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ORIGINAL PAPER

Assessing monthly habitat quality for bumblebees in grasslands using a habitat trait model: a case study in Worcestershire, UK

Andrea Tapia-Arenas[1] · **Richard F. Comont**[2] · **Fleur Visser**[1] · **Kate Ashbrook**[1]

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Abstract Bumblebee decline in the UK has been associated with land use change from diverse meadows to intensive agriculture. While grasslands can offer the resources that bumblebees need to survive and thrive, the precise availability of resources through the year and between sites can vary due to differences in species composition and management. In this study, we surveyed bumblebee abundance using transects and monitored their habitat using 1-square-meter plots in 2021 and 2022 across five semi-natural grasslands located in Worcestershire, UK. These data were used to build a monthly bumblebee abundance prediction with a Generalized Linear Effects Model (GLME), which was used to rank the sites based on the predicted number of bumblebees. The selected model indicated that bumblebee abundance was most strongly associated with the proportion of the preferred bumblebee forage species and floral richness. Vegetation height and the variation of floral resources coverage had small, non-significant coefficients in this dataset, but were retained as ecologically relevant descriptors and for their contribution to cross-validated performance. Our model successfully identified sites with the lowest bumblebee abundance, and the monthly assessments provided information to guide management actions to improve the habitat quality at a site scale. Our findings are foundational, suggesting directions for future research in broader geographical contexts to validate and refine habitat assessment methods.

Implications for insect conservation This study highlights crucial implications for insect conservation, demonstrating that targeted management actions based on monthly habitat assessments can significantly enhance the quality of grassland habitats. This approach not only supports bumblebee populations but also other pollinator species within agricultural landscapes.

Keywords Generalized linear mixed-effects modelling · Abundance prediction · Habitat management · Bumblebees

Introduction

Animal pollinators are crucial for the reproduction and thus survival of 87.5% of angiosperms worldwide (Ollerton et al. 2011; Grass et al. 2016). An estimated 35% of the global food crop production is dependent on animal pollinators (Klein et al. 2007; Senapathi et al. 2021). Despite their importance, pollinator declines have been reported both globally (Potts et al. 2010; Nieto et al. 2014), and in the United Kingdom (Williams and Osborne 2009), and bumblebees (*Bombus spp.*) are no exception.

Declining bumblebee numbers have been linked with long-term land use changes from florally-diverse meadows to developed or intensively-cropped land (Carvell et al. 2006a; Goulson et al. 2006; Fitzpatrick et al. 2007; Goulson 2009). The flower-richness of ecosystems therefore provides a key part of the habitat's suitability for bumblebees. This can be measured in multiple ways and potentially be used as indicator of habitat quality. These critical factors encompass flower abundance (Williams et al. 2007; Tuell et al. 2008; Byrne and delBarco-Trillo 2019; Tabor 2022), floral diversity (Blaauw and Isaacs 2014; Roger et al. 2017), and presence of preferred forage species (Goulson and Darvill 2004; Goulson et al. 2005; Carvell et al. 2006a). Additionally, temperature (Vogt 1986a, b; Guiraud et al. 2021; Kenna

✉ Andrea Tapia-Arenas
andrea.tapia.arenas@gmail.com

Richard F. Comont
richard.comont@bumblebeeconservation.org

Fleur Visser
f.visser@worc.ac.uk

Kate Ashbrook
k.ashbrook@worc.ac.uk

[1] School of Science and the Environment, University of Worcester, Worcester, UK

[2] Bumblebee Conservation Trust, Stirling, UK

et al. 2021) and rainfall (Lye et al. 2012; Woodcock et al. 2014; Sanderson et al. 2015; Phillips et al. 2018; McNeil et al. 2020; Descamps et al. 2021) are the abiotic factors that seem to be fundamental traits of their habitat.

Habitat heterogeneity seems to be important for bumblebees, as a varied landscape will be more likely to provide a diverse range of flowers maturing at different times of year as well as the differing habitat requirements throughout their life cycle (Kells and Goulson 2003; Goulson 2009; Lye et al. 2012). In contrast, homogeneous landscapes tend to decrease pollinator species richness (Andersson et al. 2013).

