

FORAGING PREFERENCES OF BUMBLE BEE CASTES ARE WEAKLY RELATED TO PLANT SPECIES COVER ON TWO ARABLE AGRI-ENVIRONMENT HABITAT TYPES

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Abstract—Arable field margins provide important floral resources for insect foragers. This study assessed the significance of cultivated margins and floristically enhanced margins, both English agri-environment scheme (AES) options, to foraging bumble bees (*Bombus* species). We examined plant foraging preferences in each habitat according to species and caste. Additionally, detailed botanical surveys were carried out to determine vascular plant densities on the study margins. Overall, our results emphasised the importance of spontaneous (Asteraceae) species emerging from the seed bank in the provision of forage across *Bombus* species and castes, and highlighted that *Bombus* foraging preferences appeared to be only weakly related to floral species densities. Although found only occasionally in high densities, the popularity of these dicots was likely due to high nectar sugar mass. *Bombus* queens were recorded relatively infrequently, implying that these habitats are failing to provide the preferred floral resources of all *Bombus* spp. queens. Queens that were observed were found to favour earlier-flowering species (e.g. *Anchusa arvensis*) and species with longer corollas (e.g. *Vicia sativa*). Worker bees across *Bombus* spp. showed high overlap in plant preferences (e.g. *Cirsium arvense*, *Ononis spinosa*). However, some variability in preferences between castes within a species were noted, for example, only *B. terrestris/lucorum* drones were found to forage on *Crepis vesicaria* in cultivated margins. Additionally, bumble bee abundance was only found to increase as dicot cover increased. Overall, our findings highlight the importance of continuing to utilise multiple AES types in order to fully support *Bombus* and other pollinating insect populations on farmland.

Keywords—Agroecology; pollinators; insects; wildflowers; *Bombus*; biodiversity

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INTRODUCTION

Biodiversity losses recorded across Europe are, in part, the product of changing agricultural practices, which have extensively altered the farmed landscape since World War Two (Robinson & Sutherland 2002). During the post-war period, food production became a key priority with governments focused on ensuring national self-sufficiency (Robinson & Sutherland 2002). Management changes during this period aimed to increase food production and crop stability on farmland. This intensification of farming practices

caused landscape simplification and loss of semi-natural habitats (Robinson & Sutherland 2002). To counteract these losses, the land sharing concept has been applied throughout the European Union via the Common Agricultural Policy in the form of agri-environmental schemes (AES), where since 1992 farmers have been financially incentivised to undertake environmentally friendly farming practices (EEC Regulation No 2078/92). In the UK, AES have continued to be implemented post-Brexit, with the decision to leave the EU being seen as an opportunity to develop new schemes (Bateman & Balmford 2018; Gravey 2022).

Pollinators are an essential natural resource owing to their importance in crop and wild plant pollination (Klein et al. 2007 2018). In 2005, insect pollination was estimated to have a global market value of €153 billion annually (Gallai et al. 2009) with insect pollinators contributing to the productivity of 87 of the 124 most important crops for human consumption (Klein et al. 2007). Alongside their economic value, insect pollinators contribute towards human nutrition through the pollination of certain crops (Steffan-Dewenter et al. 2005), and are recognised for their socio-cultural importance by the general public (Hall & Martins 2020). However, pollinators have been declining throughout the last century, with evidence of a 75% decrease in insect biomass over a 27-year study (Hallmann et al. 2017), parallel declines in wild pollinator and plant communities (Potts et al. 2010), and increased aculeate extinction rates recorded (Ollerton et al. 2014). These continued declines could have a profound impact on crop visits by insect pollinators (Aldercotte et al. 2022), impacting pollination services to crops, but also in the pollination of wild flowering plants (Holzschuh et al. 2011). Reversing pollinator declines on farmland have therefore been identified as a conservation priority (DEFRA 2015; Holland et al. 2015).

In the study presented here we examine the use of two AES habitats, annually cultivated margins (hereafter called “cultivated margins”) and floristically enhanced margins, which are common margins in the UK, by three bumble bee species (*Bombus* spp.). Cultivated margins were designed to conserve rare arable plants, but are an unpopular option on farmland for a variety of reason, including their perceived untidy appearance and the potential risk of weed establishment in adjacent crops. Their possible wider benefits have received little attention in the scientific literature (but see McHugh et al. 2022), despite their provision of more common annual plant species, in addition to rare plants, which may be beneficial to foraging pollinators (Powney et al. 2019; McHugh et al. 2022). In contrast to this, floristically enhanced margins are a popular option with farmers. These are non-rotational sown or naturally regenerated field edge strips and comprise of a mixture of grasses and perennial flowering plants. Floristically enhanced margins are suggested to improve pest

control in adjacent crops (Albrecht et al. 2020), as well as provide resources for various pollinating insects during and outside of mass-flowering crops (Bottero et al. 2021). Both cultivated margins and floristically enhanced margins have the potential to provide important floral resources at different life stages and periods of the year to a diverse range of pollinating insects (Cole et al. 2017; Bottero et al. 2021). Floristically enhanced margin used by pollinators have been the focus of several studies (Holland et al. 2015; Wood et al. 2015a, b), with *Bombus* abundance positively correlated with floral diversity in margins (Bottero et al. 2021). However, to our knowledge this is the first study to examine how the use of these habitats varies among *Bombus* caste, although foraging preferences of queens alone have been previously investigated (Lye et al. 2009).

