RESEARCH ARTICLE

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The effects of climate and land use on British bumblebees: Findings from a decade of citizen-science observations

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Abstract

1. Bumblebees are important pollinators but are suffering from population declines due to land use intensification and climate change. In-depth knowledge of species' relationships with different land use and climate variables is invaluable to guide conservation efforts, as well as enable predictions to be made about the impacts of future changes in these variables.

2. Here we use 10 years of bumblebee abundance data from the UK, collected by citizen scientists as part of the BeeWalk scheme, to investigate associations between 14 bumblebee species and various land use, habitat and climate variables. National-scale land cover and climate data were complemented with observer-collected habitat data.

3. Bumblebee presence and abundance showed strong relationships with environmental variables. However, interspecific variation was far stronger than commonalities, which suggests that targeted conservation work is required to effectively safeguard particular species. Within species, we found evidence of different habitat associations between reproductive and worker castes.

4. The results also showed that wetland and riparian habitats had consistently positive associations with a number of species, while semi-natural, arable and urban areas had strongly species-specific associations.

5. *Synthesis and applications*. This study reveals strong effects of specific habitats occurring within broad land cover types on the presence and abundance of bumblebees, with several distinct habitats having importance for different species and castes. Consequently, conservation efforts need to be carefully tailored to particular species. Nevertheless, reversing the loss of semi-natural areas such as wetlands may be the single most generally effective action for bumblebee conservation while improving habitats in urban and arable areas could benefit particular (rare) species. Our results also suggest that the combination of long-term, detailed monitoring data of both species and habitats, here collected by citizen scientists, with remotely sensed landcover and climate data is essential to extend knowledge of species' habitat requirements and to support future research and conservation.

1 | INTRODUCTION

Bumblebees are often considered keystone species, providing important pollination services for numerous flowering plants and contributing substantially to the global agricultural economy (Goulson, 2010; IPBES, 2016). However, many bumblebee species have suffered range declines throughout the Northern Hemisphere over the last few decades and nearly half of the 68 species recorded in Europe have decreasing population trends (Potts et al., 2015). The primary cause of these losses has been land use change towards intensive agriculture and an associated loss of habitats and floral diversity, exacerbated by increased applications of harmful pesticides (Goulson et al., 2015; Senapathi et al., 2015; Siviter et al., 2021). Anthropogenic climate change is also a contributory factor: increased frequency and severity of droughts reduces the floral resource availability for pollinators (Phillips et al., 2018), and recent research directly links population declines to the increasing frequency of temperatures that exceed species' upper thermal limits (Soroye et al., 2020). As a result, local extinctions are occurring near the edges of climatic ranges and species are retreating towards their climatic optimums (Casey et al., 2015; Kerr et al., 2015; Soroye et al., 2020; Williams et al., 2007). It is expected that climate change will continue to impact bumblebees and in Europe up to half of 56 species examined are predicted to lose the majority of their climatically suitable area by 2100 (Rasmont et al., 2015). As populations decline, they become increasingly fragmented due to the discontinuous nature of favourable habitat, and this can increase their risk of extinction due to low genetic diversity, more inbreeding, costly diploid male production and parasitism (Whitehorn et al., 2011).

In the face of such ongoing global change and predicted population declines, it is imperative to conserve bumblebees to safeguard future pollination services. A detailed knowledge base on species' relationships with different land use and climate variables is invaluable here, as it allows conservation measures to be targeted effectively. It is increasingly recognised that assessments must consider multiple global change pressures simultaneously, and not only the impact of one pressure in isolation (González-Varo et al., 2013; Naeem et al., 2019; Settele et al., 2016; Siviter et al., 2021). Indeed, progressively more studies are considering the combined effects of both land use and climate on the distributions of bumblebees. For example, Polce et al. (2018) modelled the present-day probability of occurrence for 47 European bumblebee species, including bioclimatic variables as well as land cover variables from CORINE. Additionally, European-wide studies on the projected future distributions of 48 bumblebee species showed that model performances improved when both land use and climate change were considered (Marshall et al., 2018; Marshall et al., 2020). Recently, Prestele et al. (2021) extended such future projections using integrated

modelling to achieve consistency with global climatic and socio-economic scenario frameworks.

However, these studies generally rely on Species Distribution Models, calibrated using broad land cover classes (e.g. Arable, Forest, Urban) that do not capture ecologically relevant environmental variation (see Marshall et al., 2020 for a demonstration of the value more detailed land use classes could have). To produce more conservation-relevant knowledge that can also support development of a new generation of predictive models, we need to know how specific habitat features relate to those established classes, preferably through independent approaches based on observation and/or statistical analysis. Such progression has so far been strongly limited by the temporal and spatial patchiness of most observational data, which are often collected in an ad-hoc fashion. Larger scale, longer term data collected in a standardised way are much better for analysis, but are rarer because a greater investment of time and money is required to design and test the protocol, train recorders to use it, monitor adherence and perform quality control (and in some cases even pay recorders to take part) (Breeze et al., 2021). To overcome these difficulties, citizen science is increasingly used to gather large quantities of data for use in many disciplines, including biodiversity conservation (Billaud et al., 2021; Dickinson et al., 2012; Theobald et al., 2015). Despite recognised limitations in, for example, sampling bias and data accuracy (Dickinson et al., 2010; Falk et al., 2019), citizen-science projects can yield robust and informative inferences about the changing state of our natural world, particularly when designed to minimise their limitations (e.g. Dennis et al., 2017; Matechou et al., 2018). National biological recording schemes are often used in this way and the United Kingdom is fortunate in having a number of these schemes in operation. *BeeWalk*, established in 2008 and run by the Bumblebee Conservation Trust (https://www.beewalk.org.uk/ & https://www.bumblebeeconservation.org/), is one such project. This standardised bumblebee-monitoring scheme relies on volunteer citizen scientists conducting monthly surveys from March to October along fixed transects, identifying and recording abundances of all observed bumblebees (Comont & Dickinson, 2020).

In this paper, we use 10 years of *BeeWalk* data along with (a) the most accurate national-scale, land cover and climate data available, and (b) detailed observer-recorded habitat records, to investigate the associations among a number of land use, habitat and climate variables and the abundance or the presence/absence of 14 different bumblebee species in the UK. We do this to provide the most detailed overview currently possible of bumblebee habitat requirements across the UK, and as an independent contribution to existing evidence generated via Species Distribution Modelling. We also use this analysis to assess the scope for revealing habitat associations from large citizen-science datasets, in an effort to identify both methods and objectives with the greatest promise for conservation efforts.

2 | MATERIALS AND METHODS

2.1 | Bumblebee species data

Bumblebee abundance data (from 2008 to 2019) were provided through the *BeeWalk* standardised bumblebee-monitoring scheme, run by the Bumblebee Conservation Trust (Comont & Dickinson, 2020). In this scheme volunteers register a transect, usually between 1 and 2 km in length (not necessarily in a straight line), which they then walk monthly between March and October. The location of each transect is loaded into the BeeWalk website, where it is assigned an overall grid reference (the estimated centre point of the transect). Transect walks are voluntary and so not all transects are walked each month. All bumblebees seen are recorded and identified to species level where possible and these records are later verified and validated by the BeeWalk team. Sightings are checked against the known distribution and phenology of each species using the standard NBN Record Cleaner (https://nbn.org.uk/tools-and-resources/nbn-toolbox/nbn-record-cleaner/) and records of rare or hard to identify species, or sightings which are unusual in some other way, are referred back to recorders for further evidence. If none is forthcoming, the sightings are aggregated as *Bombus* sp. Data collection did not require ethical approval.