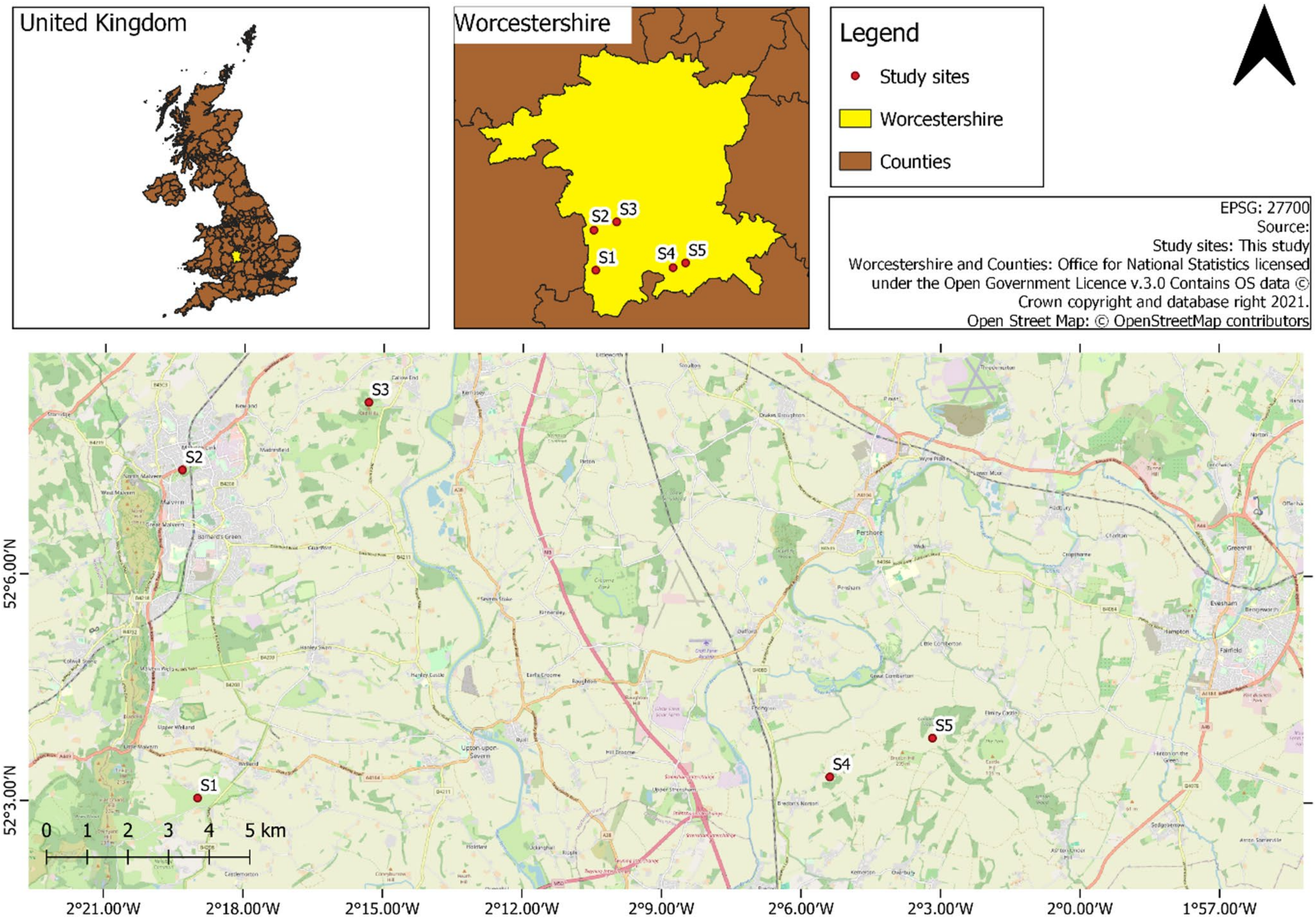
While grasslands can support bumblebee populations, individual sites tend to differ significantly in terms of the foraging, nesting, and overwintering opportunities. In particular, foraging resources in semi-natural grasslands can vary considerably throughout the bumblebee flight period (e.g., Carvell et al. 2006a; Williams et al. 2012).

In this study, we developed a bumblebee abundance prediction model with data from semi-natural grasslands located in Worcestershire. Our goal was to identify variables for this model that can be used to assess semi-natural grasslands in terms of habitat quality for bumblebees. Consequently, the model predictions will provide valuable insights to guide resource allocation for enhancing habitat quality for bumblebees in semi-natural grasslands.