The aim of this study was to understand how different *Bombus* species castes utilise floristically enhanced and cultivated margins. To address this aim we will answer the following questions:

1. Do the plant foraging preferences of *Bombus* species using cultivated and floristically enhanced margins vary among *Bombus* species and castes?
2. Does vascular plant cover on cultivated and floristically enhanced margins influence *Bombus* foraging choices i.e., are *Bombus* species more likely to forage on common plant species?
3. Do *Bombus* foraging rates relate to the monocot or dicot plant cover? And does the cover of these two plant groups differ between cultivated and floristically enhanced margins?

MATERIALS AND METHODS

MARGIN SELECTION

In 2019, pollinator and vegetation assessments were made across 15 farms in three English regions, the South (Hampshire/Dorset), East (Norfolk) and Oxford (Oxfordshire). Each farm included in the study had a cultivated margin or plot (English AES prescription codes: HF11/20 and AB11) and a floristically enhanced margin (HE10 and AB8) which were used for plant and pollinator surveys. Two of the floristically enhanced margins were established through natural regeneration and

the remainder sown with a wildflower and grass mix. They varied between one and 15 years old. The farms were selected at random within the study regions from a list of farms provided by Natural England. Preliminary checks were made to ensure the margins within the selected farms were suitable for the study, for example, if atypical management of these habitats was noted, the farm was rejected from the study.

BUMBLE BEE SURVEYS

Bumble bees were surveyed on cultivated and floristically enhanced margins using the “bee walk” method (Prys-Jones & Corbet 1991). Surveys were conducted along 100 m long transects along the centre of the focal habitat and the transects were walked at a consistent pace stopping to observe bumble bees when necessary. Transect walks were completed monthly from April until September, in a randomised order. To ensure surveys took place while bumble bees were active, they were conducted between the hours of 10:00 and 17:00, at temperatures greater than 10°C and in the absences of strong wind, heavy rain or fog.

Within 2 m of the observer all foraging bumble bees were noted, on the wing, to species and caste (worker, queen, male/drone), and the plant species they were foraging on was recorded (no other plant data was recorded at this time). Where the surveyor experienced difficulties with identification, the bumble bees were caught with a net and transferred to a transparent pot for closer inspection, or a photo of the individual was taken and sent to an external expert for verification. As *Bombus terrestris* (Linnaeus, 1758), *B. lucorum* (Linnaeus, 1761), *B. cryptarum* (Fabricius, 1775) and *B. magnus* (Vogt, 1911) workers cannot be accurately differentiated in the field, all foraging individuals (including queens and males) were grouped together for our analysis and are referred to as *B. terrestris/lucorum* throughout.

BOTANICAL ASSESSMENTS

A detailed botanical assessment was conducted mid-way through the surveying season (between June and early-July) the percentage cover of each vascular plant species present (not just those in flower) was estimated in twenty 1 m² quadrats which were placed at 5 m intervals along the 100 m survey transect. Vegetation which was obviously trampled through other sampling being

conducted as part of a wider study was avoided. Percentage occurrence of each species was averaged across the 20 quadrats for analysis.

ANALYSIS

All data analyses were conducted in R version 4.2.0 (R Core Development Team 2023). Models were built using ‘lme4’ (Bates & Maechler 2009; Bates et al. 2023), and figures created using ‘ggplot2’ (Wickham 2011).

We modelled whether *Bombus* species castes, summed across the survey period, varied in abundance between cultivated and floristically enhanced margins. Generalised Linear Mixed Effects Models (GLMMs) were initially built with “farm” included as a random effect, however the majority of modelled relationships either failed to converge or resulted in singular output. In order to simplify models and avoid model overparameterization a series of Generalised Linear Models (GLMs) were constructed to test between farm differences of abundance of each *Bombus* species caste to ensure that ‘farm’ could be excluded as a random effect in this analysis (Appendix I). Following this confirmation, GLMs were built with abundance of each *Bombus* species and caste as the response variable, and margin type as a categorical explanatory variable with two levels (cultivated margin or floristically enhanced margin). Models were initially built using a Poisson distribution, but where overdispersion was present this was corrected to a Quasipoisson distribution.

Heatmaps were created to show the average number of flower visitations by each *Bombus* species, separated by caste, on each margin type. Seasonal variation in margin use is not considered here as this was investigated in McHugh et al. (2022). We also examined if abundance of each *Bombus* species caste related to the cover of each plant species they were recorded foraging on over the surveying season. GLMMs were built with abundance of each *Bombus* species and caste as the response variable, and the plant species cover as the explanatory variable and farm as a random effect. The cover of each plant species recorded was square-root transformed to normalise its distribution.

We then analysed the relationships between *Bombus* foraging density (seasonal abundance per

survey location was summed across species and castes) and monocot or dicot cover on pooled cultivated margins and floristically enhanced margin data. Monocot and dicot cover were calculated as the sum of the average cover of each monocot and dicot species respectively in the study margins. Monocot and dicot cover were square-root transformed to normalise the data distribution. Two GLMMs were built with *Bombus* density as the response variable, and either monocot or dicot plant cover as the explanatory variable. 'Farm' was included as a random effect to improve model fit, and the Poisson distribution family was selected for analysis.

Gantt charts describing the activity periods of each *Bombus* cast and the flowering period of forage plants were also created to show when species were flowering in relation to the presence of castes (Appendix II).

Heatmaps were also used to visualise the plant coverage data. For these data visualisations, the plant data was separated into monocots and dicots and the average cover of each vascular plant species calculated within the three study regions (East, Oxford and South) for the two studied habitats, cultivated and floristically enhanced margins (see Appendix III for full list of plant species). Botanical surveys were conducted once in June/early-July, seasonal differences in plant abundance are therefore not considered.

