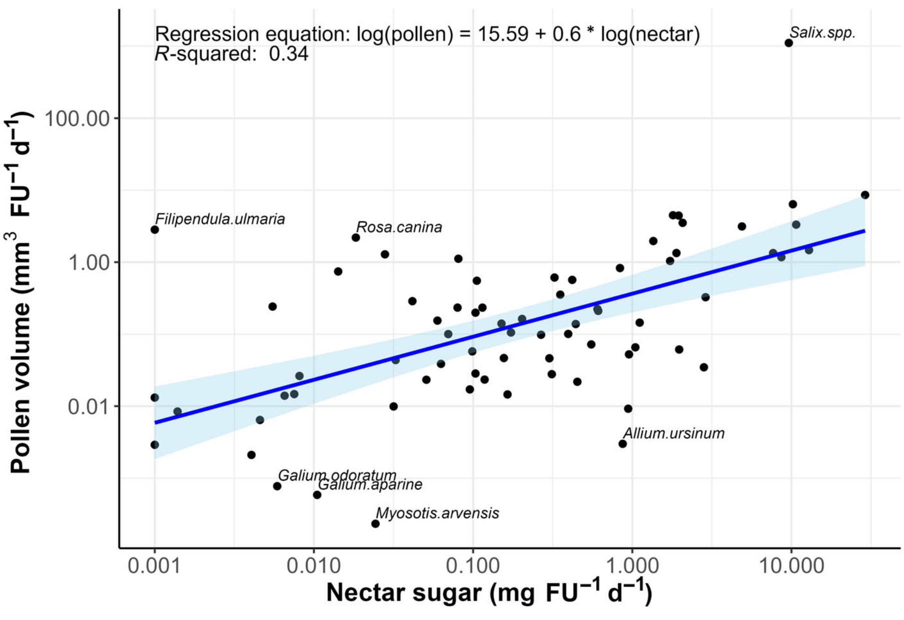

Fig. 2 Nectar and pollen production show a strong and significant association at the floral unit level ($F_{1,71}$ = 35.33, P < 0.001, adj. R^2 = 0.326), likely because they both also correlate with floral unit size. Despite this relationship, a number of species (labelled individually by name) fall relatively far from the regression line (blue line ±95% confidence intervals) demonstrating the value of one resource cannot always be predicted from the other. Note the log scale on each axis, though the scale has been back-transformed to show absolute (rather than log-transformed) values for each resource. The regression equation is shown at the top left of the figure.

However, this was highly variable amongst farms and very short-lived, being primarily limited to early April. After this, *Filipendula ulmaria*, *Rubus fruticosus* L. and *Taraxacum officinale* agg. (Weber). were the most important contributors to annual farm-scale pollen supply (Fig. 3); this was available for a longer period of the year and was more consistent amongst farms. The species that were most important for annual pollen provisioning were quite different from those that were most important for nectar provisioning; however, *Rubus fruticosus*, *Taraxacum officinale* and *Centaurea nigra* L. were important providers of both resources at the farm scale (Fig. 3).

The habitats that provided the greatest proportion of pollen throughout the year varied depending on the scale at which pollen was expressed. Per square metre unit area, hedgerows provided the highest quantity of pollen, followed by field margins and woodland, with pasture providing the smallest amount