Materials and methods

Study sites

Five open grassland areas were studied, all located in Worcestershire, in the English midlands (Fig. 1). All sites consisted of natural grassland (acid, calcareous and neutral) with some broadleaved and mixed woodland. Sites 1 (Castlemorton Common, 36.6 Ha), 2 (Link Common, 8 Ha) and 3 (Old Hills, 7.7 Ha) were managed by the Malvern Hills Conservation Trust; site 4 (Bredon Hill West, 10.7 Ha) was managed by Natural England; and site 5 was managed by a private owner (Bredon Hill East, 16.5 Ha). All sites, except for site 2, had livestock either permanently (site 1 and the northern area at site 5), or temporarily in late summer (sites 3 and 4). Bumblebee species abundance and the habitat present was assessed monthly between March and October



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Source:
Study sites: This study
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Fig. 1 Location of study sites

2021 and 2022, although there was some variation in the months surveyed between individual sites. Three sites (1, 2, and 3) were each surveyed from August to October 2021 and from March to October 2022, while sites 4 and 5 on Bredon Hill were only surveyed during 2022 (site 4 May to October 2022 and site 5 April to October 2022).

Bumblebee surveys

Bumblebee survey transects of 1.051–1.325 km were established at each site using the standard BeeWalk protocol from the Bumblebee Conservation Trust (2021). These were walked between 9:15 and 16:20, recording all bumblebee individuals which entered a 4 m wide, 4 m long and 2 m high 'recording box'. Individual bumblebees were identified to species level on transects at each site. Reliably differentiating workers of *Bombus terrestris* and the *B. lucorum* aggregate (*B. lucorum*, *B. magnus*, and *B. cryptarum*) in the field is often impossible, therefore they were recorded together as *Bombus terrestris/lucorum*. These surveys yielded the monthly abundance of bumblebees at each site, which was standardized by transect length.

When an individual was seen visiting a flower, the plant species was recorded. The temperature was measured using a Kestrel 3500 hand-held weather meter and the wind was characterised using the Beaufort scale.

Habitat surveys

A 1 m^2 quadrat was used to identify all plants that were actively flowering at the time of the survey, except for grasses. The percentage coverage of these flowering plants was estimated by sight in the field, and the average vegetation height was measured within the plot using a 1-meter ruler. The number of plots per visit varied among sites and months, ranging from 31 to 75 per survey. Details of the number of plots surveyed per site and visit are provided in Supplementary material Table S1.

We aimed to use the data collected from the habitat surveys to develop classification algorithms using remotely-sensed images. Therefore, we established the location of plots using a geospatial approach considering the pixel coordinates of Sentinel-2 and Landsat-9 images. Specifically, we randomly selected one Sentinel-2 pixel centroid for every Landsat-9 pixel within a 50-metre buffer area along each BeeWalk transect. However, it's important to emphasize that the primary focus of this paper is on the data collected during the habitat and BeeWalks surveys.

The number of plots varied depending on site and month (Supplementary material Table S1), as not all plots could be accessed throughout the season due to cattle enclosures (sites 1 and 4) and weather conditions (sites 2, 3, and 5). A Differential Global Positioning System (DGPS) device with centimetric precision was used to locate the selected centroids in the field. At sites 2, 3, and 4 this was a Trimble TSC3, but due to difficulties on receiving reference station data at sites 1 and 5 with this device, a Trimble Geo7 was used instead.

The habitat surveys and BeeWalks were carried out as closely together as possible, to ensure a good correspondence between them. They were typically carried out within two days of one another, with the longest difference between both surveys of 11 days at site 2.

Data processing and analysis

We analysed the relationship between monthly site-level bumblebee abundance and 11 habitat traits determined from the habitat surveys. All statistical analyses were performed using R version 4.3.0 (R Core Team 2023). Table 1 shows a description of the habitat traits and the variables used for this analysis. For our analysis, we used standardised bumblebee abundance values (bees seen per km walked) at each site. We used two different approaches when calculating flower preference traits: (1) by using information from Carvell et al. (2006a) species list to identify preferred flowers; and (2) using data on flower visitation from our BeeWalk surveys to identify preferred flowers.

