

## RESEARCH ARTICLE

# Ten-a-day: Bumblebee pollen loads reveal high consistency in foraging breadth among species, sites and seasons

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Grant/Award Number: NE/L002434/1**Handling Editor:** Natalia Escobedo Kenefic**Abstract**

1. Pollen and nectar are crucial resources for bees but vary greatly among plant species in their quantity, nutritional quality and timing of availability. This makes it challenging to identify an appropriate range of plants to meet the nutritional needs of bees throughout the year, though this information is important in the design of pollinator conservation schemes.
2. Using DNA metabarcoding of pollen loads, we record the floral resource use of UK farmland bumblebees at different stages of their colony lifecycle, and compare this with null models of 'expected' resource use based on landscape-scale resource availability (pollen and nectar), to identify foraging priorities and preferences. We use this approach to ask three main questions: (i) what is the foraging breadth of individual bumblebees?; (ii) do bumblebees utilise a greater or lesser diversity of plant species than expected if they foraged in proportion to resource availability?; (iii) which plant species do bumblebees preferentially utilise?
3. Individual bumblebees foraged from a highly consistent number of different plant taxa (mean:  $10 \pm 0.37$  SE per bee), regardless of their species, sampling site or time of year. This high consistency in foraging breadth, despite large changes in the quantity, identity and diversity of resource availability, implies a strong behavioural tendency towards a fixed range of foraging resources. This effect was most striking in April when foraging diversity was maintained despite very low landscape-level resource diversity.
4. Bumblebees used some plant taxa significantly more than predicted from their landscape-level floral abundance, nectar or pollen supply, implying certain desirable characteristics beyond the mere *quantity* of resource. These included *Allium* spp. and *Vicia* spp. in April; *Trifolium repens* and *Lotus corniculatus* in July and Cardueae spp. (thistles) and *Taraxacum officinale* in September.

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5. *Practical implication:* Our results strongly indicate that resource *quantity* is not the only factor driving bumblebee foraging patterns and that resource *diversity* and *quality* are also important factors. Thus, in addition to providing large quantities of floral resources, we recommend that pollinator conservation schemes also focus on providing a sufficient diversity of preferred floral resources, enabling pollinators to self-select a diverse and nutritious diet.

#### KEYWORDS

diet diversity, DNA metabarcoding, floral preference, floral resource, nectar, phenology, pollen, pollinator

## 1 | INTRODUCTION

Floral resources (pollen and nectar) are vital for supporting populations of wild and managed pollinators (Potts et al., 2003; Roulston & Goodell, 2011; Woodard & Jha, 2017), with declines in floral resources cited as one of the primary factors driving pollinator declines worldwide (Baude et al., 2016; Goulson et al., 2015; Potts et al., 2010). Reversing these trends requires us to understand which features of floral resources are most limiting for pollinators, so that we can manage landscapes to reduce these population-limiting factors (Sponsler et al., 2023). Measuring floral resources and their value to pollinators is not straightforward however, as pollen and nectar vary dramatically among plant species in their quantity (Baude et al., 2016; Filipiak et al., 2022), nutritional quality (Nicolson, 2022; Vaudo et al., 2020) and availability through the year (Guezen & Forrest, 2021; Jachula et al., 2021; Timberlake et al., 2019). The corresponding nutritional requirements of pollinator communities are also not well established but are known to vary substantially among different species, and at different stages of their lifecycle (Vaudo et al., 2015).

For generalist pollinators, selecting the most appropriate floral resources at each time of year is essential in order to support their own, and their offspring's, energetic and nutritional requirements. This is particularly important for social species with long flight seasons such as bumblebees, which need to meet the changing demands of the colony as they transition from rearing offspring in the spring, to the high energy demands of foraging workers, new queens and males later in the year (Vaudo et al., 2018). Meeting these nutritional needs relies upon foraging decisions made by individual worker bees, which consequently have a large impact on the survival and reproductive success of the colony (Woodard & Jha, 2017). It also relies upon a sufficient diversity of floral resources available within the foraging range of the colony, enabling them to balance their nutrient intake from complementary food sources with different nutritional profiles (Centrella et al., 2020; Vaudo et al., 2015). Therefore, in the design of pollinator conservation schemes, there is an increasing interest in understanding the nutritional needs of pollinators and the nutritional value of different floral resources so that planting schemes can be optimised to support pollinators' nutritional requirements throughout the year (Filipiak, 2019; Jones & Rader, 2022; Vaudo et al., 2020, 2024). However, such detailed

nutritional information is currently available for just a few plant species, rather than for whole plant communities, and it is the latter in which a pollinator operates and makes foraging decisions.

In the absence of detailed nutritional data for each plant and pollinator species, an alternative approach for designing pollinator-friendly planting schemes is to record the foraging behaviour of pollinators and look for patterns that indicate their resource preferences. For example, *which* plant species are pollinators visiting more than would be expected from their abundance (behaviour referred to hereafter as floral preferences), and *how many* different plant species are pollinators utilising to meet their nutritional needs? Understanding these two things may provide an indication of the identity and diversity of plant species required to support a pollinator population throughout the year. Motivated by this approach, our study aimed to record patterns of floral resource use by farmland bumblebees at different stages of their colony lifecycle (April, July and September) and use these patterns to identify features of floral resources that bumblebees prioritise. Foraging patterns were established using DNA metabarcoding of bumblebee pollen loads, which is an efficient method for identifying plant taxa that individual bees have chosen to utilise (Bell et al., 2022). When investigating the patterns of resource use, we wanted to separate the more obvious determinants of floral selection, such as floral abundance and pollen and nectar availability, from the less obvious features such as resource diversity and quality. To achieve this, we generated null models of consumer choice based upon the relative floral abundance, nectar supply and pollen supply of plant species recorded in the landscape. Comparing these null models of expected resource use, with recorded values of actual resource use (inferred from the DNA metabarcoding data), enabled us to identify features of floral resources that may be important to consider in the design of pollinator conservation schemes. Specifically, we asked the following three questions:

*Question 1:* What is the foraging breadth of individual bumblebees and does this vary among species, sites and periods of the year? Little is known about the individual-level foraging breadth of bumblebees and how this varies through the year, but an understanding of this may provide an indication of the range of plant species required to fulfil their basic nutritional needs. If foraging breadth remains relatively consistent among

species, sites and periods of the year, this may support the idea that bees are actively maintaining a balanced diet of floral resources.