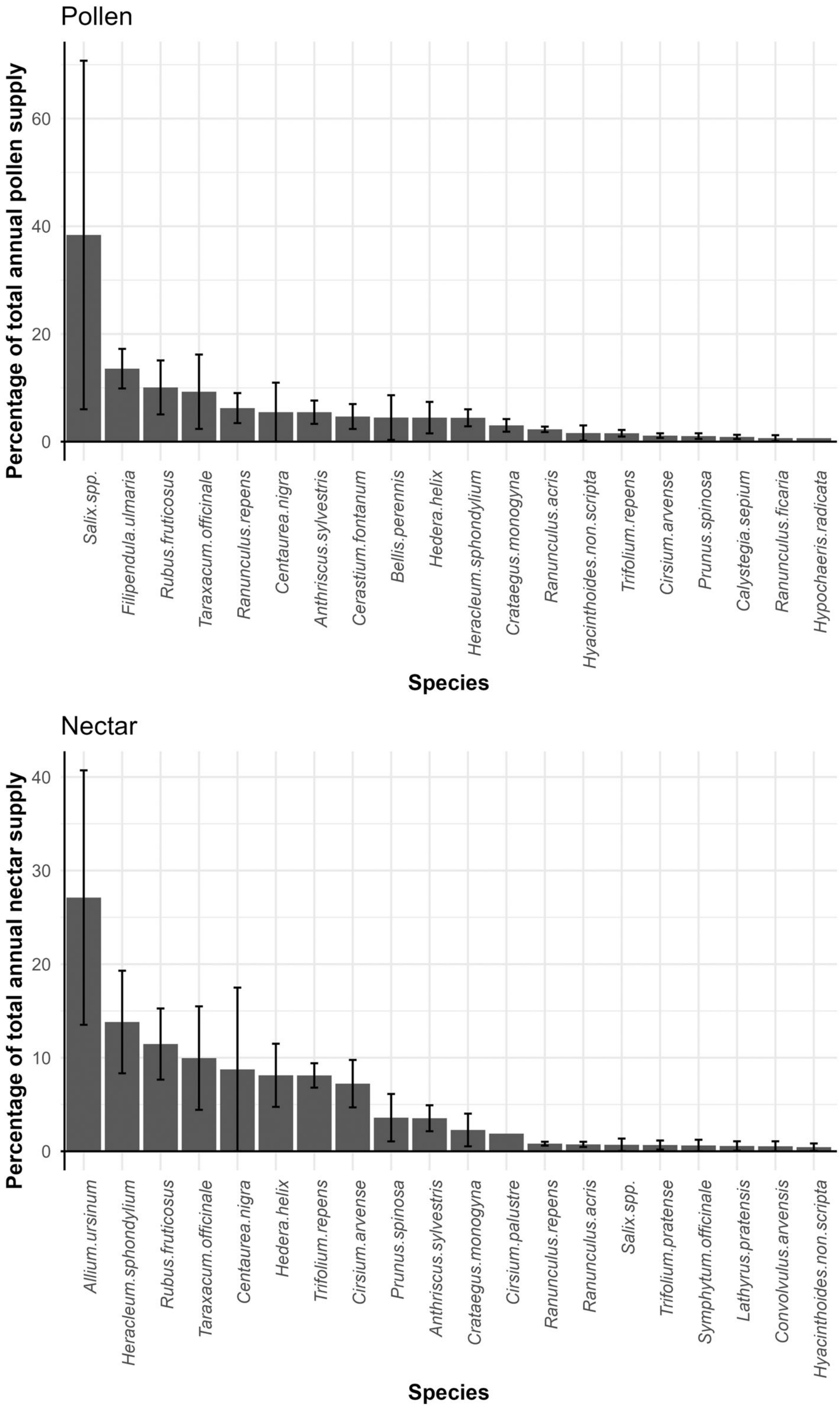

Fig. 3 Plant species providing most of the pollen at a farm-scale differ from those which provide most of the nectar. Graph shows the percentage contributions of key plant species to annual farm-scale pollen (upper panel) and nectar (lower panel) supply. Values show a mean (±SE) across the three study farms. For clarity, only the top 20 species are shown for each resource.

(Fig. 4). However, when scaled up to the level of the whole farm, pasture provided the majority of pollen, followed by woodland, hedgerows and field margins (Fig. 4). This difference occurs because pasture, while low in resources, covers by far the largest area of the farms (Table S1). Habitats varied in their pollen production value throughout the year; however, pasture remained the main provider of pollen at the farm scale throughout most of the year, until the end of September when woodland habitats (with a high abundance of late-flowering ivy) became a major source of pollen (Figs 5, S1). The pollen and nectar production of different habitats show a similar pattern of relative importance on an annual basis (Fig. 4) and through the year (Figs 5, S1) – this is true at both the metre-squared scale and the whole-farm scale.