The habitat traits were analysed using a Generalized Linear Mixed-Effects (GLME) model with the negative binomial family to avoid overdispersion, in the package lme4 (Bates et al. 2024). We assigned month as a random effect and conducted an automated model selection using function 'dredge' available in the package MuMIn version 1.47.5 (Bartoń 2023). This package can build all the possible combinations and calculate the Akaike's Information Criterion adjusted for a small sample size (AICc). Interaction terms were not included unless explicitly specified; in particular, month was treated as a random intercept only and not in interaction with floral predictors, as our objective was to test the main effects of habitat traits while accounting for seasonal variation.

Pearson correlation coefficients among predictors were calculated to assess multicollinearity prior to model selection (Supplementary material Table S2). Pairs with $|r|>0.7$ were identified, and models containing these combinations were excluded post-hoc to avoid multicollinearity issues.

Although the models were ranked according to their AICc, the selection of the final model to predict bumblebee abundance was based on a combination of model parsimony and performance. Models with $\Delta AICc <= 2$ were considered as statistically equivalent. To further evaluate performance and avoid overfitting, we applied Leave-One-Out-Cross-Validation (LOOCV). This technique involves training each

Table 1 Description of bumblebee habitat traits analysed (all variables were estimated per site and per month)

Habitat trait	Description	Variable name
Presence of flowers	Proportion of plots with flowers present during the survey (express as %).	Presence
Flower diversity	Shannon-Wiener Diversity Index estimated using the formula $Shannon = -\sum p_i * \ln(p_i)$, where pi is the proportion of the flower coverage of species i.	Shannon*
	Simpson's Reciprocal Index estimated with the formula $Simpson = 1 - \frac{\sum n(n-1)}{N*(N-1)}$, where n represents the percentage of flower coverage of species i and N the percentage of flower coverage for all species.	Simpson*
	Number of actively flowering species.	FlRichness-Num
Flower preferences	Total percentage of flower coverage considering only species found in Carvell et al. (2006a) study.	CovPrefSpCa
	Calculated by dividing the total percentage of flower coverage of species found in Carvell et al. (2006a) study by the total percentage flower coverage.	CovPrefSp-CaPr
	Total percentage of flower coverage of species visited by bumblebees according to the BeeWalks.	CovPrefSpSi
	Calculated by dividing the total percentage of flower coverage of species visited by bumblebees according to the BeeWalks by the total percentage of flower coverage	CovPrefSp-SiPr
Flower abundance	The average percentage cover of flowering species within each survey (species-based mean).	CovSpMean
	The standard deviation of the flower coverage of all species during each survey.	CovSpStd
	Average of flower coverage at plot level considering only plots where flowers were present.	CovPlt
	Average percentage cover of flowering plants across all plots within each survey, including those with no flowers (plot-based mean).	Cov-PltAllmean
Nesting conditions and heterogeneity	Standard deviation of the vegetation height across all plots.	VegHstd
	Average vegetation height across all plots.	VegHmean

*We set a value of 0 for the Shannon-Wiener and Simpson's Reciprocal diversity indices when no flowers were present during the habitat surveys

model iteratively on all observations except one and calculating the Root-Mean-Square Error (RMSE) for both training and validation sets. This analysis aimed to assess if the model is overfitting or underfitting, by comparing the mean RMSE of the training and validation set (Arlot and Celisse 2010). In our study, one observation corresponds to a site-month combination of bumblebee abundance. The model with the lowest discrepancy between training and validation RMSE was selected as the best-performing model. A similar approach has been used in ecological model selection (Hashimoto et al. 2024; Sandal et al. 2024).

Finally, we compared predicted and observed values by ranking the five study sites according to bumblebee abundance in descending order (the site with the highest abundance was assigned rank 1, the second highest rank 2, and so on). Separate rankings were generated using observed abundances and model-predicted abundances, and these were compared to assess model performance.

Results

Sites were surveyed over two years, 2021 and 2022. Data from both years were used to build the prediction model, although our results will focus more on 2022 as fieldwork this year provided a comprehensive analysis of bumblebee activity and habitat conditions throughout their entire flying season.

Bumblebee abundance and species

All the BeeWalks were conducted during dry weather, with temperatures ranging from 13 °C to 29 °C except in March, when temperatures were between 10 °C and 12 °C, while in August, they reached 32 °C at site 3. The wind speed ranged mostly from 0 to 3 on the Beaufort scale (0–12mph).