**Question 2:** Do bumblebees utilise a greater diversity of plant species than expected if they foraged in proportion to resource availability? If so, this would imply bees are prioritising the collection of resources from a range of *different* plant species (and thus potentially a range of different nutrients) instead of simply maximising resource *quantity*. Given the fitness, immunity and developmental benefits of a diverse diet for bees (Alaux et al., 2010; Centrella et al., 2020; Di Pasquale et al., 2013; Roger et al., 2017), we might expect them to maximise the number of different plants they collect resources from. However, to our knowledge, no previous studies have used null models to separate this behaviour from the effects of relative floral resource availability.

**Question 3:** Which plant species do bumblebees preferentially utilise? If certain plant species are utilised more frequently than predicted by the null model, it implies there is something inherently favourable about their floral resources, over and above the quantity of pollen or nectar they produce. This may relate to their nutritional quality, their spatial, temporal or morphological accessibility or their visual/olfactory attractiveness. In the absence of further information, the underlying driver of their attractiveness will remain unclear, but these species will nevertheless be promising targets for inclusion in conservation schemes.

We investigate these three questions on replicate farms in Southwest UK during April, July and September. For each of the questions, we examine how the results change through the year, providing us with an insight into the shifting seasonal patterns of floral resource use.

## 2 | MATERIALS AND METHODS

### 2.1 | Field sites

Fieldwork was conducted in 2017 on three medium-sized (142–213 ha) mixed farms in Somerset, Southwest UK (Birches Farm, Elmtree Farm and Eastwood Manor Farm, Figure S1). Sampling permissions were provided by all farmers. None of the farms were under any form of pollinator-friendly management and all three farms were more than 5 km from a major urban area (i.e. town or city), but within foraging range of rural villages. At each site, the centre of the farm was identified and a circle with a 1 km radius was drawn from this central point. All sampling took place within this circle. The sites contained a mixture of pasture and arable land, with fields separated by hedgerows, field margins or semi-natural woodland (Figure S2; Table S1). As is typical of much of the UK, a small number of rural gardens and households as well as artificial surfaces (roads, buildings etc.) were also found in the sampling circles and surrounding landscape. The flowering species richness and habitat composition of the three farms were broadly representative of the

wider landscape, based on data from 12 farms in Southwest UK (Timberlake et al., 2021; Figure S3).

### 2.2 | Floral resource sampling

From March to October 2017, each site was visited once per week to record floral abundance in each type of semi-natural habitat (permanent pasture, semi-natural woodland, hedgerows and field margins). These habitats are clearly delineated in most farms in this region and exhibit consistent differences in their quantity and timing of resource availability (Timberlake et al., 2021), so represent practical and informative floral resource sampling units. Gardens were not surveyed as pollen and nectar values for garden plants were not available at the time of sampling. The arable crops on the study farms (wheat, maize and barley) are not typically bumblebee-visited, so were also not sampled. 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<sup>2</sup> 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). A floral unit was defined as one or multiple flowers that can be visited by insects without flying (Carvalho et al., 2008). 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, 2011), was used to model a smooth, non-linear 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, 2011). These floral abundance estimates were then multiplied by species-level nectar production values to calculate the mass of sugar produced by each plant species over time at the landscape level. Nectar values per floral unit were recorded by measuring nectar production over 24 h and calculating the amount of sugar in the nectar of each species using nectar data from Baude et al. (2016) and Timberlake et al. (2019). The floral abundance of each species was also multiplied by their pollen production value to estimate the volume of pollen available from each plant species over time at the landscape level. Pollen values were recorded by measuring the volume of individual pollen grains, the number of pollen grains per stamen, the number of stamens per flower and the mean number of flowers per floral unit to scale up pollen volume to the floral unit level (Wright et al., 2024; Appendix A1). These landscape-scale resource values were used to generate null models of expected

resource use, based on relative resource availability (see null model methods below). Nectar and pollen data were available for all the species collectively contributing 99% of floral abundance in each flowering period.

### 2.3 | Pollinator sampling

Bumblebees were sampled on the three farms during three periods of the year: spring (4–21 April 2017), summer (26 June–14 July 2017) and late summer (4–14 September 2017), these periods corresponding to different stages in the colony lifecycle and different periods of floral resource availability. Bumblebees were chosen as a focal group as their nutritional requirements are known to change through the year; from the rearing of brood in the spring, to the high energy demands of foraging workers in the summer, and finally to the production of new queens and males later in the year (Goulson, 2010). Thus, we might expect to see changes in their pattern of resource use that reflects this transition. Moreover, their long flight season ensured they would be present in sufficient numbers throughout the entire sampling period.

Each site was visited twice per sampling period, and to ensure a representative coverage of the area a fixed 2 km transect route was established at each site, passing through each habitat in direct proportion to its area. The transect was restricted to the inner 500 m radius of each study circle so that all captured bees were at least 500 m from the outer edge of the circle and therefore likely to be primarily foraging within the study circle (Figure S2). Any bumblebee encountered within 10 metres of the route was captured and transferred to a 1.5 mL centrifuge tube and frozen to await identification and pollen removal (see Appendix A2 for more details). Only females of the five bumblebee species most frequently encountered in the study sites (*Bombus terrestris* L., *B. lapidarius* L., *B. pascuorum* (Scopoli, 1763), *B. hypnorum* L. and *B. hortorum* L.) were used in the study. We restricted our sample to female bees because it is typically only females that collect pollen for the colony.