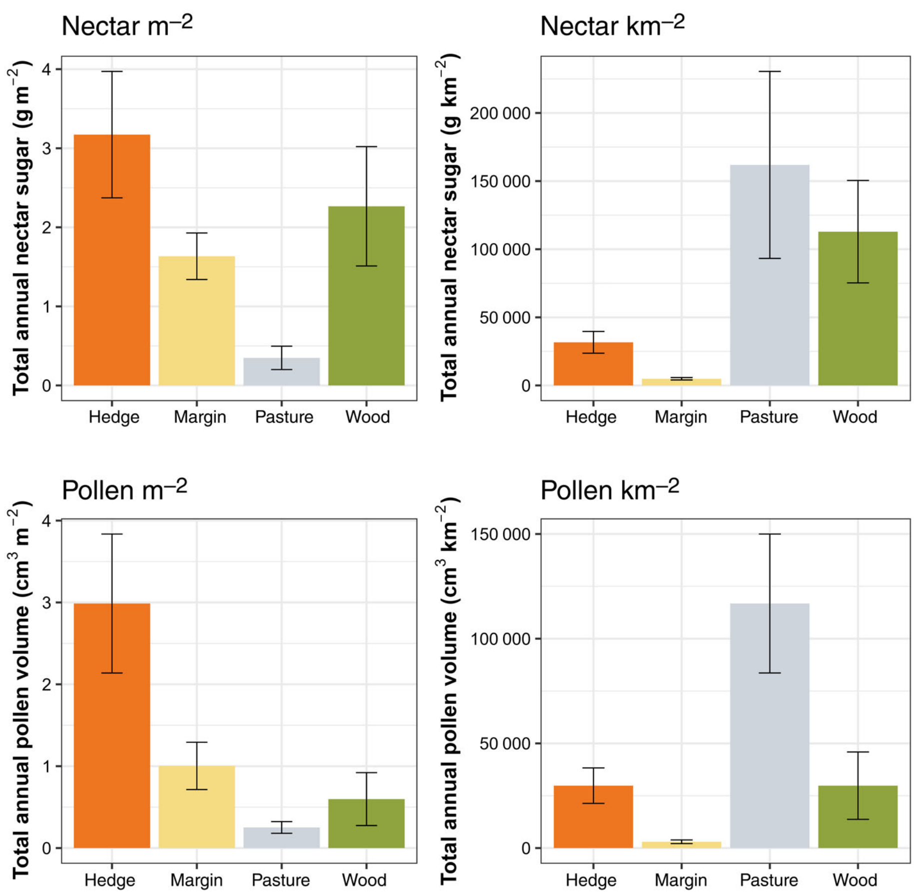

Fig. 4 Farmland habitats show similar patterns of relative importance in their annual supply of pollen and nectar. Annual nectar production (top) and pollen production (bottom) of farmland habitats are expressed per metre-squared unit area (left) and per km^2 of farmland (right). Bars show the mean $\pm$ SE of the three study farms.

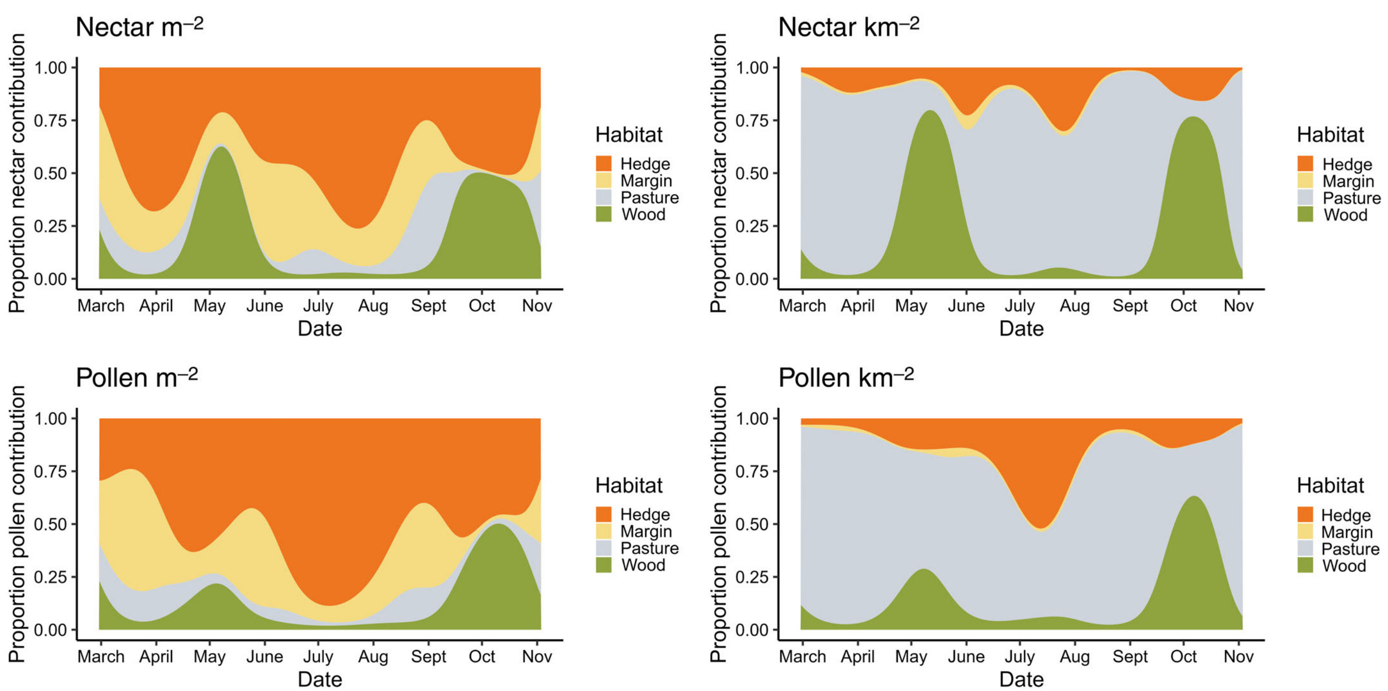

Fig. 5 Relative importance of each habitat in their provision of nectar (upper row) and pollen (lower row) differs substantially through the year, but remains relatively similar between the two resources. The left-hand column shows values at the metre-squared level while the right-hand row shows values at the km^2 (landscape level). Hedgerows provide the greatest contribution to pollen and nectar supply at the unit-area level while pasture provides the greatest contribution of both resources at the landscape level, due to its high coverage of the landscape. See Supporting Information Fig. S1 for the absolute values of pollen and nectar provided by each habitat through the year.