We recorded a total of 302 individual bumblebees, of which 56% were workers, 13% were males, 11% were queens, and 20% could not be reliably allocated to caste. The total bumblebee abundance increased from March to a peak in July (although a noticeable decline is evident in May), before declining through to October (Supplementary material S3, Fig. S3.1). At a site level, sites 2 and 4 peaked in June, whereas the other three sites peaked in July. The sites that had the highest bumblebee abundance were sites 1 and 5 in July.

In this study we recorded all 7 of the most widespread species in Britain (Bumblebee Conservation Trust 2020). The most abundant species in this study was *Bombus lapidarius*, followed by the aggregated species group (*B. lucorum* and *B. terrestris*) and *B. pascuorum*, with 91, 88 and

63 individuals, respectively. These species were found at all sites.

The least abundant species in this study, with fewer than five individuals, were only present at some sites. We counted three individuals of *B. pratorum* at site 2, two individuals of *B. hortorum* at sites 1 and 5 (one in each site), and only one individual of *B. hypnorum* at site 3. Additionally, one cuckoo (parasitic) species was identified at site 5, a *B. rupestris* male. Fifty-three individuals were not possible to identify to species level during the BeeWalk surveys.

Habitat traits

Flower presence and diversity

We surveyed 2,602 plots across the five sites between March and October. In March, no forage resources were recorded, but by April flowers were present in nearly 20% of the surveyed plots. Flower presence increased steadily, peaking in June (56%) and July (57%), before dropping sharply in August (15%) and stabilising around 10% through October (Supplementary material S3, Fig. S3.1). A total of 51 plant species were found in flower during the 2021 and 2022 habitat surveys (full list is provided in Supplementary Material Table S4). Monthly trends for flower presence and floral richness are provided in Supplementary Material S3 (Fig. S3.1; panels Presence and FLRichness, respectively). The only two species that were found at all sites were *Hypochaeris glabra* and *Lotus corniculatus*. Of these, only *L. corniculatus* has been reported of high importance to bumblebees (Carvell et al. 2006a). We also found species in genus *Ranunculus* and *Stellaria* at all sites.

In April, the average number of flower species per site (Supplementary material S3, Fig. S3.1, FLRichness panel) was only 1; however, it increased to 5 in May, and peaked at 10 in June. Species richness decreased after this point, with the most significant decline occurring from July to August, when the number of species dropped from 8 to 4 (Supplementary material S3, Fig. S3.1, FLRichness panel). Of the other two variables calculated to assess floral diversity, the Shannon-Wiener (Shannon, Table 1) and Simpson's Diversity (Simpson, Table 1) indices showed a similar pattern (Supplementary Material S3, Fig. S3.1 Shannon and Simpson panels).

Overall, observations showed that 17 flower species were visited by bumblebees during the BeeWalk surveys (a full list is provided in Supplementary Material Table S5). Some bumblebees at the sites were seen visiting flowers that did not occur in any of the habitat survey plots (*Cyclamen hederifolium*, *Digitalis purpurea*, *Epilobium angustifolium* and *Stachys* sp.). Although flower visitation does not necessarily imply that the bumblebee is collecting pollen or drinking nectar, it can be used as an indicator of the resources available to bumblebees at each site.

Flower abundance

All the flower abundance variables peaked in July, including the mean flower coverage percentage CovPltAllmean, Table 1), the mean percentage of flower coverage among plots with flowers (CovPlt, Table 1), the mean flower species coverage (CovSpmean, Table 1) and its corresponding standard deviation (CovSpStd, Table 1). Notably, CovSpmean and CovSpStd exhibited a decreasing trend from April to May, contrasting with the increasing trends observed in CovPltAllmean and CovPlt (Supplementary Material S3, Fig. S3.1 panels CovPltAllmean, CovPlt, CovSpmean and CovSpStd).

Nesting conditions and heterogeneity

The mean vegetation height (VegHeman, Table 1) and its corresponding standard deviation (VegHstd, Table 1) exhibited their lowest value in March. Their monthly trends are detailed in Supplementary Material S3, Fig. S3.1 panels VegHmean and VegHstd).