### 2.4 | Identifying the pollen

Following Lucas et al. (2018), pollen was removed from bees by covering them in a detergent solution and shaking them in a TissueLyser II (Qiagen). After removal of the bees, the remaining pollen and detergent solution was centrifuged to isolate the pollen pellet (Appendix A3). A modified version of the DNeasy 96 Plant Kit was used for DNA extraction. Samples were incubated in a water bath at 65°C for 1 h and 1 µL RNase (Qiagen) added before disruption using a TissueLyser II for 4 min at 30 Hz with 3 mm tungsten carbide beads. The remaining steps were carried out according to the manufacturer's protocol, excluding the use of the QIAshredder and the second wash stage. A negative control was included within each extraction.

DNA was amplified during two rounds of PCR using the *rbcL* DNA barcode marker region (CBOL Plant Working Group et al., 2009).

Samples were initially amplified using the universal primers *rbcLaf* and *rbcLr506* (de Vere et al., 2012). Products were then purified and indexed following Illumina's 16S Metagenomic Sequencing Library Preparation protocol (Illumina, 2013). Sequencing was carried out at the Institute of Biological, Environmental and Rural Sciences (IBERS) at Aberystwyth University on an Illumina MiSeq platform using a 2X300 base pair kit (see Appendix A4 for full details).

A data analysis pipeline available on GitHub at <https://github.com/colford/nbgw-plant-illumina-pipeline> was used to process the Illumina sequence reads and match them to taxa in a local reference database (de Vere et al., 2012; Jones et al., 2021; Appendix A5). After the assignment of each sequence to a plant taxon, results were manually checked to remove erroneous taxa (mostly likely a result of contamination) whose presence in pollen loads was considered implausible based on their distribution, phenology or rarity of the plant. For each bee specimen, we calculated the proportion of total sequence reads that each plant species made up—its relative read abundance (RRA)—to give a semi-quantitative measure of each plant's contribution to the pollen load. Relative read abundance data is known to provide a more sensitive representation of diet than presence/absence data (frequency of occurrence) as it avoids overstating rare taxa and devaluing the most abundant taxa in a sample (Deagle et al., 2019; Lowe, Jones, Witter, et al., 2022). Using the proportion of plant taxa in a sample is an effective way of controlling for differences in sequencing depth between samples, thus we used relative read abundance data for all our analyses. Despite these advantages, the quantitative signal in DNA metabarcoding data does not provide a perfect proxy for the actual abundance of a resource, and we therefore encourage readers to focus more attention on the relative patterns in the results, rather than absolute values.

To visualise the overall patterns of resource use among sampling periods, bumblebee species and sampling sites, the composition of pollen loads on individual bees (using relative read abundance data) were ordinated using non-metric multidimensional scaling (NMDS) in the package *vegan* (v. 2.5–5; Dixon, 2003). To provide a broad picture of the different types of plant being utilised by bumblebees, plant taxa in bumblebee pollen loads were categorised as either garden, non-garden or unknown based upon their introduction status. Additionally, plant growth form (e.g. trees and herbs) was categorised using the Online Atlas of the British and Irish Flora (Botanical Society of Britain and Ireland (BSBI), 2020).

### 2.5 | Generating null and observed networks of plant resource use

The relative read abundance of a given plant taxon in the pollen load of a bee (from the DNA metabarcoding data) was assumed to represent the relative strength of the interaction between that plant and bee, following Lowe, Jones, Brennan, Creer, Christie, et al. (2022). These data were used to compile a semi-quantitative individual-level resource use network which we call the 'observed' network. To differentiate the effects of resource quantity, from other potentially

meaningful factors such as diversity and quality, we developed three alternate ‘null’ networks of floral resource use which we could compare against the observed network. These null networks are not completely random (in the sense that some null models are) but instead represent a basic account of foraging: that bees visit plants in direct proportion to their resource availability, *sensu* Vaughan et al. (2018). Thus they enable us to distinguish the effects of resource quantity, from other potentially meaningful drivers of foraging. These three null networks were generated using the package *econullnetr* (Vaughan et al., 2018) and were based upon three different measures of floral resource availability recorded on the farms. These were: (1) the floral abundance of each plant species; (2) the nectar supply of each plant species and (3) the pollen supply of each plant species. For each individual bee in the observed resource use network, the model repeatedly redistributes its interactions (inferred from the DNA metabarcoding data) among all plant taxa present on the farm, with the probability of each plant being used directly proportional to its resource abundance. Each model was subdivided by bumblebee species, farm and season and was run with 10,000 iterations. Modelling resource choices made by individual bees in this way allows variation between species, sampling periods and sites to be assessed and enabled us to answer our three main questions.

## 2.6 | Answering the three questions

### 2.6.1 | Question 1: What is the foraging breadth of individual bumblebees and does this vary among species, sites and periods of the year?

The range of plant taxa being utilised by individual bumblebees (hereafter referred to as foraging breadth) was measured by calculating the number of unique plant taxa detected in the pollen load of each bee. For this analysis we used only presence-absence data as we were purely interested in the richness of plant taxa being used by each bee and how this varied among species, sites and periods of the year. A general linear model (function *glm* in base R) was used to test for differences in foraging breadth between the different levels of these three factors (sampling period, site and bumblebee species). The model residuals were confirmed to be normally distributed. A post-hoc Tukey test using the function *glht* in the package *multcomp* (Hothorn et al., 2016) was used to conduct pairwise comparisons for each month—our variable of primary interest. Model coefficients and their confidence intervals were plotted using *ggplot* (Wickham et al., 2016).