Finally, we examined if differences in monocot and dicot cover existed between the two margin types. A linear mixed effect model using the *lmer* function in 'lme4' was built with monocot or dicot cover as the response variable, margin type (floristically enhanced or cultivated margin) as the explanatory variable, and 'farm' specified as a random effect. Only monocot cover was square-root transformed to normalise its distribution, as dicot cover distribution was near normal and unimproved by transformation. The dicot cover resulted in singular model output and results are not reported.

RESULTS

Our results highlight both differences and similarities in foraging plant preferences among bumble bee species and between castes within these species. During the surveys, although 126 *Bombus* were recorded to caste while foraging on

cultivated margins, and 185 *Bombus* were identified to caste on floristically enhanced margins, no significant differences in *Bombus* species caste abundances between cultivated and floristic margins were found.

Bumble bees were found foraging on 16 flowering plant species in cultivated margins (Fig. 1), and 17 species in the floristically enhanced margins (Fig. 2). Six species of plant were visited by bumble bees in both margin types: *Cirsium arvense*, *C. vulgare*, *Crepis vesicaria*, *Knautia arvensis*, *Lotus corniculatus* and *Trifolium pratense*. *Cirsium arvense* was the only species to be used by all three *Bombus* species in both the cultivated margins and the floristically enhanced margins; and *Cirsium arvense* and *Crepis vesicaria* were the only species to be visited by all castes when combining *Bombus* observations over both margin types.

Queen *B. terrestris/lucorum* observations were made across a range of species in both margin types, whereas *B. lapidarius* (Linnaeus, 1758) queens were only observed visiting a single species in both margin types (*Papaver* spp. in cultivated margins and *C. vesicaria* in floristically enhanced grass margins), and no queen *B. pascuorum* (Scopoli, 1763) observations were made. Drones were recorded foraging from a far narrower range of species (1/3 or less) than that of their worker counterparts for both *B. lapidarius* and *B. terrestris/lucorum*. No drone *B. pascuorum* were recorded.

Although surveys were conducted during April, no *Bombus* individuals were recorded to caste level during this period (Appendix II). Drones were recorded later than workers for *B. lapidarius*, but not for *B. terrestris/lucorum*, and only *B. terrestris/lucorum* workers and queens were recorded into the September surveys.

On cultivated margins, *Bombus lapidarius* workers were most frequently seen foraging on *L. corniculatus* and *C. vesicaria* (Fig. 1). Foraging attempts on the former were not observed by the other castes within this species, however, both worker and queen *B. terrestris/lucorum* bumble bees utilised this plant species. Worker bees from *B. lapidarius*, *B. pascuorum* and *B. terrestris/lucorum* showed high overlap in plant preferences e.g., *C. arvense*, *Ononis spinosa* (but this species was only in one margin in the East and was not picked up in