Objective 3: Quantify the phenology of pollen supply at the landscape level and compare this with the phenology of nectar supply

Farmland pollen availability showed a strongly seasonal pattern with a large spring bloom peaking in April, followed by a steep decline in June and then remaining relatively low throughout the year (Fig. 6). The phenology of pollen and nectar supply were remarkably similar at a landscape level, which is not surprising given that the availability of both resources is largely driven by the abundance of flowers in the landscape (Fig. 6a). However, the magnitude of the peaks and troughs differed slightly between the two resources. After the spring peak of pollen and nectar production, pollen supply dropped more slowly than nectar, buffered in part by the blooming of *Filipendula ulmaria*. This results in a less obvious 'June Gap' and more steady decline through to August, compared with a clear trough and then mini-peak in July for nectar production. These differences are driven by the specific identity of the flowering species, as while pollen and nectar are broadly correlated, there are exceptions to this (Fig. 2), and these exceptions will alter the magnitude of peaks and troughs. The phenology of floral abundance showed a similar pattern to both pollen and nectar supply, but there was a much more obvious peak in the late summer (September/October), which was largely driven by ivy, *Hedera helix* L., which produces a very large number of flowers, but relatively small amounts of nectar sugar and pollen per-flower.

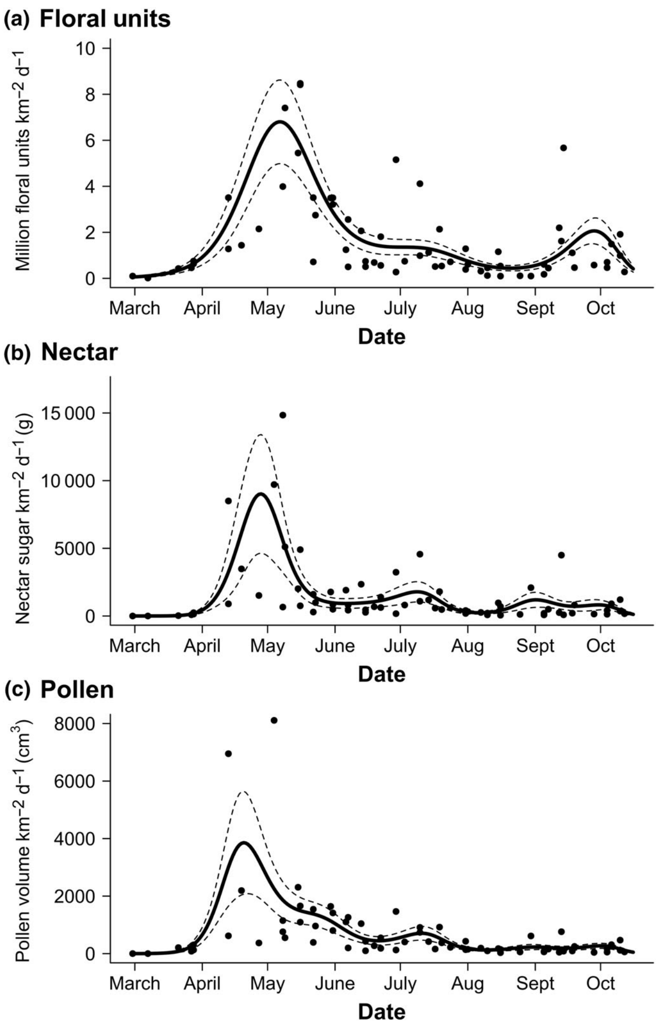

Fig. 6 Quantity of pollen, nectar and floral units all follow a similar seasonal pattern on farmland. Graph shows the phenology of three different measures of farmland floral resources: (a) number of floral units; (b) mass of nectar sugar and (c) volume of pollen, at a whole-farm scale throughout the flowering season. Points represent individual sampling events on the three study farms (Birches, Eastwood and Elmtree) and the data from all three farms are smoothed with a generalised additive model (±SE; dashed lines).

Discussion

In this study, we recorded the pollen production of common farmland plant species and combined these data with floral longevity values and floral abundance data to characterise and quantify daily pollen production at the species, habitat and landscape scale. The results show that the flowers of most plant species produce pollen for between 1 and 4 d and that the daily pollen production of individual plant species is significantly correlated with their daily nectar production. Willows (*Salix* spp.) produced around one-third of all pollen at a landscape scale (perhaps because they are partially wind-pollinated), but this was very short-lived, and many other species were important for maintaining pollen supply through the year. Per unit area, hedgerows provided the highest quantity of both pollen and nectar, but at the landscape level, pasture and woodland provided the highest quantity due to their high landscape coverage. The phenology of pollen production at the farm scale showed a broadly similar trend to nectar production, though the 'June gap' (a period of relatively low nectar production reported by European beekeepers during June) was much less pronounced for pollen than for nectar. In general, landscape-level pollen and nectar availability are relatively good proxies for one another, though the species providing most of the landscape-scale pollen are not the same as those providing most of the nectar. In what follows, we consider the limitations of the study, put our results into the context of previous research in this field and consider some recommendations for management and possible future research directions.