### 2.6.2 | Question 2: Do bumblebees utilise a greater diversity of plant species than expected if they foraged in proportion to resource availability?

To test whether the bumblebee community as a whole was utilising a greater diversity of plant taxa than expected if they simply foraged in proportion to floral abundance, pollen or nectar

availability, we compared the diversity of observed resource use with the diversity of expected resource use based on the null models of floral abundance, pollen and nectar availability. ‘Observed’ resource use diversity was measured by calculating the Shannon diversity of interactions in the observed resource use network (inferred from DNA metabarcoding data) using the function *bipartite\_stats* within the R package *bipartite* (Dormann et al., 2008). All bumblebee species were pooled into one single community in this analysis so that our results purely reflected the diversity of resource use, not the diversity of bumblebee species. ‘Expected’ resource use diversity was calculated in the same way, except that the Shannon diversity calculations were made on the three alternate null models of resource use. In each of the three sampling periods (April, July and September), diversity values for the observed network were compared against the 95% confidence intervals of the three null networks to test whether they differed significantly from the expectations of the null model. We took a conservative approach in our analyses and trimmed both the null and observed networks to include only those plant taxa that were recorded in the floral abundance surveys *and* in bumblebee pollen loads. This ensured that any differences between null and observed networks were not simply a result of sampling incompleteness, for example, the omission of gardens from floral abundance surveys.

### 2.6.3 | Question 3: Which plant species do bumblebees preferentially utilise?

To identify plant taxa that were utilised significantly more or less frequently than expected from their floral abundance, pollen and nectar availability, we compared the ‘observed’ use of each plant taxon (inferred from relative read abundances in the pollen barcoding data), to the *expected* use of each plant taxon based on the three null resource use networks (floral abundance, nectar and pollen). The observed resource use value for each plant taxon was compared against the 95% confidence intervals of the three null models to identify disproportionately visited plants whose use could not be explained by any measure of resource *quantity*. All analyses were carried out in R, version 3.5.1 (R Core Team, 2018).

## 3 | RESULTS

A total of 235,322 floral units from 125 flowering plant species (88 on Birches farm, 77 on Eastwood Manor farm and 63 on Elmtree farm) were recorded on the three study farms during March to October 2017. Pollen loads from a total of 187 individual bumblebees of five different species (63 *B. terrestris*, 37 *B. lapidarius*, 83 *B. pascuorum*, 3 *B. hypnorum* and 1 *B. hortorum*) were DNA metabarcoded, with a total of 178 unique plant taxa identified from the samples, with 65 identified to species level, 77 to genus, 3 to tribe and 33 to family (Table S2). The plant species that each insect was captured on is shown in Table S3. The composition of pollen on bees’ bodies

changed markedly through the year but differed very little between study sites and bumblebee species (Figure 1; Table S4). Plants of garden origin were identified on 46% of all bumblebee specimens (increasing to 70% in the late summer) and made up a mean of 6% of the taxa recorded in pollen loads. Plants classified as herbs made up the greatest proportion of taxa in bumblebee pollen loads, followed by shrubs and trees, though this varied somewhat through the year, with more tree taxa being utilised in the early spring (Figure 2).

### 3.1 | Question 1: What is the foraging breadth of individual bumblebees and does this vary among species, sites and periods of the year?

The number of plant taxa recorded in the pollen loads of individual bumblebees (foraging breadth) was highly consistent among species and study sites, with a mean of 10.27 ( $\pm 0.37$  SE) and a median of 10 plant taxa per individual bee (Figure 3a). No significant differences in foraging breadth were recorded among bumblebee species or farms, though values were slightly lower in July ( $8.82 \pm 0.48$  SE) than in April ( $11.3 \pm 0.83$  SE) and September ( $12.0 \pm 0.71$  SE) and this difference was significant (GLM  $t$ -value<sub>1,2</sub> = -2.65, Estimate = -2.55, Std. Err = 0.96,  $p = 0.009$ ) (Figure 3b).

### 3.2 | Question 2: Do bumblebees utilise a greater diversity of plant species than expected if they foraged in proportion to resource availability?

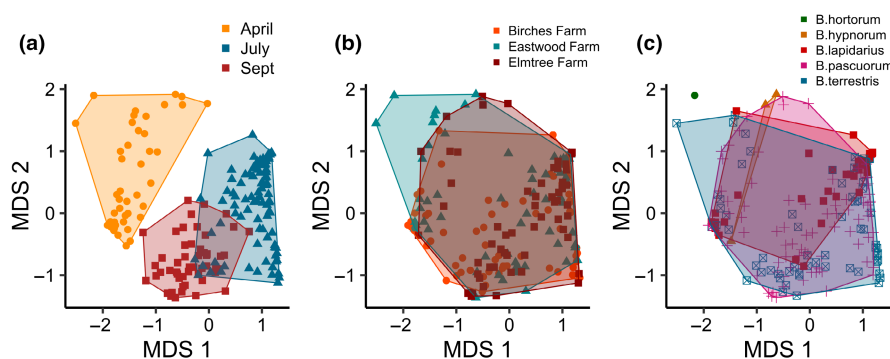
At the community level, the Shannon diversity of interactions among plants and bumblebees (i.e. resource use diversity) was highest in April, followed by September and then July (Figure 4). In July and September, the diversity of resource use was in-line with expectations based on the diversity of floral resources available to bees (i.e. no significant difference from the null models). However, resource use diversity was significantly higher in April than predicted by either the pollen, nectar or floral unit-based null models.