The worker castes of the morphologically similar species *B. terrestris*, *B. lucorum*, *B. magnus* and *B. cryptarum* are impossible to reliably differentiate in the field (Carolan et al., 2012; Scriven et al., 2016) and so were grouped together here and denoted as *B. terrestris* agg. As the reproductives (queens and males) of *B. terrestris* are morphologically distinct from the more similar *B. lucorum*, *B. magnus* and *B. cryptarum*, analyses were carried out on the reproductives alone, this time only grouping the latter three species as *B. lucorum* agg. Cuckoo bumblebees (subgenus *Psithyrus*) were not considered due to the absence of a worker caste and any unidentified bumblebees were discarded from the dataset. In total, 14 species (including the *B. terrestris* agg. Species group) were analysed (see Table 1).

The total number of individuals in a species or species group observed on a transect was summed (the total number of queens, workers and males observed) and if no individuals were recorded on a transect it was given a zero. For the more common species, it was also possible to analyse the workers and reproductives separately, to assess whether these castes had different relationships to land use and climate. As transects were walked multiple times a year, the totals were summed for each year, giving an annual transect count. To minimise false zeros, only transects that were walked three or more times within 1 year were included in this annual transect count. The early trial years of *BeeWalk*, 2008 and 2009, were discarded from the dataset due to their small sample size and patchiness, leaving 10 years of data for analysis (2010–2019 inclusive). Transects that had centre points less than 250 m apart were combined. This left a total of 2,361 annual transect counts (comprising summed values across three or more walks of each transect) at 1,001 unique grid references (Figure S1; Table S1).

2.2 | Land cover data

Land cover data were obtained from the Coordination of Information on the Environment (CORINE) Land Cover (European Union, 2020). The original CORINE classes were grouped into the following nine classes: pasture, peri-urban, arable, deciduous/mixed forest, water/wetland, semi-natural, urban, coniferous forest and heterogeneous agricultural areas (see Table S2 for information on the reclassification). The latter two classes were later discounted as they were present in only extremely small proportions and had no effect in any statistical model (see Table 2). Buffer

TABLE 1 Summary of the total numbers of each bumblebee species considered for analysis

	Total count	Mean transect count (± *SE*)		Percentage presence on 2,361 annual transect counts
Bombus terrestris agg.	150,919	63.92	± 1.57	98.73
Bombus pascuorum	90,463	38.32	± 1.09	93.35
Bombus lapidarius	63,190	26.76	± 1.03	86.19
Bombus pratorum	20,173	8.54	± 0.35	69.42
Bombus hypnorum	14,974	6.34	± 0.31	58.66
Bombus hortorum	13,697	5.80	± 0.33	59.97
Bombus humilis	2414	1.02	± 0.16	8.09
Bombus muscorum	1399	0.59	± 0.21	5.46
Bombus jonellus	719	0.29	± 0.04	7.41
Bombus sylvarum	425	0.18	± 0.04	2.41
Bombus ruderatus	386	0.16	± 0.04	3.52
Bombus monticola	229	0.09	± 0.02	2.08
Bombus ruderarius	126	0.05	± 0.04	1.74
Bombus soroeensis	52	0.02	± 0.01	0.34

TABLE 2 Mean proportions and standard deviation for each land use type at each buffer size around all transects (*n* = 1,001). For further details, see Table S2

	500 m buffer		1,000 m buffer		2,000 m buffer	
	Mean proportion (*n* = 1,001)	*SD*	Mean proportion (*n* = 1,001)	*SD*	Mean proportion (*n* = 1,001)	*SD*
Pasture	0.2643	0.3160	0.2582	0.2636	0.2557	0.2306
Peri_urban	0.2588	0.3374	0.2439	0.2958	0.2198	0.2581
Arable	0.2211	0.3219	0.2388	0.2936	0.2597	0.2733
Forest	0.0720	0.1771	0.0612	0.1234	0.0513	0.0839
Water/wetland	0.0639	0.1658	0.0780	0.1663	0.0909	0.1645
Semi-natural	0.0592	0.1818	0.0565	0.1568	0.0577	0.1444
Urban	0.0352	0.1222	0.0370	0.0952	0.0381	0.0718
Coniferous	0.0173	0.0871	0.0189	0.0736	0.0200	0.0677
Heterogeneous	0.0083	0.0654	0.0076	0.0502	0.0066	0.0322

TABLE 3 Climatic and topographic variables, with definitions and units, used in the analysis

Variable	Definition	Units
Growing degree days (gdd)	Annual number of growing degree-days (daily average temperature above 5 degrees)	day (annual)
Extreme days (extremedays)	Days with extremely hot maximum temperature with respect to historic distribution (annual no. days with daily max. Temp. > 95th percentile of historic daily temp.)	day (annual)
Mean diurnal range (diurnalavg)	Annual mean of daily difference between daily max. and min. Temperatures.	degree C (annual)
Annual temperature range (temprange)	Maximum daily temp. of warmest month – minimum daily min temp of coldest month	degree C (annual)
Temperature seasonality (tsd)	Standard deviation of monthly mean temperature per year	degree C (annual)
Total annual precipitation (precip_mm)	Sum of monthly total precipitation in each year	mm (annual)
Precipitation seasonality (precip_cv)	Coefficient of Variation in monthly precipitation in a year	% (annual)
Elevation	Metres above sea level	metres

sizes of radius 500 m, 1,000 m and 2,000 m were created around the grid reference at the centre point of each transect. These buffer sizes were chosen to relate to the foraging ranges of different bumblebee species (see e.g. Walther-Hellwig & Frankl, 2000), and to explore the effects of habitats at different scales around observed bumblebee activity. The proportion of each land use type present within each buffer zone was calculated (see Table 2 for mean proportions of each LU type, and Table S2 for further details including a comparison to national mean values), using the vector CORINE LC data, in ESRI Geodatabase format. Collinearity among LU types was tested and no combination of variables had a Pearson's correlation >0.45 (Figure SF4). As CORINE LC data are produced every 4–6 years, we used the most relevant data to the year of sampling (CORINE 2006 for 2008–2010 observations, CORINE 2012 for 2011–2014 and CORINE 2018 for 2015–2019). The Shannon diversity of land use types (of a potential 21 classes from the initial CORINE LU classes, see Table S2) was also calculated for each grid reference and each buffer size to give a measure of land use heterogeneity.

Through the *BeeWalk* scheme, habitat descriptions were also recorded for each transect from a defined list of 40 habitat types, following the Joint Nature Conservation Committee standardised habitat classification. We grouped the original list of 40 habitat types into 15 combined types (Table S3).

2.3 | Climatic and topographic data

We obtained climate data from Had-UK 1 km observational data (2010–2019) (Met Office, 2020). We initially considered 11 climate variables but discarded four due to high collinearity with other variables (>0.7 Pearson correlation coefficient was chosen as the cut-off following Dormann et al., 2013; Marshall et al., 2018, see Figure SF5). The remaining seven variables are detailed in Table 3 and were calculated for each grid reference, at each buffer size, for each relevant year. The elevation of each grid reference, at each buffer size, was also calculated, using SRTM 90 m data (Jarvis et al., 2008) via the R package 'RASTER' (Hijmans, 2020).

The collinearity of each climatic and topographic variable against each LU type was also checked. No combination of variables had a Pearson's correlation >0.53 and the majority were substantially lower (Figure SF6). Summaries of climatic and topographical variable ranges across the transects and nationally are provided in Table S2.