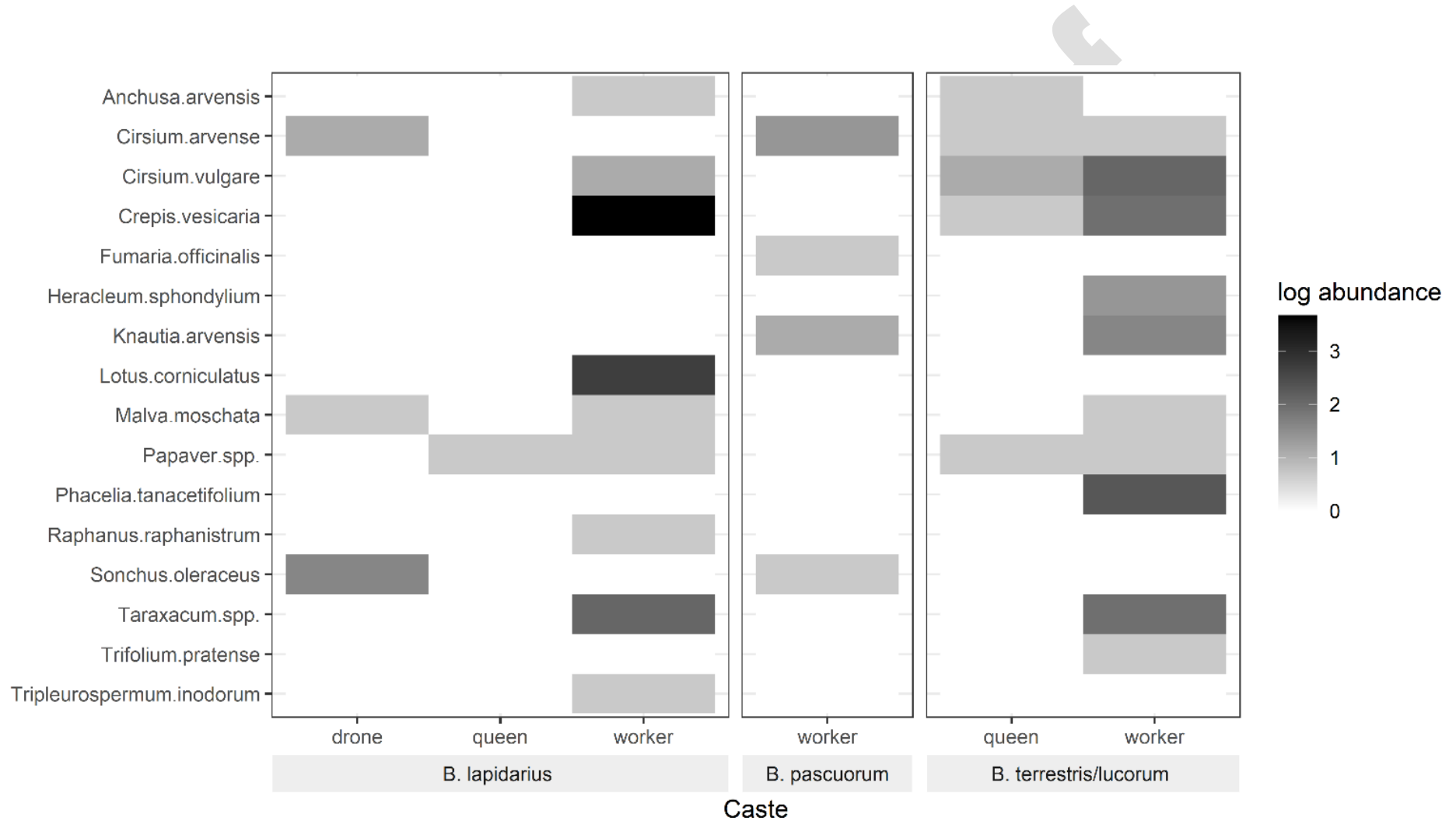


Figure 1. *Bombus* foraging activity on cultivated margins. *Bombus* abundance on different flower species averaged across farms and log-transformed, separated into species and caste. *Bombus lapidarius*: drones: $N = 7$, queens: $N = 1$, workers: $N = 66$; *Bombus pascuorum*: workers: $N = 7$; *Bombus terrestris/lucorum*: queens: $N = 6$, workers: $N = 39$.

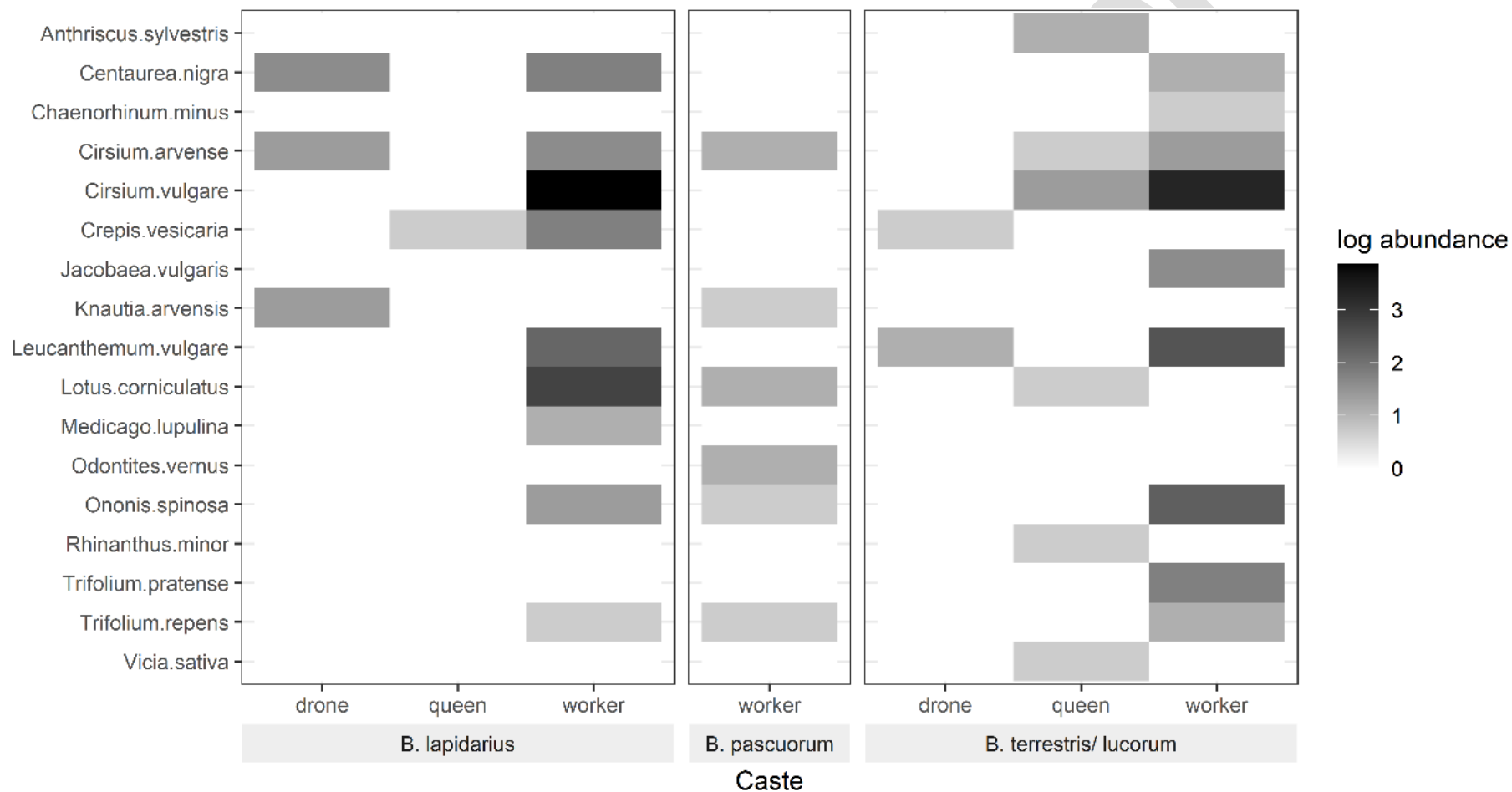


Figure 2. *Bombus* foraging activity on floristically enhanced margins. *Bombus* abundance on different flower species averaged across farms and log-transformed, separated into species and caste. *Bombus lapidarius*: drones: N = 10, queens: N = 1, workers: N = 90; *Bombus pascuorum*: workers: N = 9; *Bombus terrestris/lucorum*: drones: N = 3; queens: N = 9, workers: N = 63.

botanical surveys) and *T. pratense*. Some variation in preferences among castes within species were noted, however, for example only *B. lapidarius* drones were found to forage on *C. vulgare*. *Bombus* queens were found on commonly visited Asteraceae species, but also *Anchusa arvensis* and *Papaver* spp.