### 3.3 | Question 3: Which plant species do bumblebees preferentially utilise?

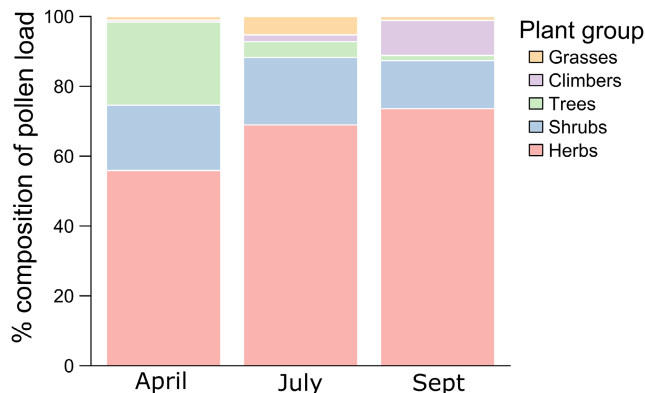
Throughout the year, certain highly rewarding plant species were utilised significantly less than expected from their landscape-scale floral abundance, pollen or nectar supply, whilst other less abundant or rewarding taxa were utilised significantly more than expected by chance (Figure 5). The most extreme of the preferred resources (utilised significantly more than their landscape floral abundance, pollen or nectar supply would predict) were *Allium* spp. and *Vicia* spp. in April; *Trifolium repens* L. and *Lotus corniculatus* L. in July and *Cardueae* spp. (thistles) and *Taraxacum officinale* agg. (Weber) in September. Meanwhile, plant taxa utilised significantly less than expected from their pollen and nectar supply including *Prunus* spp. in April; *Ranunculus* spp. in July and *Hedera helix* L. in September.

## 4 | DISCUSSION

Our study compared the use of different floral resources by farmland bumblebees with the availability of these same resources to identify foraging priorities and preferences at different stages of their life-cycle. Individual bumblebees utilised a highly consistent number of different plant taxa, regardless of their species or location (a mean of 10 plant taxa per bee). This remained relatively constant throughout the year, despite large differences in the quantity, identity and diversity of floral resources available to them. This effect was most striking in early spring (April) when the diversity of resource use by bumblebees was significantly higher than expected based on the diversity of resource availability. Although the breadth and diversity of resource use remained relatively constant throughout the year, the identity of plant species being utilised by bumblebees changed dramatically. Certain plant species were used more than predicted from their floral abundance, pollen or nectar availability, implying additional desirable qualities beyond the mere quantity of their resource provision. Overall, our results suggest that floral resource diversity and quality are important factors influencing bumblebee



**FIGURE 1** Non-metric multidimensional scaling (NMDS) plots show that the composition of pollen loads on individual bumblebee samples (from relative read abundance data) differs among the three sampling periods (panel a), but remains consistent among sites (panel b) and bumblebee species (panel c). Each point represents an individual bumblebee and points are clustered by (a) sampling period, (b) study site and (c) bumblebee species.

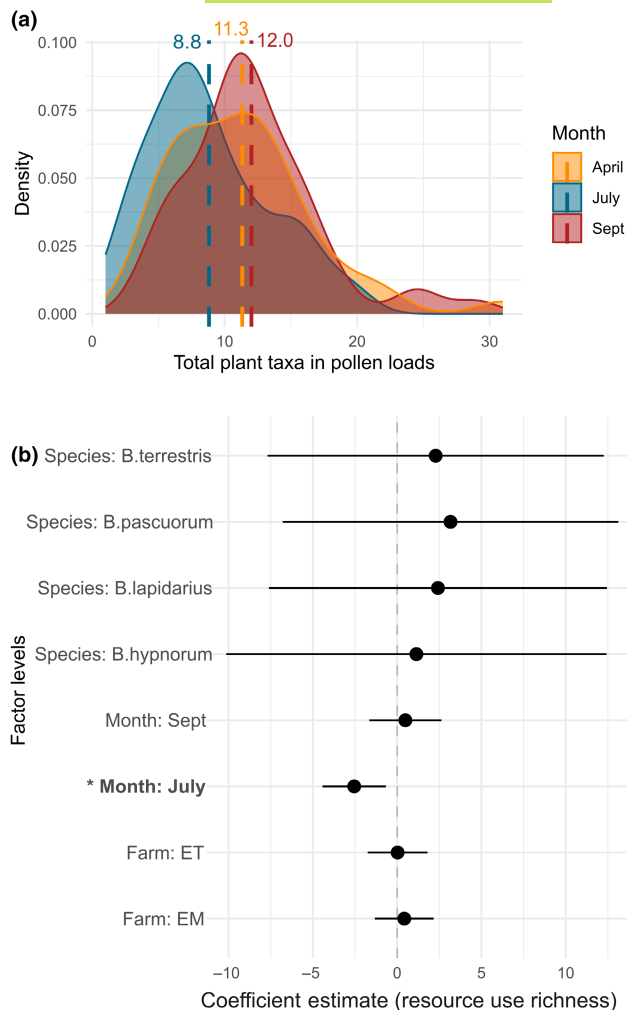


**FIGURE 2** Bumblebees utilised resources from a range of different plant groups (herbs, shrubs, trees, climbers and grasses) and this changed slightly through the year. Values show the mean number of plant taxa from each plant group as a percentage of all taxa recorded in bumblebee pollen loads. Note the substantially higher use of tree taxa in the early spring (April).

foraging patterns, alongside the more obvious influence of resource quantity. In what follows, we discuss the relevance of this work to our understanding of bumblebee ecology, as well as the conservation management implications of these findings.