2.4 | Statistical analysis

Data were analysed in R, version 3.4.1 (R Core Team, 2017). To identify whether there were trends in land cover and climatic variables over the 10-year period, trend analyses were carried out for the predictors individually prior to the main analyses. As land cover data had three samples per grid reference location, that is, 2006, 2012, 2018, no statistical trend analysis was applicable; therefore, the land use proportions from the first and the last years were compared to each other and the +− signs were counted for the 1,001 grid references as 'no change', 'increase' or 'decrease'. For climatic variables, we carried out a nonparametric Mann–Kendall trend analysis, as the data were not normally distributed (Mann, 1945), using the Kᴇɴᴅᴀʟʟ package in ʀ (McLeod, 2011). This analysis tests whether there is a monotonic trend based on rank correlation under the 95% confidence level and gives 'no trend', 'positive trend' and 'negative trend' to each climatic variable.

2.4.1 | Count analyses

As there were no significant temporal trends in the land use or climate, each bumblebee species was analysed separately to assess how their abundance and/or presence were affected by the land use and climate variables. The total annual counts of the six more common species (*B. terrestris* agg. [workers only], *B. pascuorum*, *B. lapidarius*, *B. pratorum*, *B. hypnorum* and *B. hortorum*) were analysed with generalised linear mixed-effect models (glmms), with a negative binomial distribution to account for over-dispersion. All models were run using the ɢʟᴍᴍTMB package in ʀ (Brooks et al., 2017), with grid reference and year as random effects, the latter due to nonlinear variations in bee abundance among years. Models were offset by the number of times the transect was walked in a year. Each buffer size was analysed separately and the CORINE land use variables, the Shannon diversity of LU types within that buffer zone and the climatic and topographic variables were covariates in the model. Model selection was done using a step-wise backward comparison of AICc (Burnham et al., 2011), and the model with the lowest AICc was chosen as the final model. Models were visually inspected with diagnostic plots (residuals vs. predicted values and QQ-Plots) with ʀ package DHARMᴀ and were found to fulfil assumptions (Hartig, 2018).

2.4.2 | Spatial autocorrelation

Further analyses were carried out to check and correct for spatial autocorrelation in model residuals. Again using the DHARMᴀ package,

we tested within-year residuals for autocorrelation for each species and year. Where we found significant levels of autocorrelation, we used hierarchical clustering (ʀ package 'sᴛᴀᴛs') to identify clusters of transects within geodesic distances of 2,000 m for each year, and retained only one record from each of these clusters. We then re-ran the relevant model on the thinned data, before once again checking the residuals. We repeated this where necessary for the full (multi-year) models for each species, as well as for specially constructed single-year models. In each case, the thinned data produced models without residual spatial autocorrelation. The results of models based on the full and thinned data were compared and it was found that no differences occurred in the direction or significance level of effects.

2.4.3 | Presence/absences analyses

To assess whether the presence of each species gave different results to their abundance, additional analyses were carried out for *B. pratorum*, *B. hypnorum* and *B. hortorum* using the annual presence/absence on each transect, instead of the annual count, and glmms with a binomial distribution. All other model variables were kept as above. This presence/absence analysis was not possible for the three most common species (*B. terrestris* agg., *B. pascuorum* and *B. lapidarius*) because they were present in the great majority of annual transect counts (Table 1), leaving insufficient absences. The three species *B. humilis*, *B. muscorum* and *B. jonellus* were not common enough for analyses on their abundance, so only their annual presence/absence were modelled with binomial glmms and, again, all other model variables were as above.

2.4.4 | Detailed habitat analyses

To investigate how more detailed habitat affected bumblebee abundance and/or presence, similar analyses were carried out on the subset of data that had observer-recorded information on habitat. This dataset included a total of 2021 annual transect counts at 880 unique grid references. We checked the representativeness of these data against the full dataset by comparing the distributions of land use and climate variables and bee abundances and found no significant differences. Again, each species was analysed separately (abundance models for *B. terrestris* agg., *B. pascuorum*, *B. lapidarius*, *B. pratorum*, *B. hypnorum* and *B. hortorum* using glmms with negative binomials distributions and presence/absence models for *B. pratorum*, *B. hypnorum*, *B. hortorum*, *B. humilis*, *B. muscorum* and *B. jonellus* using glmms with binomial distributions). Grid reference and year were entered as random effects and models were offset by the number of times the transect was walked in a year. In these models, the 15 habitat classes were entered as covariates, along with the climatic variables that were found to be important for each species in the previous analysis, at one buffer size of 1,000 m. This buffer size was chosen as the most relevant for bumblebees because, although foraging ranges are variable for different species, the mean range

is approximately 1,000 m (Goulson & Osborne, 2009). Models were simplified according to AICc scores as before.

2.4.5 | Reproductives versus workers

The sample size of the more common species was sufficient to allow additional analyses on the reproductives (queens and males) and workers separately. The annual presence/absence of queens and males on each transect were calculated for *B. terrestris*, *B. lucorum* agg., *B. pascuorum*, *B. lapidarius*, *B. pratorum*, *B. hypnorum* and *B. hortorum*. For the workers, the abundances of *B. terrestris* agg., *B. pascuorum* and *B. lapidarius* were used (due to insufficient absences) and the presence/absence of *B. pratorum*, *B. hypnorum* and *B. hortorum*. Binomial/negative binomial glmms were used to investigate how land use and climate as well as the more detailed habitat data affected the castes of each species, with all other model variables kept as above.

2.4.6 | Rare species analyses

The five species, *B. sylvarum*, *B. ruderatus*, *B. monticola*, *B. ruderarius* and *B. soroeensis*, were too rare to allow the full statistical analyses described above. Instead the proportions of CORINE land use within each buffer size on the transects on which these species were found were compared to the proportions of land use on transects on which the species were not found using two-sample Wilcoxon rank-sum tests. Additionally, climatic variables on transects where species were found were compared to those where species were not found using two sample *t*-tests. To fulfil assumptions of normality, climatic variables were transformed with the orderNorm function in the BEST-NORMALIZE package in R (Peterson, 2020).

3 | RESULTS

There were no significant trends in the seven climatic variables at more than 93% of transect locations (at 95% significance level), with the diurnal average increasing at 6% of transect locations and the precipitation seasonality decreasing at 3% of transect locations (Figure SF2). The three available land use datasets were too few to establish significance of any trends, but mean changes in land use proportions were all less than 1% (Figure SF3). The largest changes were an overall decrease in arable areas of 0.9% and an increase in water and wetland areas of 0.7%. Because trends were absent or very small, we did not analyse them further.

Strong effects of climate and land use variables on bumblebee presence and abundance were found across species. The results were characterised by substantial interspecific variation more than commonalities, with multiple, often strong effects of land use and climate for some species (e.g. *B. lapidarius* and *B. hypnorum*) and few effects on others (e.g. *B. humilis* and *B. jonellus*) (Figure 1). No single

buffer size had more significant effects than others, but results were never inconsistent across buffer sizes.

3.1 | Land use

Peri-urban and semi-natural were the two land use classes associated with the most significant effects. Semi-natural land had a negative association with *B. terrestris* agg., *B. pascuorum* and *B. pratorum* (Figures 1 and 2; Tables S5, S6 and S8) but a positive one with the less common *B. hortorum*, *B. humilis* and *B. muscorum* (Figure 1; Tables S10, S18 and S19). In contrast, a higher proportion of peri-urban land was positively correlated with *B. terrestris* agg. and *B. hypnorum* but negatively correlated with the less common *B. jonellus*, *B. hortorum* and *B. muscorum*. The latter two species also both had negative associations with urban areas. A higher proportion of water/wetland was positively correlated with a higher abundance of *B. terrestris* agg., *B. pascuorum* and *B. muscorum* (Figures 1 and 2). *Bombus lapidarius* appears to be more of a generalist, with significantly positive associations with all land use types at all scales (Figure 1; Table S7).