Unlike cultivated margins, floristically enhanced margins were also able to support *B. terrestris/lucorum* drones alongside queens and workers (Fig. 2). Four flower species were used by all three *Bombus* species: *C. arvensis*, *L. corniculatus*, *O. spinosa*, and *Trifolium repens*. However, *C. vulgare* received the greatest number of visits from both *B. lapidarius* and *B. terrestris/lucorum* workers, as well as queen *B. terrestris/lucorum*. *Bombus terrestris/lucorum* queens were also observed visiting *Anthriscus sylvestris*, *Rhinanthus minor*, and *Vicia sativa*. Drones showed no overlap in their foraging preferences between *B. lapidarius* and *B. terrestris/lucorum* observations in floristically enhanced margins, though both *B. lapidarius* drones and workers were observed in similar numbers on *Centaurea nigra* and *C. arvensis*. We note however that drones were recorded in low numbers on floristically enhanced margins ($N = 13$).

We expected that foraging preferences would relate to the frequency of plant occurrence, however our plant cover data (Fig. 3 & 4), and analysis of *Bombus* density and plant species cover (Appendix IV) indicated that this was not the case. Few relationships between *Bombus* species castes and plant species cover were detected. However, positive associations were found between *Bombus lapidarius* workers and *Cirsium vulgare* (Est = 0.71 ± 0.30 , $P < 0.05$), and near significant associations with *Leucanthemum vulgare* (Est = 0.49 ± 0.67 , $P = 0.05$). *Bombus terrestris/lucorum* queens were positively associated with the widest range of plant species, namely *Anchusa arvensis* (Est = 0.93 ± 0.24 , $P < 0.01$), *Crepis vesicaria* (Est = 0.70 ± 0.24 , $P < 0.01$) and *Anthriscus sylvestris* (Est = 0.90 ± 0.41 , $P < 0.05$).

On cultivated margins, bumble bee plant preferences included *C. vesicaria*, *L. corniculatus*, *C. arvensis* and *Phacelia tanacetifolium*. Of these species, only *C. arvensis* was abundant during vegetation

monitoring and this was only true in one region, Oxford (Fig. 3). All other species had low cover in all regions, apart from *P. tanacetifolium* which was not recorded in any vegetation surveys. Although *Bombus* foraging visits were highest to *C. vulgare* in floristically enhanced margins, this plant species was infrequently recorded across all regions (Fig. 4). Similarly, *L. corniculatus* was frequently foraged on but occurred at medium frequencies on the study plots.

Additionally, margins were found to attract a greater number of foraging *Bombus* as dicot cover increased, but no relationship with monocot cover was noted (Tab. 1).

Overall, we found that monocot cover was highest on floristically enhanced margins (Tab. 2).

Fifty-three plant species were recorded on the floristically enhanced margins across the three surveyed regions, 20 monocots and 33 dicots. Twenty species of grass were recorded on floristically enhanced margins. Some were more common than others, for example, *Festuca rubra* and *Dactylis glomerata*, were common across all regions. Other species of grass were also recorded in high densities, but their occurrence varied across the surveyed regions e.g. *Agrostis stolonifera* was most common in the East and recorded infrequently in the South and at medium densities in Oxford. Dicot densities showed more regional variation than the monocot data. No dicots were dominant across all regions, but the most commonly recorded species included *Achillea millefolium* (East), *C. nigra* (Oxford and South), *Leucanthemum vulgare* (South), *Medicago lupulina* (South), *Plantago lanceolata* (East) and *T. repens* (Oxford).

Cultivated margins supported a wider range of plant species with 68 plant species being recorded across the three regions, 16 of which were monocots and 52 which were classified as dicots (Fig. 3). Compared to floristically enhanced margins, cultivated margins showed a higher degree of regional variation. Monocots occurred at relatively low densities in the South and were highest in the East due to the prevalence of *Holcus mollis* and *Triticum aestivum*. The East has the most even spread of dicot species. In Oxford the most common species included *C. arvensis*, *Persicaria*