Limitations

There are three main limitations to our research. First, the phenology work is based on 1 yr floral counts, and there is no measure of year-to-year variation in flowering, which may occur due to variation in weather conditions and farm management. The general patterns and dominant species are likely to be broadly conserved from year to year however (Timberlake *et al.*, 2019). Second, we only collected data on the *volume* of pollen and not the *mass* or nutritional *quality*. Pollen quantity alone may not provide the most relevant measure of pollinator requirements as pollen varies substantially amongst species in its nutritional value (Vaudo *et al.*, 2015). Data on the nutritional content of pollen are currently limited for whole plant communities, although it could be readily combined with these data when it becomes available. Third, we do not include any wind-pollinated species such as grasses in our assessments of pollen availability, though pollinators are occasionally known to consume pollen from these plants. Thus, our estimates of pollen availability may represent a slight under-estimate of the true quantity of pollen available to insects.

Pollen availability through the year

While there is very little floral longevity data for the UK, there are some studies from the rest of the world. For example, Song *et al.* (2022) collates information from over 416 papers, many of which studied the floral longevity of species in Asia and the Americas. Few of these studies include any pollen data though, making it impossible to calculate daily pollen production. Indeed, aside from a handful of studies, pollen production is rarely quantified at all, despite being a vital component of pollinator nutrition. By recording both the pollen production and floral longevity values of a whole community of common farmland plants, we are able to calculate their daily pollen production values and quantify pollen resources at a landscape level. Similar to the nectar production data reported by Timberlake *et al.* (2019), our data show that that even though hedgerows produce the highest volume of pollen per unit area, their contribution to landscape-level floral resource production is relatively low, due to their low coverage of the landscape. By contrast, pasture has the lowest pollen production per unit area, but the highest landscape-level production of pollen, due to its high coverage of UK farmland. Farmland pasture covers *c.* 40% of UK land (GOV, 2015) and has become less florally diverse over time due to increased fertiliser use and the shift from hay to sileage production (Woodcock *et al.*, 2014). This reduction in floral diversity and abundance is thought to have played an important role in reducing the abundance and diversity of pollinators on farmland (Carvell *et al.*, 2006; Wratten *et al.*, 2012; Jönsson *et al.*, 2015). It should be noted that although we can quantify the *supply* of pollen through the year, our understanding of pollen *demand* by bees and other insects is highly limited, making it difficult to infer anything about the limitation of this resource at different times of year (Sponsler *et al.*, 2023). In the absence of detailed data on pollinator nutritional requirements, other approaches can be used to assess resource limitation including foraging assays (Sponsler *et al.*, 2020) and pollen depletion studies (Harris *et al.*, 2023).

Comparing nectar and pollen availability

Nectar and pollen are broadly correlated at the floral-unit level, likely due to their co-variance with floral unit size. The floral organs that produce pollen and nectar are likely to be scaled up in larger flowers, resulting in a greater production of both resources. Moreover, in cases where floral units are comprised of many individual flowers (such as *Salix* spp. and Asteraceae spp.), both pollen and nectar are multiplied up by the number of individual flowers, and will both therefore co-vary with flower number. Despite this general pattern of association, there were several species that did not conform closely to the regression line, meaning the supply of one resource could not be reliably predicted from the other; these included *Salix* spp., *Myosotis arvensis* and *Allium ursinum*. When scaling up to the landscape level, the phenology of pollen and nectar supply were also closely correlated due to the fact that both resources are largely determined by floral abundance. Although our data enable us to quantify daily pollen production at the landscape scale, the nutrient content of pollen remains largely unknown, preventing a full assessment of nutrient availability through the year. While there is some information published on specific nutrients contained within pollen, for example by Todd & Bretherick (1942), Roulston & Cane (2000), Vaudo *et al.* (2020), these studies focus on a small subset of plant taxa and do not provide an overall picture of the pollen nutrients available to foraging pollinators. Moreover, many of the studies on pollen focus on the pollen collected by bees, which is mixed with nectar and bee secretions and so does not give an accurate estimation of its nutrient content (Kostić *et al.*, 2015; Taha, 2015; Li *et al.*, 2018). Looking forward, improving our understanding of the nutrient content of pollen is an important research area in need of further study.

Conservation implications

Management strategies implemented by the UK Government for improving pollinator resources mainly focus on creating field margins planted with wildflowers and reduced mowing (Natural England, 2012; DAERA, 2022). Although these areas do provide floral-rich habitats, which have been found to improve pollinator abundance (Haaland *et al.*, 2011; Jönsson *et al.*, 2015), they represent a tiny percentage of most farmland habitats and Baude *et al.* (2016) report that they contribute a trivial amount of nectar. Of the three study farms within this study, only Birches and Elmtree had field margins, and they comprised just 1% of the land on the farms. Hedgerows provide high quantities of pollen and nectar per unit area and have been found to support high bee richness as well as facilitating the movement of pollinators across agricultural landscapes (Cranmer *et al.*, 2012; Dicks *et al.*, 2015; Sardiñas & Kremen, 2015). However, they also make up a very small percentage of most farmland landscapes; in our case, *c.* 5% of each farm. Focussing on improving pollinator resources in the widespread habitats such as pasture may be a more effective way in increasing the abundance of pollinators within farmland landscapes (Orford *et al.*, 2016; EIPWALES, 2021). Overall though, both the improvement of existing habitats such as pasture and further development of floral-rich field margins and hedgerows are key ways to improve pollinator resource availability on farms. Our results show that a few key species including *Salix* spp., *Filipendula ulmaria*, *Rubus fruticosus* and *Taraxacum officinale* provide a very large proportion of farmland pollen and may therefore offer particularly important targets for conservation. Losing these species could have profound consequences for the community of pollinators – particularly bees – which would likely lose a large proportion of their protein and lipid supply. On the other hand, increasing the abundance of these pollen-rich plant species on farmland – including shrubs and trees such as willow – is likely to greatly benefit populations of farmland pollinators.