3.2 | Climate and topography

Climatic and topographic associations were also very species dependent. For example, *B. terrestris* agg., *B. pascuorum* and *B. hypnorum* all had positive associations with higher elevations, but the opposite was found for *B. hortorum*, *B. humilis* and *B. muscorum*. The mean diurnal range was an important positive predictor for both *B. pascuorum* and *B. pratorum*, while temperature seasonality was more important for *B. lapidarius*, *B. hypnorum* and *B. jonelllus*, with a relatively strong negative association with the latter. All the final glmm models with parameter estimates for climate and land use variables and their associated 95% confidence interval and test statistics (Wald's *z*-score and *p* values) are detailed in Tables S5–S10 and S18–S20.

3.3 | Observer-recorded habitats

Moving beyond the general land cover categories, we found substantial further effects of the observer-recorded habitat types. Freshwater edges, bogs, scrub and horticulture/orchards were consistently found to have positive effects on the presence and/or abundance of a number of species. Other habitats had species dependent effects, for example *B. pratorum* and *B. hypnorum* were positively associated with gardens but the opposite was true for *B. lapidarius* (though not significant) and *B. humilis*. Woodland had negative associations with *B. terrestris* agg., *B. pascuorum* and *B. lapidarius* but positive with *B. pratorum*. Figure 5 shows the variables that remained in the final models and their significance for the analyses of workers and reproductives (for full information on all the final models, see Tables S5–S20).
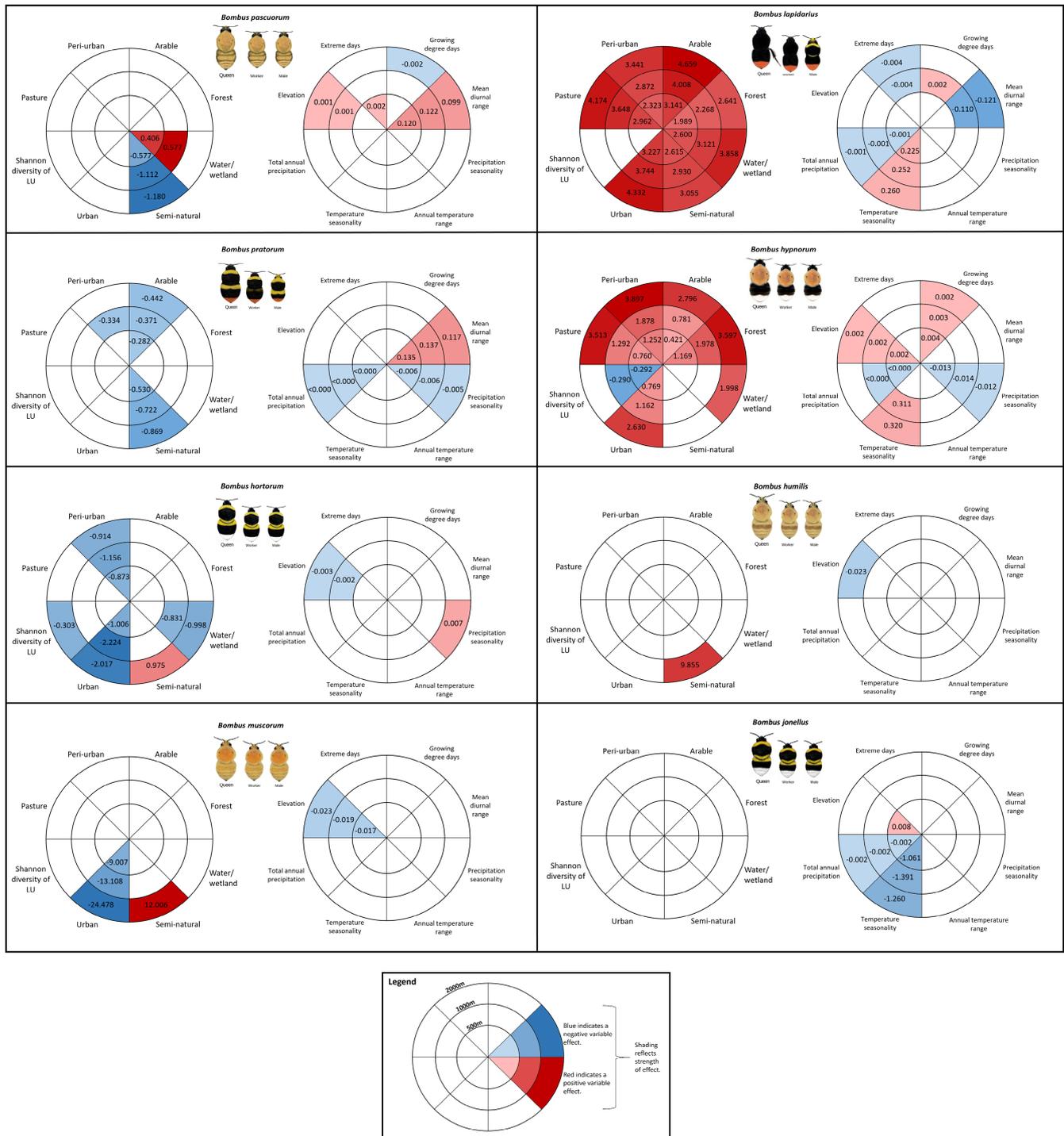
FIGURE 1 Model estimates for the significant CORINE land use and climatic variables at each buffer size in the final glmm models for eight species (count analyses for *B. pascuorum*, *B. lapidarius*, *B. pratorum*, *B. hypnorum*, *B. hortorum* and presence/absence analyses for *B. humilis*, *B. muscorum*, *B. jonellus*). Positive effects are shown in red, negative in blue with shading to illustrate the strength of effect. Complete information on final models can be found in Tables S5–S10 and S18–S20

3.4 | Abundance versus presence/absence

Analysing both the presence/absence and abundance of *B. pratorum*, *B. hypnorum* and *B. hortorum* produced broadly similar results but did reveal some additional interesting detail (Tables S7–S9). For *B. pratorum*, the presence at the largest buffer size of 2 km was significantly, positively correlated with the proportion of pasture. However, this