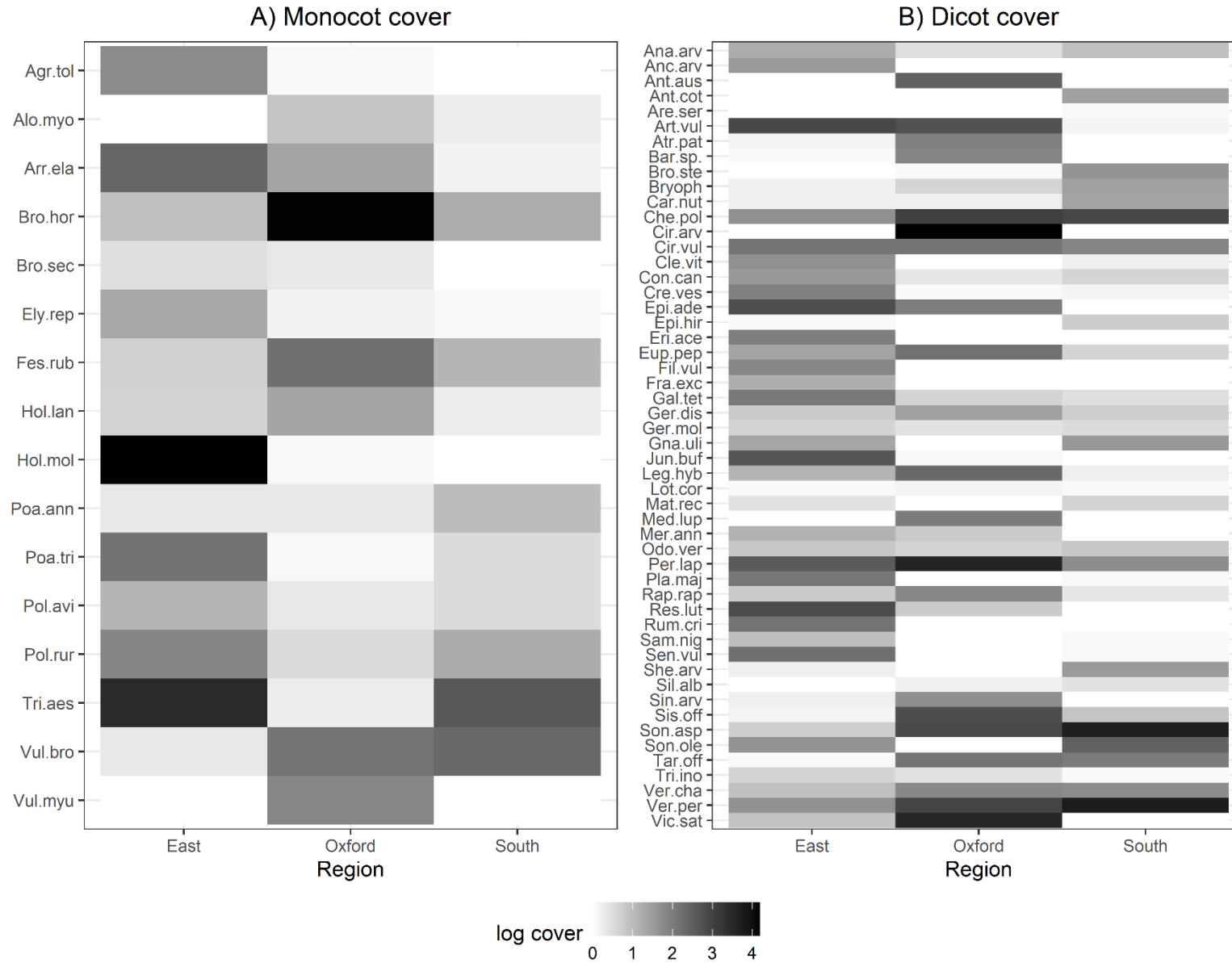


Figure 3. Plant cover on cultivated margins. The average cover (log-transformed) of each vascular plant species calculated within the three study regions (East, Oxford and South), separated into A) monocots, and B) dicots.