#### 4.1 | Bumblebee floral use diversity

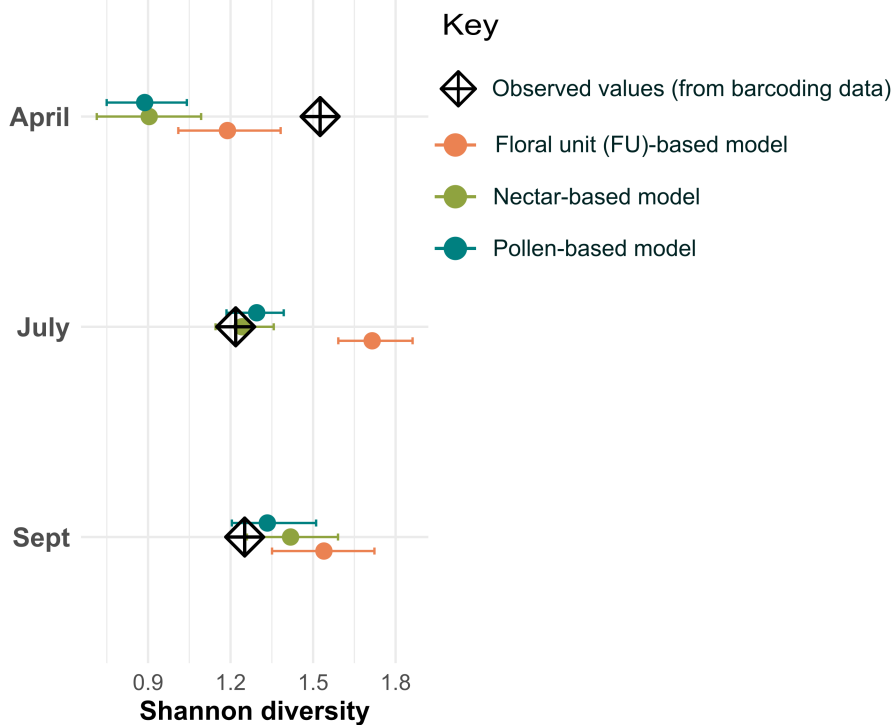
The number of different plant taxa used by individual bees (foraging breadth) remained remarkably consistent among species, sites and—to a lesser extent—seasons, despite large differences in the richness of available resources. This relatively consistent value of c.10 plant taxa recorded on each individual bee, against a background of high floral turnover, suggests a strong behavioural tendency towards a fixed number of forage resources. It is possible that this behaviour may represent a balance between two opposing selective pressures which are thought to drive the foraging patterns of generalist pollinators. The first of these is the pressure to maximise foraging efficiency by preferentially visiting resource-rich patches and maintaining a relatively high level of resource fidelity (Grant, 1950; Slaa et al., 2003), as predicted by optimal foraging theory (Pyke et al., 1977). This is expected to reduce handling time and the cognitive costs of learning and recalling new collection routines (Chittka et al., 1999; Russell et al., 2017). Foraging in this manner would result in a relatively low diversity of highly rewarding plants being visited, as predicted from the null models in which individuals forage in proportion to relative resource availability. An alternative, opposing pressure is the drive to maximise diet diversity and ensure a balanced intake of nutrients (Kaluza et al., 2017). A greater diversity of floral resources, particularly pollen, is known to increase the immunocompetence (Alaux et al., 2010; Di Pasquale et al., 2013), larval development (Genissel et al., 2002; Tasei & Aupinel, 2008) and fitness (Kaluza et al., 2018) of bees and there is evidence that bees actively increase their diet diversity where possible (Jha & Kremen, 2012; Kaluza et al., 2017). However, to our knowledge, no previous



**FIGURE 3** The number of unique plant taxa utilised by individual bumblebees (foraging breadth) remained highly consistent through the year (panel a). Dashed vertical lines show the mean for each sampling period. Panel (b) shows the coefficients and 95% confidence intervals of the general linear model used to test for differences in foraging breadth among bumblebee species, sampling months and field sites (farms). Although there were no significant differences in foraging breadth among bumblebee species or farms, values were slightly lower in July than in April or September (GLM  $t$ -value<sub>1,2</sub> = -2.65, Estimate = -2.55, Std. Err = 0.96,  $p$  = 0.009).

studies have used null models to separate this behaviour from neutral mechanisms such as relative resource abundance.

Potentially as a compromise between the conflicting priorities of increasing diet diversity and maximising foraging efficiency, the bumblebees in our study appeared to 'major and minor' on floral resources, with one or two dominant pollen taxa recorded on each individual bumblebee, but a number of other minor taxa occurring at lower frequencies (Table S4). This phenomenon has previously been reported in bumblebees and is thought to be a strategy for keeping track of changing resources in a dynamic environment and ensuring that the diet of individual bees and the colony remains nutritionally balanced (Heinrich, 1979a). The high diversity of resource use in early spring was particularly striking as it is a period of low floral resource diversity on farmland (Timberlake et al., 2019). This indicates



**FIGURE 4** The community-level Shannon diversity of ‘observed’ floral resource use by bumblebees (black crosses) remains relatively constant through the year and largely independent of the diversity of floral resources available in the landscape. Shown alongside the ‘observed’ resource use value for each season are the three ‘expected’ values of resource use ( $\pm 95\%$  confidence intervals) based on the three null models. These null models assume that bees are utilising plants in proportion to either their floral abundance (FU; orange dots); their nectar supply (green dots) or their pollen supply (blue dots). If observed resource diversity values fall outside of the confidence intervals of all three models, it implies that the diversity of resource use cannot be explained by patterns in relative resource availability.

a pattern of foraging behaviour that prioritises resource diversity over resource quantity, perhaps because of the more complex nutritional demands of the colony during this time (Vaudo et al., 2015). Alternatively, this could be a result of more neutral factors such as the dispersion of resource patches, weather conditions or increased resource competition with other bees. Enhanced competition is known to increase bumblebee diet breadth and generalisation (Fontaine et al., 2008) and this period of the year (early spring) is a substantial resource deficit for farmland bumblebees in this region (Timberlake et al., 2019), likely resulting in greater levels of competition for resources (Sponsler et al., 2023, 2024). This pattern has been observed in honeybees too, which increases their diversity of resource use at the community level during periods of resource limitation (Lowe, Jones, Brennan, Creer, Christie, et al., 2022).