was not so for the abundance and instead a negative effect of arable land was observed. The negative effects of peri-urban and arable land at smaller scales and semi-natural land at all scales were consistent across models. Climatic variables produced more variable results, with precipitation (seasonality and total) having negative effects on the abundance of *B. pratorum*, but the annual temperature range having negative effects on the presence of this species. The
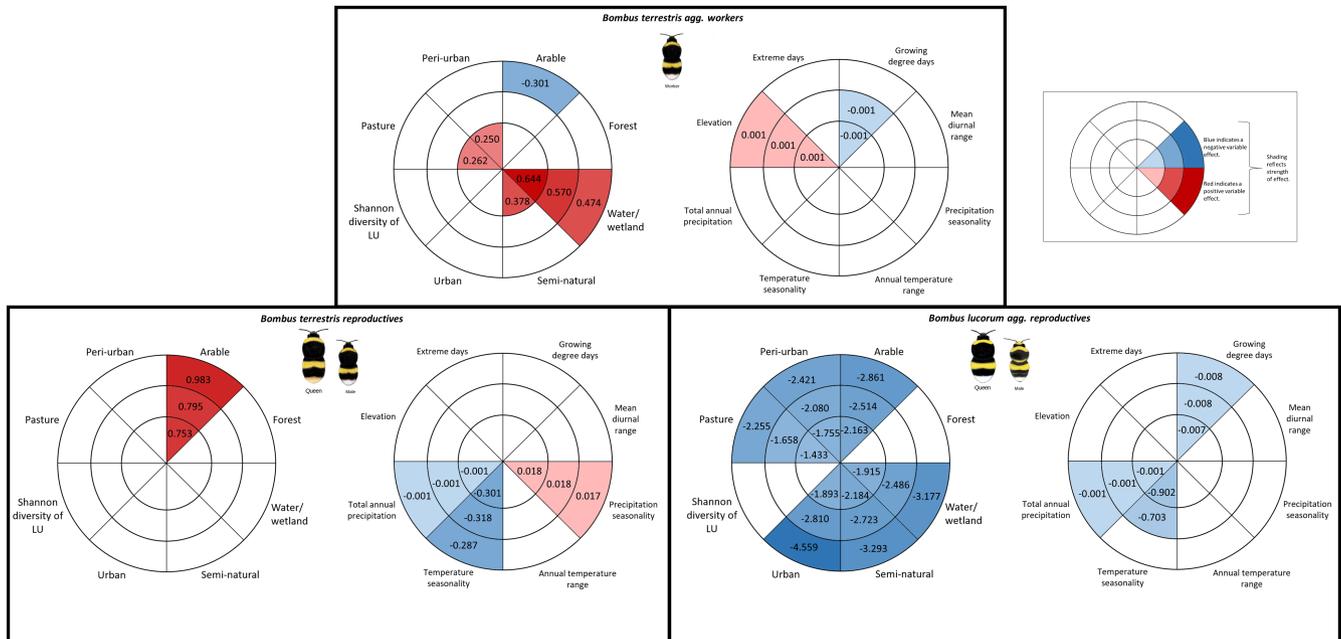
FIGURE 2 Model estimates for the significant CORINE land use and climatic variables at each buffer size in the final glmm models for *B. terrestris* agg. Workers (top), the *B. terrestris* reproductives (bottom left) and *B. lucorum* agg. Reproductives (bottom right). Positive effects are shown in red, negative in blue with shading to illustrate the strength of effect. Complete information on final models can be found in Tables S5, S11 and S12

most important climatic variable for this species, the mean diurnal range, had consistent, positive effects across models. Gardens and freshwater edges also had consistent positive effects, but scrub, bracken and herbs and bog, marsh and mire had positive associations with the annual abundance of *B. pratorum*, while woodlands and hedges and lanes were positively associated with their presence. For *B. hypnorum*, the presence/absence and abundance models produced very consistent results with only a very few small differences. The majority of land uses had significant positive relationships with this species but, interestingly, forests were revealed to be the most important variable in predicting the presence of this species and this strong effect was not seen for the abundance. The presence/absence and abundance of *B. hortorum* was consistently, negatively associated with peri-urban and urban land (and water/wetland at larger scales), but this effect was stronger for the presence/absence of the species. Semi-natural land was revealed as a positive predictor of the abundance of this species at large scales, but this effect was not seen for the presence alone. Climatic variables were broadly consistent for *B. hortorum*, but the mean diurnal range was positively associated with the presence at small scales and the precipitation seasonality positively associated with the abundance at large scales. The habitat horticultural and orchard was most important for this species and was positively associated with both the presence and abundance.

3.5 | Reproductives versus workers

Further interesting results were revealed from the separate analyses on the reproductive and worker castes of the more common

species. For *B. terrestris* agg., analysing the reproductives allowed for some distinction within this species group, showing that there are indeed different land use and climate preferences (Figure 2). For example, *B. terrestris* reproductives had a strong positive association with the arable land use class, while the *B. lucorum* agg., reproductives had negative associations with all land use classes, except forest, and this effect was strongest for urban areas. The total annual precipitation was negatively associated with reproductives of both species (and, indeed, this negative association was found for all the reproductives of the common species analysed). In contrast, *B. terrestris* reproductives were positively associated with precipitation seasonality and both *B. terrestris* and *B. lucorum* agg. reproductives had negative associations with temperature seasonality, with this effect being strongest in the latter species group. The habitat analyses provided more information (Figure 3), for example, *B. terrestris* reproductives were positively associated with set-aside areas, as well as hedges and lanes. *B. lucorum* agg. Reproductives were positively associated with woodland and scrub, bracken and herbs and negatively associated with improved grassland. The positive effect of freshwater edges and gardens was found for all.

The separate analyses on the workers and reproductives of the other common species, *B. pascuorum*, *B. lapidarius*, *B. pratorum*, *B. hypnorum* and *B. hortorum*, provided additional detail on the preferences of these species (Figure 3; Tables S13–S17). For *B. pascuorum*, *B. lapidarius* and *B. hypnorum*, hedges and lanes were positively associated with the abundance of workers, while scrub, bracken and herbs were important for the presence of the reproductives. In contrast, improved grassland had negative
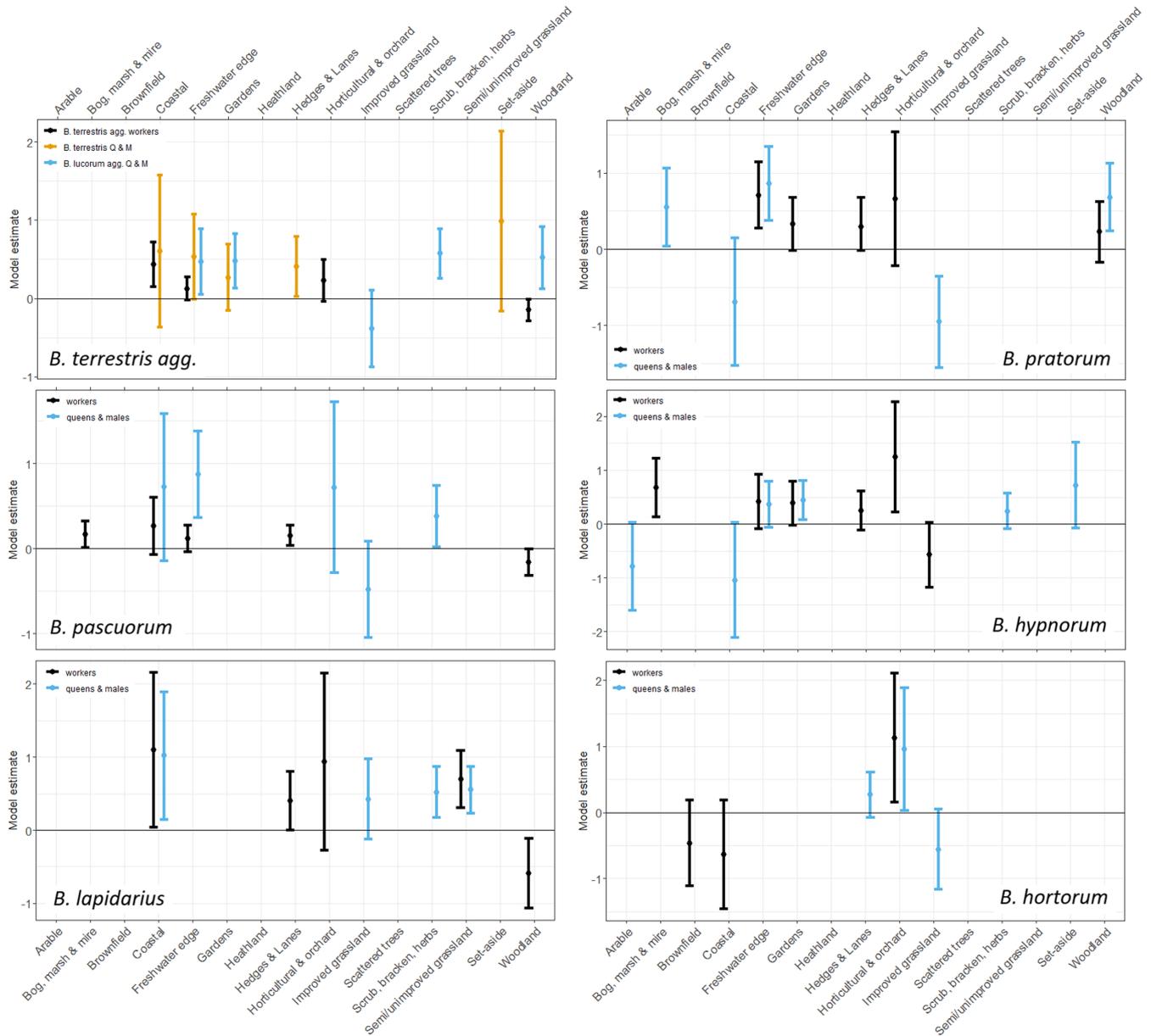
FIGURE 3 Parameter estimates and 95% confidence intervals for the final glmms assessing associations between bumblebee worker and reproductive abundance/presence and 15 habitat variables. Lines that do not cross zero are significant at $p < 0.05$. In the top left panel (*B. terrestris* agg.), the results for workers are shown in black, *B. terrestris* queens and males are shown in brown and the *B. lucorum* agg. Queens and males are shown in blue. In all other panels, the results for workers are shown in black and the queens and males of that species are shown in blue