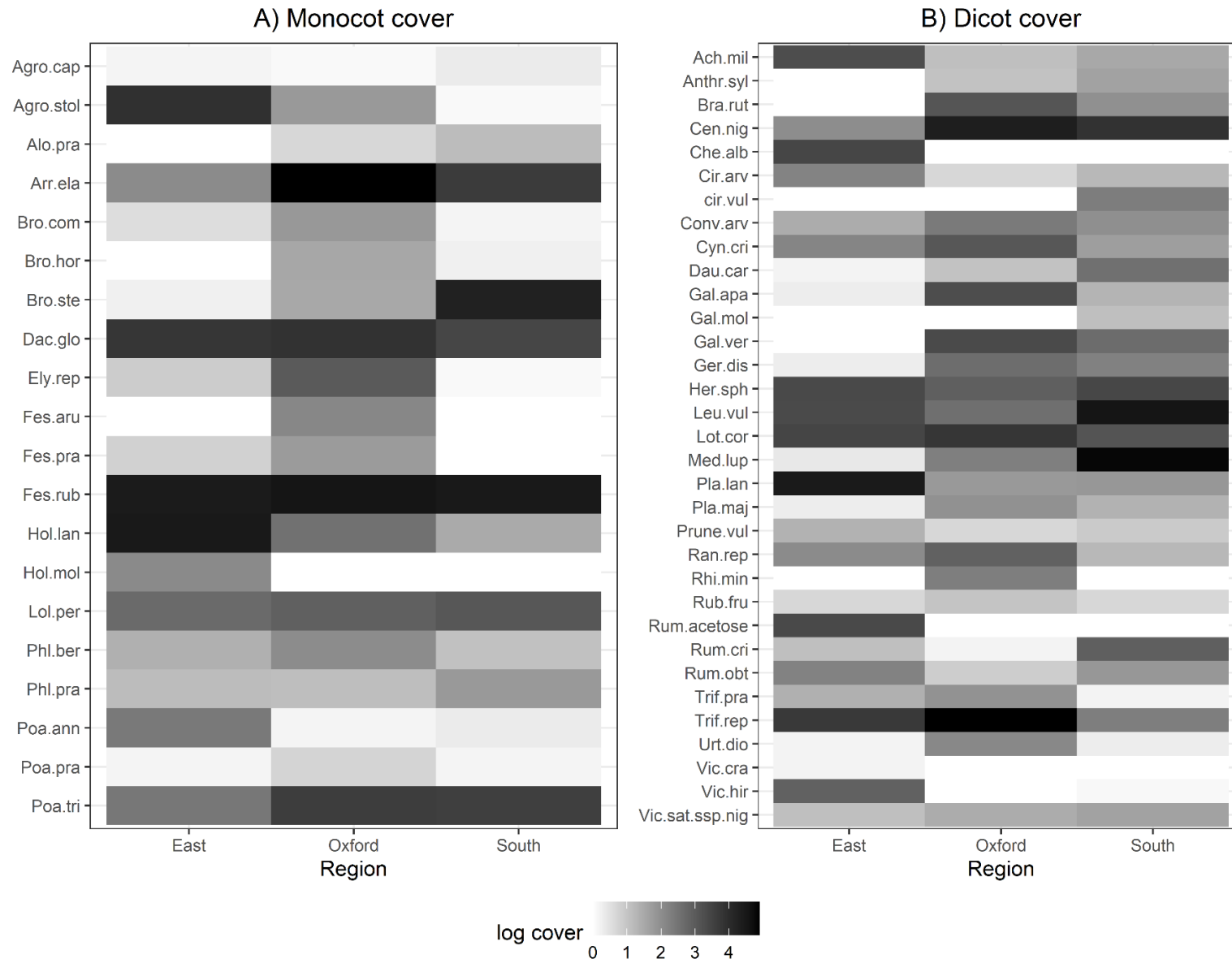


Figure 4. Plant cover on floristically enhanced margins. The average cover (log-transformed) of each vascular plant species calculated within the three study regions (East, Oxford and South), separated into A) monocots, and B) dicots.

lapathifolium and *V. sativa*, whereas in the South *Sonchus asper* and *Veronica persica* were most common.

DISCUSSION

This study provides an interesting insight into the foraging preferences of three *Bombus* species and their castes. Our findings highlight the importance of certain spontaneous Asteraceae species found on cultivated and floristically enhanced margins. *Crepis vesicaria*, *Cirsium arvense* and *C. vulgare* were all significant foraging resources for *Bombus* species across both margin types, despite the latter two being considered as ‘injurious weeds’ (UKGOV 1959). Species such as these have particularly high nectar sugar mass (Hicks et al. 2016), and make a significant contribution to the national nectar provision for pollinating insects (Baude et al. 2016). Multiple studies have demonstrated their significance for flower-visiting insects (Balfour & Ratnieks 2022; McHugh et al. 2022; Nichols et al. 2023) and the importance of agri-environment schemes continuing to offer options in which these species are allowed to flower without causing a disservice to agriculture. This further provides evidence for the continued inclusion of both cultivated and floristically enhanced margins as AES options on farmland, as both areas contain diverse flora including important “weed” species, and given that they attract different suites of pollinators, with solitary bees preferring cultivated and bumble bees the floristically enhanced margins (McHugh et al. 2022).

Differences and similarities among castes were also observed. The lack of sightings early and late in the season (Apr and Sept) suggests these habitats are not providing suitable forage for all *Bombus* species and castes. However, *Bombus* workers were recorded relatively evenly across species, though *B. terrestris/lucorum* queens were seen far more regularly than *B. lapidarius*, and no *B. pascuorum* queens were recorded. This could also suggest that cultivated and floristically enhanced margins are failing to provide the preferred floral resources for these *Bombus* spp. queens. *Bombus terrestris/lucorum* queens were found to prefer *Prunus* blossoms while *B. pascuorum* preferred flowers with longer corollas such as *Lamium album*, *L. purpureum* and *Symphytum officinale* (Lye et al., 2009), none of which were recorded during our botanical surveys. Therefore, it is important farmland contains a range of semi-natural habitat types that can provide resources at different times of the year and to different species and castes.

The *Bombus* queens that were observed were found foraging on a range of species, including earlier-flowering species (*A. arvensis*, *A. sylvestris*, and *Papaver spp.*), and species with longer corollas (*R. minor* and *V. sativa*). These early flowering species are particularly important to ensure queens can collect enough pollen and nectar to establish a brood of workers. *Papaver spp.* have particularly high pollen volume (Hicks et al. 2016), making them a great resource for nest stores of pollen. However, these observations were skewed by *B. terrestris/lucorum* counts and surveys of only

Table 1. Relationship between *Bombus* abundance and plant cover (monocot and dicot) across both cultivated and floristically enhanced margins.

Model	Covariates	Estimate	Standard Error	z-value	P
Monocot	Intercept	2.03	0.31	6.60	< 0.001
	Sqrt (monocot)	-0.02	0.02	-0.90	0.37
Dicot	Intercept	-2.41	0.63	-3.83	< 0.001
	Sqrt (dicot)	0.54	0.06	8.57	< 0.001

Table 2. Differences in plant cover (monocot) between cultivated and floristically enhanced margins.

Model	Covariates	Estimate	Standard Error	Df	t-value	P
Monocot	Intercept (CM)	3.60	0.50	28.00	7.17	< 0.001
	FEM	3.99	0.71	14.00	5.64	< 0.001

two farmland habitats. Therefore, these conclusions may not be representative of other *Bombus* species queens, and further research in this area is needed in order to better support a diverse range of *Bombus* species to establish populations on farmland.

Bombus drones were also found in limited numbers and foraged from a narrower range of species. However, they were observed on species of high sugar nectar content (e.g., *C. arvensis*, *C. nigra*) that flower later in the year (e.g., *C. nigra*, *M. moschata*; Hicks et al 2016). The eggs that will become drones are laid by the queen in late summer (Bumblebee Conservation Trust 2021). Drones may remain in the nest for a few days before leaving to find a queen to mate with, and do not return (Belsky et al. 2020). These flower preferences are therefore typical of a drone, as they forage from high sugar nectar flowers late in the flight season to maintain energy levels whilst waiting or searching for a queen to mate with (Villalobos & Shelly 1987).