## 4.2 | Bumblebee floral preferences

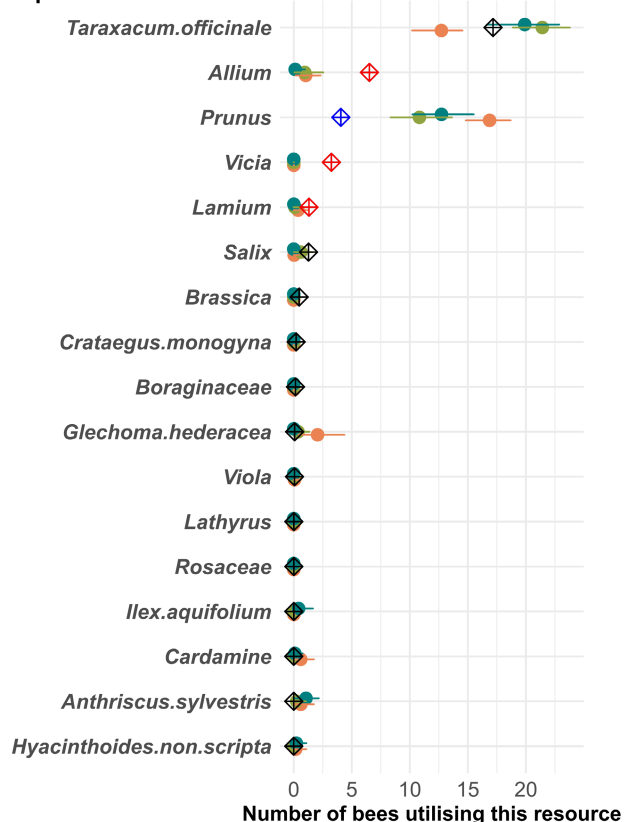
In general, plants with high floral abundance and pollen and nectar availability were utilised by bumblebees more frequently than less abundant and rewarding plants, in line with previous studies (Butler, 1945; Fowler et al., 2016; Heinrich, 1979b; Konzmann & Lunau, 2014). However, there were a number of plant taxa which

bumblebees showed a particular preference for, beyond what would be predicted based on their floral abundance or nectar and pollen production alone. These included wild garlic (*Allium ursinum* L.), vetches (*Vicia* spp.), clover (*Trifolium repens*), bird's-foot trefoil (*Lotus corniculatus*), thistles (*Cardueae* spp.) and dandelions (*Taraxacum officinale* agg.). Thus, in addition to making foraging decisions based on resource quantity, bumblebees also appeared to be discriminating between resources based on their quality – whether that be their nutritional quality (Hanley et al., 2008; Vaudo et al., 2016), their physical quality such as nectar viscosity (Kim et al., 2011) or their floral morphology (Sponsler et al., 2022). Indeed, many of these preferred species possess deep corollas which bumblebees are well adapted to exploiting. Certain other species such as ivy (*Hedera helix*) and buttercups (*Ranunculus* spp.) were utilised significantly less than expected, perhaps because of a surplus of resources provided (previously reported in the case of ivy; Harris et al., 2023) or the presence of toxic or unpalatable compounds, for example, the toxic ranunculin compound present in *Ranunculus* pollen (Sedivy et al., 2012). The floral preferences of bumblebees shifted through the year, with some plants favoured at one point in the year, but not another. For example, *Taraxacum officinale* agg. was utilised slightly less than expected in April, but significantly more than expected in September, emphasising the

**FIGURE 5** Comparing ‘observed’ values of resource use (crosses) with ‘expected’ values based on the three null models (dots and lines) reveals plant species that are utilised significantly more (red crosses) or less (blue crosses) than expected based on their floral abundance or pollen and nectar availability. If observed resource use values fall outside of the confidence intervals of all three models, it implies that utilisation of this plant taxa cannot be explained by any aspect of their relative resource availability. Taxa are only shown here if information was available on both their farm-scale floral abundance and their species-level pollen and nectar production, enabling expected interaction strengths to be calculated.