associations with the reproductives of *B. pascuorum, B. pratorum* and *B. hortorum*, but this was positive for *B. lapidarius* reproductives. When considered separately, *B. pascuorum* workers and reproductives had negative associations with peri-urban land uses, an effect that was masked when all individuals were considered together. For *B. lapidarius*, the positive effects of arable and pure urban land uses were stronger when workers and reproductives were considered separately and the same was true for *B. hypnorum* and the peri-urban and forest land uses. Other main effects of land use, climate and habitat were broadly similar between the analyses of all individuals together and those with the castes separate (see Tables S13–S17).

3.6 | Rare species

The five rarer species, *B. sylvarum, B. ruderatus, B. monticola, B. ruderarius* and *B. soroeensis*, also show significant variation and some clear significant associations with CORINE land use classes (Figure 4) and the climate variables (Figure 5). For example, the presence of *B. sylvarum* was positively associated with higher proportions of water/wetland, while *B. ruderatus* was found in areas with more arable land. Both *B. monticola* and *B. soroeensis* had a higher presence in areas with a greater proportion of semi-natural land (Figure 4). The climatic niche of *B. sylvarum* and *B. ruderatus* appears to be broadly similar, with a greater presence on transects that have lower elevations, a
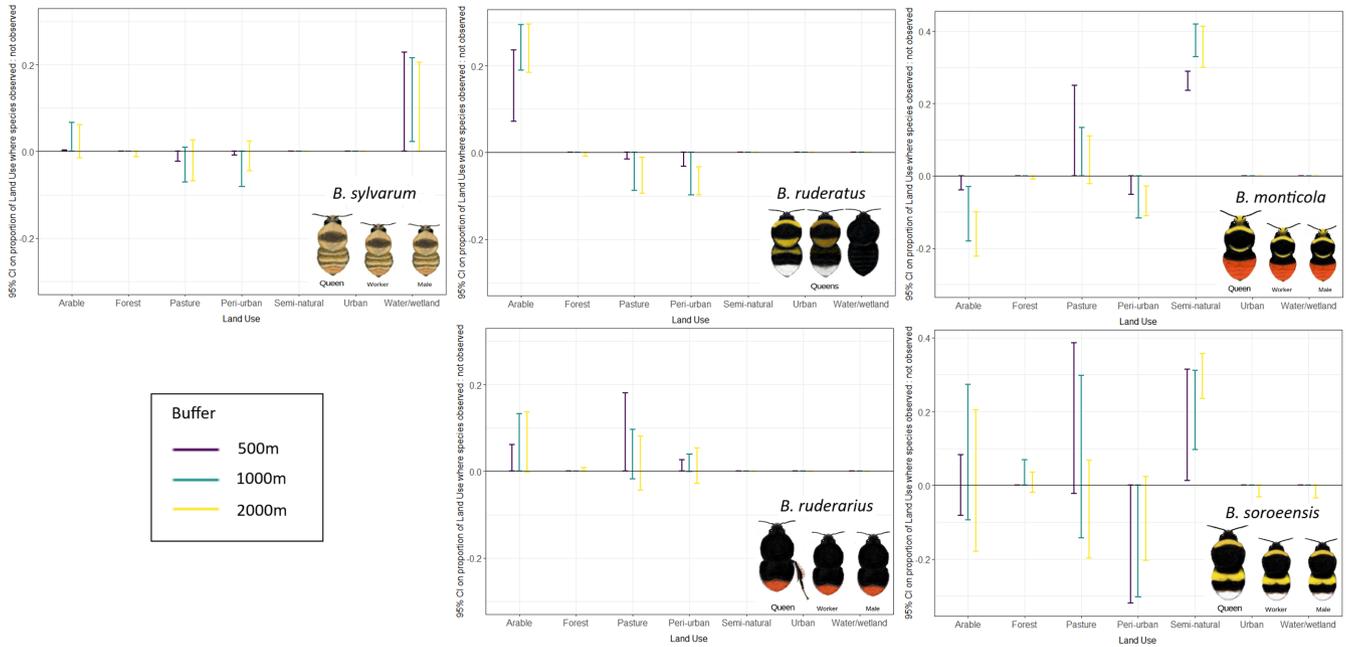
FIGURE 4 95% confidence intervals from the Wilcoxon rank-sum tests comparing proportions of CORINE land use on the transects where the five rare species were observed, relative to transects where not observed at the three buffer sizes. Lines that do not cross zero show significant differences in these proportions
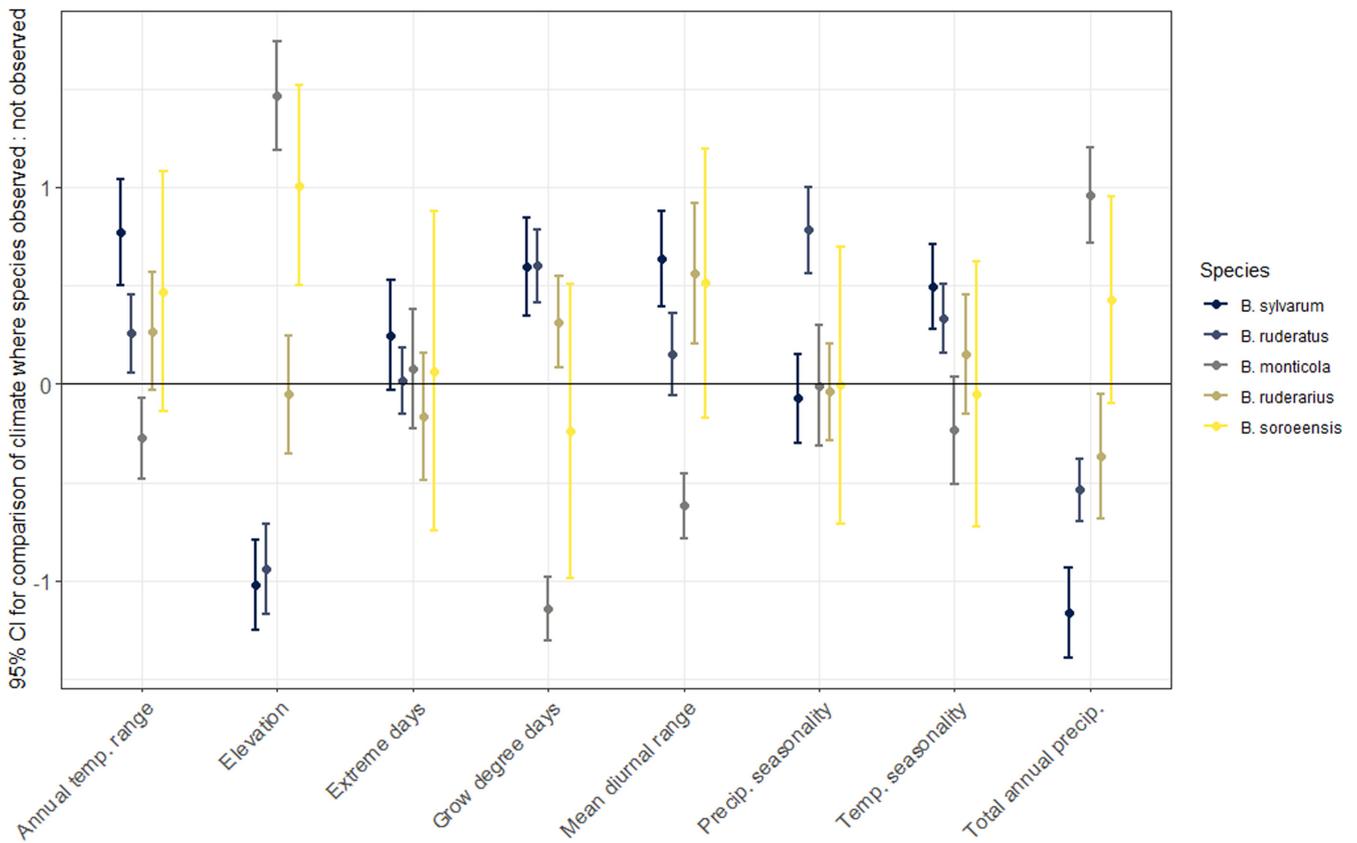
FIGURE 5 95% confidence intervals from the two sample *t*-tests comparing climate variables on the transects where the five rare species were observed, relative to where not observed. Lines that do not cross zero show significant differences in these proportions