Conclusion

Quantifying the pollen production, floral longevity and floral abundance of a whole community of common farmland plants throughout the year enabled us to conduct the first landscape-level assessment of pollen supply in the UK. Looking ahead, this approach – especially in combination with measures of pollen nutritive value and information on the nutritional requirements of pollinators – will provide more targeted approaches for conserving pollinators and the pollination services they provide.

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Competing interests

None declared.

Author contributions

JM, TPT and EKW conceived the ideas and designed the methodology. EKW collected the floral longevity data. TPT collected the floral abundance data. MB and EKW collected the pollen data. EKW, TPT and IPV analysed the data. EKW and TPT led the writing of the manuscript. All authors contributed critically to drafts and gave final approval for publication.

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Data availability

Fully reproducible R script and source data are available from: https://github.com/tom-timberlake/farm_pollen. Pollen volume and floral longevity values for all 72 plant species in this study are available in Table S2.

References

Barnsley S, Lovett A, Dicks L. 2022. Mapping nectar-rich pollinator floral resources using airborne multispectral imagery. *Journal of Environmental Management* **313**: 114942.

Baude M, Kunin WE, Boatman ND, Conyers S, Davies N, Gillespie MA, Morton RD, Smart SM, Memmott J. 2016. Historical nectar assessment reveals the fall and rise of floral resources in Britain. *Nature* **530**: 85–88.

Biesmeijer JC, Roberts SPM, Reemer M, Ohlemuller R, Edwards M, Peeters T, Schaffers AP, Potts SG, Kleukers RMJC, Thomas C *et al.* 2006. Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. *Science* **313**: 351–354.

Buchman S. 1986. Vibratile pollination in Solanum and Lycopersicon: a look at pollen chemistry. In: D'Arcy W, ed. *Solanaceae II: biology and systematics*. New York, NY, USA: Columbus University Press, 237–252.

Bukovinszky T, Rikken I, Evers S, Wäckers FL, Biesmeijer JC, Prins HHT, Kleijn D. 2017. Effects of pollen species composition on the foraging behaviour and offspring performance of the Mason Bee *Osmia bicornis* (L.). *Basic and Applied Ecology* **18**: 21–30.

Carvalheiro LG, Barbosa ERM, Memmott J. 2008. Pollinator networks, alien species and the conservation of rare plants: *Trinia glaucaas* a case study. *Journal of Applied Ecology* **45**: 1419–1427.

Carvell C, Meek WR, Pywell RF, Goulson D, Nowakowski M. 2007. Comparing the efficacy of agri-environment schemes to enhance bumble bee abundance and diversity on arable field margins. *Journal of Applied Ecology* **44**: 29–40.

Carvell C, Roy DB, Smart SM, Pywell RF, Preston CD, Goulson D. 2006. Declines in forage availability for bumblebees at a national scale. *Biological Conservation* **132**: 481–489.

Cranmer L, McCollin D, Ollerton J. 2012. Landscape structure influences pollinator movements and directly affects plant reproductive success. *Oikos* **121**: 562–568.

DAERA. 2022. *Guide to the environmental farming scheme for agreements commencing 01 Jan 2022*. [WWW document] URL https://www.daera-ni.gov.uk/publications/guide-environmental-farming-scheme-agreements-commencing-01-jan-2022 [accessed 14 November 2023].

Dicks LV, Baude M, Roberts SPM, 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.

Donkersley P, Rhodes G, Pickup RW, Jones KC, Wilson K. 2014. Honeybee nutrition is linked to landscape composition. *Ecology and Evolution* **4**: 4195–4206.

EIPWALES. 2021. *European Innovation Partnership (EIP) Wales: a guide to pollinator friendly grassland farming*. [WWW document] URL https://businesswales.gov.wales/farmingconnect/sites/farmingconnect/files/documents/EIP_Pasture_for_pollinators.pdf [accessed 13 July 2023].

FAO. 2018. *FAOSTAT statistical database*. Rome, Italy: Nations Faaootu.

Filipiak M. 2019. Key pollen host plants provide balanced diets for wild bee larvae: a lesson for planting flower strips and hedgerows. *Journal of Applied Ecology* **56**: 1410–1418.

Furse S, Koch H, Wright GA, Stevenson PC. 2023b. Sterol and lipid metabolism in bees. *Metabolomics* **19**: 78.

Furse S, Martel C, Yusuf A, Shearman GC, Koch H, Stevenson PC. 2023a. Sterol composition in plants is specific to pollen, leaf, pollination and pollinator. *Phytochemistry* **214**: 113800.