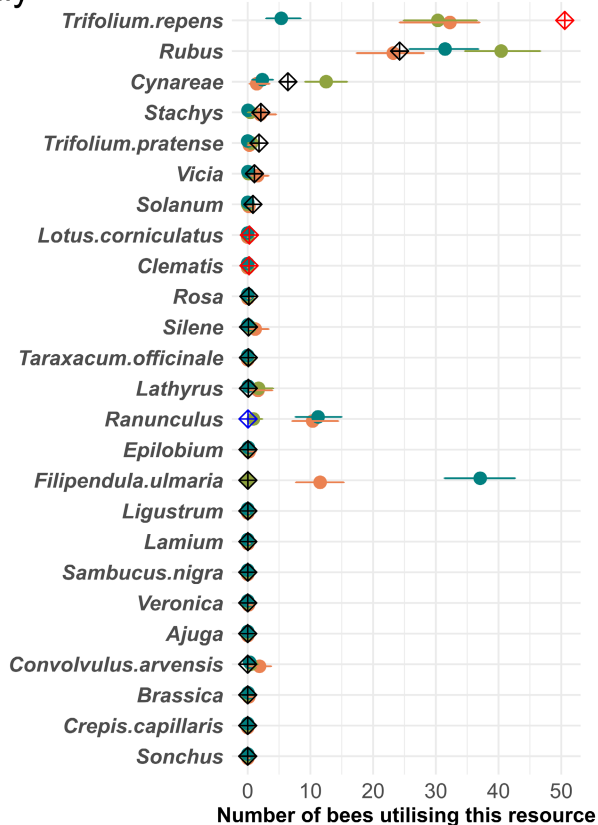
### April



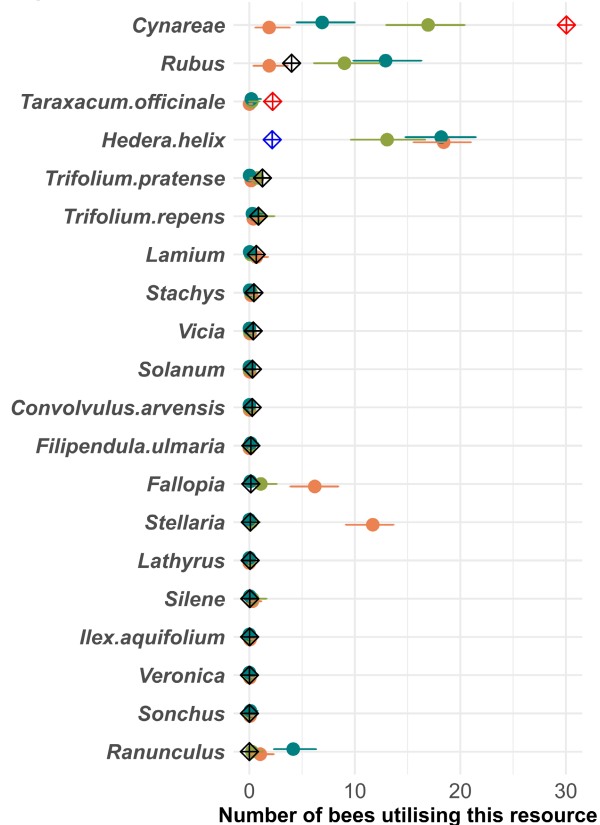
### Key

- Observed values (from barcoding data)
- Values ±95% CI predicted by floral unit (FU)-based
- Values ±95% CI predicted by nectar-based model
- Values ±95% CI predicted by pollen-based model

### July



### Sept



fact that preferences for a species are not fixed, but are influenced by the relative attractiveness of other resources in the landscape, and perhaps by the changing nutritional value of the resource and requirements of the colony (Morán-López et al., 2022; Vaudo et al., 2018).

### 4.3 | Management implications

The striking consistency in foraging breadth by bumblebees in this study suggests resource diversity is important to bumblebees and highlights the value of ensuring a sufficient diversity of floral resources on farmland throughout the year, as well as a sufficient quantity of resources. Our limited understanding of pollinator nutritional requirements and the nutritional composition of wild plant species currently prevents us from identifying the most nutritionally appropriate mix of plant species for pollinators. Further research into the nutritional quality of floral resources and nutritional requirements of wild pollinators will likely improve the success and cost-effectiveness of pollinator conservation schemes by enabling us to target planting schemes more effectively. However, in the meantime, plants which are visited more than expected based upon the quantity of their floral resources (e.g. *Allium* spp., *Vicia* spp., *Trifolium repens*, *Lotus corniculatus*, *Cardueae* spp. and *Taraxacum officinale* agg.), may represent good targets for inclusion in conservation schemes. Alongside these highly preferred species, it is also important to conserve the abundant, highly rewarding species such as *Rubus* spp., *Prunus* spp., *Hedera helix* and *Trifolium pratense* L. which were not disproportionately visited, but nevertheless comprised a major part of bumblebee diets.

A high proportion of the plants in bumblebee pollen loads, particularly in the early spring, were characteristic of woodland or hedgerows, such as *Prunus* spp., *Allium* spp., *Fraxinus* spp., *Hyacinthoides non-scripta* (Mill.), *Crataegus monogyna* Jacq., *Salix* spp., *Rubus* spp., *Rosa* spp., *Hedera helix*, *Lamium* spp. and *Stachys* spp. This highlights the importance of maintaining such habitats in farmland and ensuring they are managed to accommodate these species. Grasses were also detected as a minor but potentially important component of bumblebee diets, likely providing an additional source of protein and lipids. The widespread use of garden plants by bumblebees (particularly in the late summer) suggests rural gardens may play an important role in supplementing the often-impooverished floral resource supply of farmland landscapes, as demonstrated by Lowe, Jones, Brennan, Creer, and de Vere (2022). However, the generally low proportion of garden plants (<10%) in bumblebee pollen loads demonstrates that while gardens may be important in supplementing farmland floral resources, they cannot substitute for diverse semi-natural habitats such as woodland, hedgerows and unimproved pasture.

#### AUTHOR CONTRIBUTIONS

Thomas P. Timberlake, Jane Memmott, and Natasha de Vere conceived the ideas and designed the methodology; Thomas P. Timberlake collected the field data; Thomas P. Timberlake, Laura

E. Jones, and Natasha de Vere conducted the molecular analysis; Thomas P. Timberlake and Ian Vaughan conducted the statistical analysis; Mathilde Baude provided the nectar and pollen data; Thomas P. Timberlake and Jane Memmott led the writing of the manuscript. All authors contributed critically to drafts and gave final approval for publication.

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#### CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest in this work.

#### PEER REVIEW

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/10.1002/2688-8319.12360>.

#### DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.3ffbg79s7> (Timberlake et al., 2024). R code and source data available in Zenodo: <https://doi.org/10.5281/zenodo.11639291> (Tom-Timberlake, 2024).

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

**Appendix A1.** Pollen quantification.

**Appendix A2.** Bumblebee sample collection.

**Appendix A3.** Pollen removal.

**Appendix A4.** Amplification and Sequencing: Illumina Miseq.

**Appendix A5.** Bioinformatic analysis.

**Table S1.** Landscape composition.

**Table S2.** Pollen metabarcoding taxa.

**Table S3.** Plant species which bumblebees were captured on.

**Table S4.** Species composition of bumblebee pollen loads.

**Figure S1.** Study location.

**Figure S2.** Landscape composition maps.

**Figure S3.** Representativeness of study sites.

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