Predicting bumblebee abundance using habitat traits

All the equivalent models (with a ΔAICc<=2.00) showed low standard errors, except for model 5 (CovSpStd, CovPrefSpSiPr, Shannon & Simpson) where the "Simpson" variable had the highest value (Table 2). The most parsimonious model (1) to predict bumblebee abundance was based on traits linked to flower diversity, abundance, and flower preference (Table 2).

While model 7 achieved the lowest LOOCV, it was excluded from further analysis because it incorporated highly correlated predictors (Presence and FlRichnessNum $|r|>0.7$, Supplementary material Table S2) indicating possible multicollinearity issues. Similarly, model 5 which had the second lowest LOOCV error included highly correlated predictors (Shannon and Simpson $|r|>0.7$, Supplementary material Table S2). Model 3, the third-ranked by LOOCV, also incorporated correlated predictors (CovPltAllmean and CovSpMeanwith $|r|>0.7$, Supplementary material S2). Therefore, model 8, the next-best model by LOOCV that did not suffer from multicollinearity, was selected as the habitat model.

According to the habitat model, the site that should have had the highest bumblebee abundance (54 individuals) from May to October 2022 was site 4, followed by site 1 with 47, site 3 with 44, site 2 with 43 and site 5 with 36. With

Table 2 Equivalent models to predict bumblebee abundance using GLME with negative binomial family and habitat traits

Rank	Predictor	Estimate	SE	*p*-value	ΔAIC	LOOCV
1	CovSpStd	0.00	0.00	<0.05	0.00	0.47
	FLRichnessNum	0.13	0.03	<0.0001		
	CovPrefSpSiPr	1.11	0.46	<0.05		
2	CovSpMean	0.01	0.00	<0.05	0.06	1.06
	FLRichnessNum	0.14	0.03	<0.0001		
	CovPrefSpSiPr	0.96	0.47	<0.05		
3	CovPltAllmean	−0.14	0.09	0.123	0.58	0.36
	CovSpMean	0.02	0.01	<0.05		
	FLRichnessNum	0.19	0.05	<0.0001		
	CovPrefSpSiPr	0.99	0.48	<0.05		
4	CovPltAllmean	−0.10	0.08	0.199	1.22	0.77
	CovSpStd	0.01	0.00	<0.05		
	FLRichnessNum	0.16	0.04	<0.0001		
	CovPrefSpSiPr	1.25	0.48	<0.01		
5	CovSpStd	0.00	0.00	0.052	1.36	0.28
	CovPrefSpSiPr	1.15	0.47	<0.05		
	Shannon	2.82	0.80	<0.001		
	Simpson	−5.21	1.84	<0.01		
6	CovSpMean	0.01	0.00	<0.01	1.55	0.86
	FLRichnessNum	0.12	0.03	<0.001		
7	CovSpMean	0.01	0.00	<0.05	1.64	0.26
	FLRichnessNum	0.18	0.05	<0.001		
	Presence	−0.01	0.01	0.265		
	CovPrefSpSiPr	0.87	0.48	0.070		
8	**CovSpStd**	**0.00**	**0.00**	**0.097**	**1.88**	**0.42**
	FLRichnessNum	**0.13**	**0.03**	**<0.0001**		
	CovPrefSpSiPr	**1.06**	**0.46**	**<0.05**		
	VegHmean	**0.01**	**0.01**	**0.340**		
9	FLRichnessNum	0.12	0.03	<0.001	1.95	0.80
	CovPrefSpSiPr	1.02	0.47	<0.05		
	VegHstd	0.01	0.01	0.056		

Data of the chosen model is highlighted in bold text

the habitat model, abundance increased with the proportion of flower coverage of preferred forage species (CovPrefSpSiPr) and floral richness (FLRichness), whereas vegetation height (VegHmean) and variability in flower cover (CovSpStd) had small, non-significant coefficients. We retained the latter variables because the habitat model had the lowest LOOCV indicating better generalisation compared to the other models.

The habitat model developed in this study enables monthly predictions of bumblebee abundance, providing valuable insights into the assessment of grassland quality as habitat for bumblebees. To evaluate the predictive performance of the model, we compared the monthly site rankings of observed and predicted bumblebee abundance (Table 3.). This tables highlights the degree of agreement between observed and predictive rankings, identifying cases where predictions aligned with field observation and where discrepancies occurred.