Goulson D, Nicholls E, Botias C, Rotheray EL. 2015. Bee declines driven by combined stress from parasites, pesticides, and lack of flowers. *Science* **347**: 1435.

GOV. 2015. *UK natural capital land cover in the UK*. [WWW document] URL https://www.ons.gov.uk/economy/environmentalaccounts/articles/uknaturalcapitallandcoverintheuk/2015-03-17#:~:text=Close%20to%2040%25%20of%20the,UK%20is%20covered%20by%20woodlands [accessed 10 June 2023].

Guezen JM, Forrest JRK. 2021. Seasonality of floral resources in relation to bee activity in agroecosystems. *Ecology and Evolution* **11**: 3130–3147.

Haaland C, Naisbit RE, Bersier LF. 2011. Sown wildfower strips for insect conservation: a review. *Insect Conservation and Diversity* **4**: 60–80.

Harris C, Ferguson H, Millward E, Ney P, Sheikh N, Ratnieks FLW. 2023. Phenological imbalance in the supply and demand of floral resources: half the pollen and nectar produced by the main autumn food source, *Hedera helix*, is uncollected by insects. *Ecological Entomology* **48**: 371–383.

Hemberger J, Bernauer OM, Gaines-Day HR, Gratton C. 2023. Landscape-scale floral resource discontinuity decreases bumble bee occurrence and alters community composition. *Ecological Applications* **33**: e2907.

Hicks DM, Ouvrard P, Baldock KC, Baude M, Goddard MA, Kunin WE, Mitschunas N, Memmott J, Morse H, Nikolitsi M *et al.* 2016. Food for pollinators: quantifying the nectar and pollen resources of Urban Flower Meadows. *PLoS ONE* **11**: e0158117.

Jachuła J, Denisow B, Wrzesień M. 2021. Habitat heterogeneity helps to mitigate pollinator nectar sugar deficit and discontinuity in an agricultural landscape. *Science of the Total Environment* **782**: 146909.

Jachuła J, Denisow B, Wrzesień M, Ziółkowska E. 2022. The need for weeds: man-made, non-cropped habitats complement crops and natural habitats in providing honey bees and bumble bees with pollen resources. *Science of the Total Environment* **840**: 156551.

Jones J, Rader R. 2022. Pollinator nutrition and its role in merging the dual objectives of pollinator health and optimal crop production. *Philosophical Transactions of the Royal Society, B: Biological Sciences* **377**: 20210170.

Jönsson AM, Ekroos J, Dänhardt J, Andersson GKS, Olsson O, Smith HG. 2015. Sown flower strips in southern Sweden increase abundances of wild bees and hoverflies in the wider landscape. *Biological Conservation* **184**: 51–58.

Kämper W, Werner PK, Hilpert A, Westphal C, Blüthgen N, Eltz T, Leonhardt SD. 2016. How landscape, pollen intake and pollen quality affect colony growth in *Bombus terrestris*. *Landscape Ecology* **31**: 2245–2258.

Klein AM, Vaissière BE, Cane JH, Steffan-Dewenter I, Cunningham SA, Kremen C, Tscharntke T. 2007. Importance of pollinators in changing landscapes for world crops. *Proceedings of the Royal Society B: Biological Sciences* **274**: 303–313.

Kostić AŽ, Barać MB, Stanojević SP, Milojković-Opsenica DM, Tešić ŽL, Šikoparija B, Radišić P, Prentović M, Pešić MB. 2015. Physicochemical composition and techno-functional properties of bee pollen collected in Serbia. *LWT - Food Science and Technology* **62**: 301–309.

Langlois A, Jacquemart AL, Piqueray J. 2020. Contribution of extensive farming practices to the supply of floral resources for pollinators. *Insects* **11**: 818.

Li Q-Q, Wang K, Marcucci MC, Sawaya AC, Hu L, Xue X-F, Wu L-M, Hu F-L. 2018. Nutrient-rich bee pollen: a treasure trove of active natural metabolites. *Journal of Functional Foods* **49**: 472–484.

Moerman R, Vanderplanck M, Fournier D, Jacquemart A-L, Michez D. 2017. Pollen nutrients better explain bumblebee colony development than pollen diversity. *Insect Conservation and Diversity* **10**: 171–179.

Natural England. 2009. *Agri-environmental schemes in England 2009. A review of results and effectiveness.* [WWW document] URL http://publications.naturalengland.org.uk/publication/46002 [accessed 28 September 2023].

Natural England. 2012. *Entry level stewardship: environmental stewardship handbook, 4th edn – January 2013 (NE349).* [WWW document] URL http://publications.naturalengland.org.uk/publication/2798159?category=45001 [accessed 14 June 2023].

Ogilvie JE, Forrest JR. 2017. Interactions between bee foraging and floral resource phenology shape bee populations and communities. *Current Opinion in Insect Science* **21**: 75–82.

Orford KA, Murray PJ, Vaughan AP, Memmott J. 2016. Modest enhancements to conventional grassland diversity improve the provision of pollination services. *Journal of Applied Ecology* **53**: 906–915.