greater number of growing degree days and a lower total annual precipitation. In contrast, *B. monticola* was associated with transects at higher elevations, fewer growing degree days and more precipitation (Figure 5) (see Tables S21–S25 for the full Wilcoxon and *t*-test results).

4 | DISCUSSION

This comprehensive analysis of UK bumblebees found strongly species-specific, often very different, responses to several land use and climate variables. This highlights the value of species-specific data and analyses, and suggests that, although generic one-size-fits-all policies may be of some benefit to bumblebees as a group, targeted species-level conservation work is required to effectively safeguard particular species and the ecosystem services they provide across the UK. These efforts require in-depth understanding of species' requirements, and as such must be supported by detailed species and habitat survey data, as provided here by a long-term citizen-science project. Our findings suggest that these data are essential complements to more established but less well-resolved data, such as remotely sensed land cover classifications, and are key in revealing the smaller scale, ecologically relevant conditions within broad habitat classes.

Nevertheless, the broad CORINE land cover classes that we analyse here, despite lacking habitat detail, do show strongly significant relationships for some species. The classes do not correlate directly to levels of land use intensity but it can be assumed that the classes 'arable' and, to some extent, 'pasture' are managed more intensively than 'semi-natural' and 'water/wetland'. Bumblebees have been negatively impacted by land use intensification (Hemberger et al., 2021), so we would expect that these latter land use classes, associated with lower land use intensity, would have positive correlations with bumblebee presence and abundance. This is certainly the case but not in a uniform manner. Semi-natural land accounts for a tiny proportion of the land in this study (mean proportion in buffer areas = 0.058), but there were still strong positive effects in many cases, particularly for the less common species (*B. hortorum*, *B. humilis*, *B. muscorum*, *B. monticola* and *B. soroeensis*). Perhaps surprisingly, we found negative effects on some common species (*B. terrestris* agg., *B. pascuorum*, *B. pratorum*), which may reflect the ability of the more widespread, human-impacted land covers to meet the requirements of these species (in terms of, e.g., timing of floral forage provision) better than they do for the rarer, declining species. Generally, the literature shows that landscape containing some semi-natural vegetation is beneficial for bumblebees (Carvell et al., 2017; Papanikolaou et al., 2017), and this can have knock-on positive effects on crop yield (Pywell et al., 2015). The broad CORINE class of semi-natural land does not capture smaller pockets of semi-natural vegetation that are important for all bumblebees, but our results suggest that the rarer species require larger areas of continuous semi-natural vegetation, which are therefore likely to be important in maintaining higher levels of species richness.

The other 'less intensive' CORINE category, 'water/wetland', also had positive associations with a number of species, for example *B. pascuorum* and *B. sylvarum*. This is supported by the higher presence/abundance of many different species in the observer-recorded habitat classes of freshwater edges and (to a lesser extent) bogs, marsh and mire. This is likely to result from several different interacting factors. First, wetland areas are often the primary undeveloped land use in lowland areas (Palta & Stander, 2020) and so act as a proxy for the availability of flower-rich ruderal vegetation and for a lower intensity of use (i.e. fewer pesticides). Likewise in arable areas, the remaining patches of habitat suitable for bees are often buffer strips associated with water courses, so it is possible that bumblebees are associating with wetlands and riparian habitats simply because these remain more often than other natural areas in human-dominated landscapes. Additionally, these wetter areas have intrinsic value as habitats for bees as they are likely to be less affected by droughts, which reduce floral resource availability for pollinators in drier habitats (Phillips et al., 2018). It is also possible that observer bias is contributing to the positive associations. Volunteer BeeWalkers select their own transect locations, which may therefore tend to include bee-rich habitats (e.g. nature reserves) close to urban areas; places that are often associated with wetlands. Nevertheless, the representation of wetland areas around the transects is in-line with their national extent (Table S2).

Positive associations with wetlands are also likely to reflect genuine ecological benefits. Wetlands have declined enormously in the UK and elsewhere (Verhoeven, 2014) and the areas where they still persist have become havens for many of the UK's rare bumblebee species (Williams, 1986). Species such as *B. sylvarum* and *B. muscorum* have survived (and are monitored) in the wetland areas of the Somerset, Gwent and Pevensey Levels, the Hythe and Romney Marshes and the Thames Estuary creeklands, where ditches break up the intensively managed agricultural or developed land, increasing connectivity and providing food, nesting and overwintering habitat (Natural England, 2014). Reversing the long-term land use changes that have resulted in the loss of so many of these crucial habitats and resources could therefore have huge benefits for bumblebee persistence in the future.