While disagreements exist between the observed and predicted rankings, there are also notable agreements in the monthly site rankings. Specifically, the habitat model consistently identifies the lowest-ranked sites, providing valuable insights for improving bumblebee habitat quality at a site level.

Discussion

We modelled monthly bumblebee abundance using habitat traits and found it was most strongly associated with the proportion of preferred forage species present, and overall floral richness. Although the effects of vegetation height and variability in flower cover were not significant, they were retained in the model for their ecological relevance and their contribution to cross-validated accuracy. These findings align with previous research highlighting the importance of preferred forage species and florally diverse areas for

Table 3 Comparison of observations (O) and predictions (P) in monthly site rankings from May to October 2022

Site	May		June		July		August		September		October	
	O	P	O	P	O	P	O	P	O	P	O	P
S1	2	2	4	3	2	2	5	5	1	4	5*	5*
S2	1	1	2	1	4	4	2	4	1	1	1	2
S3	5*	4	3	4	5	3	4	3	5*	5	2	1
S4	5*	5	5	5	1	1	1	2	5*	3	5*	5*
S5	5*	3	1	2	3	5	2	1	5*	2	5*	5*

Where the numbers indicate the ranking position, green cells indicate ranking agreements, orange disagreements by one position and red more than one position disagreement. Ranks marked with an asterisk (*) had zero bumblebees

bumblebees (Carvell 2002; Carvell et al. 2006b; Pakeman and Stockan 2013; Blaauw and Isaacs 2014; Hülsmann et al. 2015). A detailed ecological interpretation of the habitat traits included in the final model is provided in Supplementary Material S6.

Month-by-month assessments identified key limiting periods, helping to explain why some sites may have low bumblebee populations despite having abundant flowers at certain times of the year. This temporal insight can inform targeted habitat improvements throughout the season and offers a framework for modelling potential management interventions. Future iterations of habitat model could be strengthened by incorporating broader-scale analyses and including forage resources from trees and shrubs.

Habitat quality assessment

During 2022, site 4 had the highest bumblebee abundance, suggesting that it had the best habitat for bumblebees. However, examination of monthly counts shows that bumblebees were only present between June and August, coinciding with abundant flower coverage of Creeping Thistle, *Cirsium arvense*. This can be attributed to bumblebees' preference for *Cirsium* nectar (Goulson et al. 2005), and it strongly suggests that the site could not sustain the full colony cycle due, in particular, to the lack of spring forage. However, the site was clearly a well-used forage area for bees from nests established elsewhere during these three months.

This shows that relying solely on measures which do not take continuity into account, such as single site visits, the peak monthly abundance, or the total annual bumblebee abundance, as indicators of habitat quality may be misleading. Instead, monthly based assessments provide more balanced and informative insights on habitat quality.

Monthly habitat quality assessments for conservation

The habitat model predictions tend to agree more often with the observed rankings of the lowest-ranked sites compared to the highest-ranked sites. This indicates that, although the model may have limitations, it is particularly useful for identifying sites with the smallest bumblebee populations. Consequently, it provides valuable information on the shortcomings of poor sites, which can be used to guide conservation management actions to improve bumblebee habitat quality at those sites most in need of it.

In May, both observed and predicted abundance values suggest that bumblebees are likely to have been primarily foraging outside the study sites, all of which were grassland which reached floral peaks during June, July and August. Our sites were set in a landscape-scale matrix of semi-natural habitats (woodland, scrub, riparian corridors, and grassland), agricultural systems (including hedgerows, orchards, and mass-flowering field crops of *Brassica napus ssp. napus*), and suburban gardens, so bumblebees had a wide range of forage resources available, several of which are likely to have been more attractive to bumblebees than the few available floral resources at the sites at this point. The virtual absence of spring-colony species such as *Bombus pratorum* and *B. hypnorum* at our study sites suggested that these species were never able to utilise the available forage here.