Potts SG, Biesmeijer JC, Kremen C, Neumann P, Schweiger O, Kunin WE. 2010. Global pollinator declines: trends, impacts and drivers. *Trends in Ecology & Evolution* **25**: 345–353.

Powney GD, Carvell C, Edwards M, Morris RK, Roy HE, Woodcock BA, Isaac NJ. 2019. Widespread losses of pollinating insects in Britain. *Nature Communications* **10**: 1–6.

R Core Team. 2022. *R: a language and environment for statistical computing.* [WWW document] URL http://www.R-projects.org/ [accessed 7 May 2023].

Rotheray EL, Osborne JL, Goulson D. 2017. Quantifying the food requirements and effects of food stress on bumble bee colony development. *Journal of Apicultural Research* **56**: 288–299.

Roulston TH, Cane JH. 2000. Pollen nutritional content and digestibility for animals. *Plant Systematics and Evolution* **222**: 187–209.

Roulston TH, Goodell K. 2011. The role of resources and risks in regulating wild bee populations. *Annual Review of Entomology* **56**: 293–312.

Ruedenauer FA, Spaethe J, Leonhardt SD. 2016. Hungry for quality—individual bumblebees forage flexibly to collect high-quality pollen. *Behavioral Ecology and Sociobiology* **70**: 1209–1217.

Sardiñas HS, Kremen C. 2015. Pollination services from field-scale agricultural diversification may be context-dependent. *Agriculture, Ecosystems and Environment* **207**: 17–25.

Song B, Sun L, Barrett SC, Moles AT, Luo YH, Armbruster WS, Gao YQ, Zhang S, Zhang ZQ, Sun H. 2022. Global analysis of floral longevity reveals latitudinal gradients and biotic and abiotic correlates. *New Phytologist* **235**: 2054–2065.

Sponsler D, Iverson A, Steffan-Dewenter I. 2023. Pollinator competition and the structure of floral resources. *Ecography* **2023**: e06651.

Sponsler DB, Shump D, Richardson RT, Grozinger CM. 2020. Characterizing the floral resources of a North American metropolis using a honey bee foraging assay. *Ecosphere* **11**: e03102.

Taha E-KA. 2015. Chemical composition and amounts of mineral elements in honeybee-collected pollen in relation to botanical origin. *Journal of Apicultural Science* **59**: 75–81.

Tew NE, Memmott J, Vaughan IP, Bird S, Stone GN, Potts SG, Baldock KC. 2021. Quantifying nectar production by flowering plants in urban and rural landscapes. *Journal of Ecology* **109**: 1747–1757.

Timberlake TP, Vaughan IP, Baude M, Memmott J. 2021. Bumblebee colony density on farmland is influenced by late-summer nectar supply and garden cover. *Journal of Applied Ecology* **58**: 1006–1016.

Timberlake TP, Vaughan IP, Memmott J. 2019. Phenology of farmland floral resources reveals seasonal gaps in nectar availability for bumblebees. *Journal of Applied Ecology* **56**: 1585–1596.

Todd FE, Bretherick O. 1942. The compositions of pollens. *Journal of Economic Entomology* **35**: 312–317.

Vaudo AD, Dyer LA, Leonard AS. 2024. Pollen nutrition structures bee and plant community interactions. *Proceedings of the National Academy of Sciences, USA* **121**: e2317228120.

Vaudo AD, Tooker JF, Grozinger CM, Patch HM. 2015. Bee nutrition and floral resource restoration. *Current Opinion in Insect Science* **10**: 133–141.

Vaudo AD, Tooker JF, Patch HM, Biddinger DJ, Coccia M, Crone MK, Fiely M, Francis JS, Hines HM, Hodges M *et al.* 2020. Pollen protein: lipid macronutrient ratios may guide broad patterns of bee species floral preferences. *Insects* **11**: 132.

Willmer P. 2011. *Pollination and floral ecology.* Princeton, NJ, USA; Oxford, UK: Princeton University Press.

Wood SN. 2010. Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *Journal of the Royal Statistical Society Series B: Statistical Methodology* **73**: 3–36.

Woodard SH, Jha S. 2017. Wild bee nutritional ecology: predicting pollinator population dynamics, movement, and services from Floral Resources. *Current Opinion in Insect Science* **21**: 83–90.

Woodcock BA, Savage J, Bullock JM, Nowakowski M, Orr R, Tallowin JR, Pywell RF. 2014. Enhancing floral resources for pollinators in productive agricultural grasslands. *Biological Conservation* **171**: 44–51.

Wratten SD, Gillespie M, Decourtye A, Mader E, Desneux N. 2012. Pollinator habitat enhancement: benefits to other ecosystem services. *Agriculture, Ecosystems and Environment* **159**: 112–122.

Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Fig. S1 Phenology of pollen and nectar supply in each farmland habitat.

Notes S1 Detailed methods for collecting and quantifying pollen volume.

Table S1 Habitat composition of each of the three study farms.

Table S2 Pollen volume and floral longevity values of all 72 plant species in the study.

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