In contrast, some species did have positive associations with the more intensively used land cover classes. For example, *B. ruderatus* and *B. terrestris* reproductives were positively correlated with arable areas, *B. pratorum* with pasture and *B. terrestris* agg. and *B. hypnorum* were both positively correlated with peri-urban land cover. It is likely that variation hidden within each of these broad classes is impacting bumblebee population dynamics. The presence or absence of flower strips and the rate and type of pesticide use can have large impacts within arable areas (Carvell et al., 2017; Geppert et al., 2020; Rundlöf et al., 2015), while the extent and contents of private gardens can determine forage and nesting potentials in urban and peri-urban areas (Osborne et al., 2008; Samuelson et al., 2018). Such effects are implied by our analysis of detailed habitat classes, which showed positive associations between *B. terrestris* reproductives and the habitat classes 'set-aside' and 'hedges and lanes', both of which could

provide valuable forage and potential nesting sites within areas classified as 'arable' in the CORINE data. Understanding how these landscape features can also support rarer species in arable areas is an important objective for further policy-relevant research, and complementing land cover data with information on field size, organic farming practices and micro/meso-habitat provision in the form of, for example, flowering hedgerows or field margins is likely to reveal significant relationships (Carrié et al., 2018; Geppert et al., 2020).

Our analyses also suggest habitat associations may differ between workers and reproductives. For example, the *B. lucorum* agg. Reproductives were associated with 'forest' land cover class and 'woodland' habitat, suggesting that the presence of forested areas is important for the reproductive success of this species group, perhaps through the provision of suitable nesting sites. Hedges and lanes evidently provide important forage for workers as they were positively associated with the abundance of *B. pascuorum*, *B. lapidarius*, *B. pratorum* and *B. hypnorum* workers, while scrub, bracken and herbs were important for the presence of the reproductives of *B. pascuorum*, *B. lapidarius* and *B. hypnorum*. Such habitat could provide nesting sites as well as late season forage such as ivy, which is known to be important for reproductives (Timberlake et al., 2021). The differences between abundance and presence analyses may indicate similar sensitivities. For instance, 'Scrub, bracken and herbs' and 'bog, marsh and mire' had positive effects on the annual count of *B. pratorum* (Table S6), hinting at the importance of these areas for forage. In contrast, 'woodland' and 'hedges and lanes' had positive effects only on the presence of this species, suggesting that these areas may be important in providing nesting sites. The negative effect of 'arable' land and the positive effects of 'gardens' and 'freshwater edge' were found in both presence and abundance models, indicating the consistent effects of these habitats.

The strong interspecific differences in land use and climate preferences were again highlighted when analysing the reproductives of *B. terrestris* and *B. lucorum* agg. Separately. While a shared negative association with total annual precipitation was observed (as for all reproductives, regardless of species), only *B. lucorum* agg. Had a negative association with the number of growing degree days. *B. terrestris* reproductives had a positive association with precipitation seasonality, suggesting alternative climatic niches for these species. *B. terrestris* does indeed have a more southerly distribution in the UK, compared to *B. lucorum* (Edwards & Roy, 2009). It must be noted that *B. lucorum* agg. is a species group, containing three morphologically identical species but which themselves have divergent climatic niches and habitat preferences (Scriven et al., 2016). The impossibility of distinguishing these species correctly in the field is certainly a limitation of citizen science collected data, but one that may be overcome with the development of more technologically advanced survey techniques such as eDNA metabarcoding (Thomsen & Sigsgaard, 2019).

Contrary to expectations, the Shannon diversity of land use types had no positive relationships with bumblebee presence or abundance. A more heterogeneous landscape has often been found to be beneficial for bumblebees and other pollinators (Mallinger et al., 2016;

Rundlöf et al., 2008), but this heterogeneity is often derived from smaller scale habitat variables not assessed here, for example field size and the number of field boundaries (Geppert et al., 2020; Hass et al., 2018). The Shannon diversity indices calculated in this study were dominated by the more common land cover classes (such as pasture and arable) and therefore higher measures did not necessarily reflect an increase in more natural areas or other habitat.

Our findings suggest some key priorities for conservation and research. Because bumblebee populations are sustained through the exploitation of ephemeral resources across a broad area, the landscape context is particularly important (e.g. Carvell et al., 2017). At this landscape scale, our results reveal a number of specific habitat and general land cover components that favour certain species, assisting in the identification of areas that can potentially function as core habitats or corridors. One aim of the *BeeWalk* scheme is indeed to directly inform the Bumblebee Conservation Trust's large-scale conservation planning, and our results feed directly into this landscape-based prioritisation. Information on how species are affected by different climatic variables also allow us to anticipate species dynamics in the medium to long term, and so to focus on particular areas of their range, or the provision of corridors to areas that are likely to become more suitable in the future. For research, there is a clear need to investigate the precise requirements of rarer species, and how common land uses such as arable production can be modified to support them. Additionally, it is important to establish how gardens, as a substantial land cover and potential habitat, can be made more suitable for those species, such as *B. humilis*, that this study showed to have a negative association with them. Such questions are particularly pertinent given the likelihood that climate change will reduce the habitat area for many species, making it essential to provide more habitat support at species' range edges if dangerous declines are to be avoided (Schweiger et al., 2019).

It is also important to highlight the limitations of studies such as this. Fundamentally, our analyses rely on statistical models that detect correlations, making them useful guides for further research but inappropriate for direct use in conservation unless supported by other ecological information. We have highlighted such corroborating information above, where available. There is also some scope for mistakes and biases in the data, albeit constrained by the quality checks and analyses described above. The most obvious source of bias here is the independent selection of transect sites by volunteers, with the likely result that transects are close to where people live, and where they like to walk. Indeed, Table S2 shows there is a bias towards urban areas and away from semi-natural areas with high elevation and rainfall, a finding which is likely to be mirrored in other studies that rely on volunteers to collect data. Despite this bias, the scale and distribution of volunteer effort nevertheless covers a wide range of land system conditions, and provides a set of statistically robust findings. Further but relatively small additions to this effort could have substantial benefits, for instance in ensuring that observational habitat information is available for all records, and in extending the data over longer time periods to robustly detect impacts of changes in climate and land use.

Notwithstanding these caveats, our study also highlights the value of citizen science, showing how an unprecedented dataset can be built up and used in ways that would be difficult to replicate with traditional methods and research projects. The national-scale overview that we derive would not be possible using standard land cover and species presence-only datasets at either small or large scales. Instead, the combination of long-term citizen-science monitoring data with more established sources is especially powerful, notably in demonstrating the importance of adding field-level habitat information to remotely sensed land cover data. Perhaps most promisingly, the sense of engagement with scientific research that such a scheme engenders could pay important dividends in support of practical and political interventions to improve habitats for threatened species across our landscapes.

AUTHORS' CONTRIBUTIONS

P.R.W., C.B., B.S. and M.R. conceived the idea and designed the analysis; R.F.C. manages the citizen-science project and provided the bumblebee data; P.R.W., C.B. and B.S. analysed the data; P.R.W. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The full BeeWalk dataset is available on Figshare at https://figshare.com/articles/dataset/BeeWalk_dataset_2008-19/12280547 (Comont, 2020). The CORINE land cover data is available at https://land.copernicus.eu/pan-european/corine-land-cover and the climatic data used was HadUK-Grid Gridded Climate Observations on a 1 km grid over the UK, v1.0.2.1 (1862–2019), available at https://catalogue.ceda.ac.uk/uuid/89908dfcb97b4a28976df806b4818639. Finally, topographic data, SRTM (90 m), is available at https://cgiarcsi.community/data/srtm-90m-digital-elevation-database-v4-1/. Analyses code is available on Zenodo at https://doi.org/10.5281/zenodo.6496771 (Whitehorn et al., 2022).

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SUPPORTING INFORMATION

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