The density of each floral species appeared to have little impact on *Bombus* foraging preferences. This suggests that *Bombus* workers are foraging for specific pollen or nectar sugar content (Konzmann & Lunau 2014) or demonstrating high levels of floral constancy (Goulson 2010), as they continue to search for flowers they know how to handle even when in low density. Although floral diversity is important when supporting the insect community as a whole, 'key species' are needed to attract a wider range of *Bombus* species and their castes (Warzecha et al. 2018; Nichols et al. 2019).

Previous research has demonstrated the importance of floristically enhanced margins, primarily HE10, as a foraging resource for pollinators (Pywell et al. 2006; Heard et al. 2007; Holland et al. 2015; McHugh et al. 2022). Here we expand on those findings and show that that relationship is likely to be related to dicot cover. We found that the number of foraging *Bombus* increased with dicot cover across both habitats, but that cultivated margins were found to support a broader range of vascular plant species than floristically enhanced margins, including species not typical of these habitats (e.g. *L. corniculatus*, *P. tanacetifolia*). We expect this is due to the latter generally being sown with specific mixtures in line with current prescriptions. The current guidelines

for a floristically enhanced margin in England recommend sowing a mixture with a minimum of four grass species and ten wildflower species (DEFRA 2023a). Alternatively, cultivated margins involve cultivating the soil to a depth of 5 - 15 cm to allow seeds to germinate that are already present deep in the soil or have populated the soil from neighbouring habitats. Cultivated margins may therefore support a more diverse range of plants nationally (DEFRA 2023b), and despite their unpopularity, should be integrated more regularly in farmland through AES.

Both habitats supported a range of grass species, many of which are known to provide an invaluable resource for other foraging insects and farmland wildlife (Smith et al. 2020). One such grass species, *Arrhenatherum elatius*, is native to Britain and is commonly used by field voles (*Microtus agrestis*) for shelter and nesting material (The Wildlife Trusts (n.d.)). The presence of this grass should therefore also improve the habitat's suitability for hunting barn owls (*Tyto alba*; Glue 2009). A second monocot common across the study habitats was *Poa annua*, their seeds are known to be eaten by a wide range of vertebrates (e.g. birds, deer) and invertebrates (Hutchinson & Seymour 1958; Holland et al. 2006). This grass was also identified as supporting invertebrates consumed by farmland birds (Smith et al. 2020). *Alopecurus myosuroides* which is one of the most agronomically damaging monocot species was observed, notably in cultivated margins, but only at low densities. This weed inhibits wheat growth rates, reducing its yield and therefore damaging farm productivity. Monocot cover down to species level is not regularly included in floral habitat surveys, and our findings suggest it should be considered more often in order to obtain a better understanding of the habitat that AES are providing different taxa as a whole.

It is important to note that these findings are only indicative due to the relatively small dataset presented here. Where it was not possible to record a *Bombus* to caste level, the individual was eliminated from the analysis, resulting in a reduced dataset. Furthermore, certain species are more difficult to identify to caste level. For example, the lack of *B. pascuorum* males may be a result of the difficulty in distinguishing males and females on the wing. Additionally, the low

numbers of males and queens overall could be an indicator that the survey methods should be adjusted in future studies where caste is of interest. Surveying earlier in the year to capture more emerging queens, and later in the summer to capture more males looking to mate with the new generation of queens should be considered. Finally, we chose to consider the overall measure of monocots and dicots in the environment rather than the cover of floral resources being directly utilised by observed *Bombus* individuals. Therefore, any relationships described between plant cover and *Bombus* abundance/castes in the results must be considered with caution as they are not directly linked to the availability of forage at the time of bee surveys. Larger datasets generated through increased survey time and over multiple years are necessary to explore annual variations in both *Bombus* populations and plant cover within these AES habitats and others.

Overall, our results highlight the importance of both sown and spontaneous species in the provision of forage across *Bombus* species and castes. Additionally, we show that *Bombus* foraging preferences appear to be weakly related to floral species densities. Further research is needed to understand the foraging preferences of less common *Bombus* species and the castes within these groups. As the government continues to develop and make changes to AES options (DEFRA 2021), it is important we continue to assess their value to pollinators, and determine how such habitats may complement each other at a landscape scale (e.g., grassland restoration, nectar mixes; but see Carvell et al. 2015). We recommend the continued implementation of cultivated margins and floristically enhanced margins on English farmland as they both provide valuable forage across species and castes, but acceptance of some agricultural weed species in the margin, particularly those providing high nectar resources, will improve the value of both margin types to *Bombus*.

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AUTHOR CONTRIBUTION

Concept and design NM & JH, data collection AM, BB, RP & PW, data analysis NM, writing NM & RN, edits and approval for publication AM, BB, RP, PW, ES & JH.

DISCLOSURE STATEMENT

No potential conflict of interest was reported by the author(s).

DATA AVAILABILITY STATEMENT

Please contact the corresponding author for data requests.

APPENDICES

Additional supporting information may be found in the online version of this article:

Appendix I. Results of GLM for between farm differences in *Bombus* abundance.

Appendix II. Gantt chart species presence.

Appendix III. List of vascular plants identified during botanical surveys.

Appendix IV. Results of GLM for *Bombus* density and foraging plant species cover.

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