The significant surge of bumblebee abundance at site 4 in July attributable to the presence of *Cirsium arvense* flowers prompted a more in-depth analysis. Interestingly, the pollen of *Cirsium* has been reported to have a negative impact on brood masses in *Bombus terrestris* colonies (Vanderplanck et al. 2018). However, *C. arvense* is known to be a top performer in nectar sugar production per floral unit (Hicks et al. 2016). Additionally, *C. arvense* appeared to produce nectar despite the dry conditions reported by Kendon et al. (2023) in July 2022. This implies that *C. arvense* is an exceptionally valuable resource for bumblebees, particularly in the context of climate change, where extreme weather events such as heatwaves and high temperatures are expected to be more frequent. We found *B. lapidarius* males (4) and workers (24) visiting this flower, as well as *B. terrestris/lucorum* (16) workers. This may justify future research into the adaptability of *C. arvense* as a nectar source in the face of a changing climate, especially as abundant mid- and late-season nectar is important for new queens, enabling them to accumulate the carbohydrates needed for overwintering (Woodard et al. 2019).

September and October mark the end of the bumblebee colony cycle in the UK, and we only recorded males of *B. pascuorum* during these months. This limits the relevance to bumblebees of forage availability in these months, although it may be more useful in late years, or for late-flying species. This also suggests that single-species models may provide finer-scale insights into forage resources available to bumblebees and its implications in their population dynamics.

Overall, the monthly bumblebee abundance predictions allowed a more comprehensive analysis of the resources available to bumblebees during their entire flying season compared to the total bumblebee abundance. The habitat model provides a comprehensive assessment of habitat traits, enabling the ranking of sites and informing about possible management actions to improve the bumblebee abundance.

Habitat model assessment limitations and improvements

Bumblebee species have different forage flight ranges (Vinet and Zhedanov 2011), which indicates that bumblebee habitat assessment should consider both local and landscape scales (Spiesman et al. 2017). While our study primarily focuses on a local-scale assessment, it's important to acknowledge that landscape-scale context likely influence bumblebee abundance at our study sites, potentially contributing to the difference between the model predictions and the observed numbers.

Bumblebee species show peak abundances in different months, which could significantly influence the habitat model. For example, although the habitat model predicted a peak in bumblebee abundance across all sites in July, the observed data revealed that sites 2 and 5 reached their peak in June. This discrepancy can be primarily attributed to the high estimate of the random effect for July in the model, which is likely influenced by the substantial bumblebee abundance observed at sites 1 and 4. This also corresponds to the high bumblebee abundance of *Bombus lapidarius* at these sites, and although we found this species at sites 2 and 5, it wasn't the most abundant species. Hence, the model reflects overall abundance but cannot separate species-specific dynamics, with random effects shaped by the most abundant species. This limitation may bias site rankings and management priorities toward common species, overlooking vulnerable ones.

Discrepancies between the observed and predicted ranking sites, involving differences of more than one position, were frequently attributed to overprediction by the habitat model across different sites. These findings suggest that limiting factors may be preventing the establishment of larger bumblebee populations. These limiting factors could include more attractive forage resources in neighbouring areas or the impact of agrochemical usage, which were not addressed in this study.

Another possibility is that low or poor habitat conditions during the early stages of the bumblebee life cycle influenced the reduced abundance observed later in the year. These findings highlight the complexity of bumblebee population dynamics and suggest the need to consider multiple factors, both local and landscape-level, in habitat management strategies.

Future research could explore incorporating variables to account for various aspects of bumblebee behaviour beyond foraging, such as potential nesting and overwintering sites, and their impact in the model's accuracy to predict bumblebee populations. For instance, the presence of abandoned rodent burrows, dry grass, tussocks, or leaf litter, could provide valuable insights about nesting bumblebee habitat conditions (Svensson et al. 2000; Kells and Goulson 2003; O'Connor 2013). By incorporating these variables, a more comprehensive understanding of habitat quality beyond foraging needs of bumblebees, can be achieve.

Conclusions

Overall, the habitat model successfully identified sites with the lowest bumblebee abundance and the monthly assessments can provide information to guide management actions to improve the habitat quality. The model can also provide a framework for assessing habitat interventions by comparing the habitats and supported bumblebee numbers resulting from alternative habitat changes.

While our model provides insights into habitat quality to support bumblebee population, its application to wide contexts should be approached with caution. The model is based on data collected from a limited number of semi-natural grasslands over two seasons, which may not fully capture the variability and complexities of different ecosystems or the requirements of rarer species. Future research involving a broader range of habitats and extended temporal coverage is necessary to verify the model's effectiveness and to refine its applicability for guiding the conservation of more diverse pollinator species.

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Data availability The data that support the findings of this study are available from the corresponding author upon reasonable request.

Declarations

Conflict of interest The authors declare no competing interests.

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