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Localised patterns of wild bee abundance indicate woodlands play multiple roles in supporting farmland populations

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Abstract

1. Higher woodland cover has been linked to increased wild bee abundance and diversity in temperate agricultural landscapes. However, our understanding of the roles played by the upper and lower strata of woodlands in supporting on-farm bees through spring and summer is lacking.
2. To explore these roles, we sampled bees (Anthophila) in deciduous woodland canopies and understories, and in an open habitat (at field margins), from May to July, at 12 sites across agricultural landscapes in Norfolk, England.
3. Before canopy closure in late spring, relative abundance in the two woodland habitats was generally higher, and canopies with flowering *Acer pseudoplatanus* L. supported more bees. However, throughout the season, open-habitat bee abundance was consistently higher closer to woodlands. After canopy closure, more open areas within woodlands were linked to greater bee abundance, except during a spike in temperatures when understory relative abundance was also at its highest.
4. These results indicate that deciduous woods on farmland provide floral resources to bees before canopy closure, which can be augmented with nectar-producing canopy trees. They also indicate that more open woodlands likely extend the availability of understory floral resources and that farmland woods, regardless of management, may continue to provide non-floral resources—including respite from hot weather—throughout the season.

KEYWORDS
bumblebees, canopy, floral resources, forest, nesting, patrolling, shade, temperate agricultural landscape, temperature, understory

INTRODUCTION

A significant proportion of global food production is dependent on insect pollinators (Siopa et al., 2024), and wild bees (Anthophila) are considered among the most important contributors (Potts et al., 2016). Within agricultural landscapes, this group depends on semi-natural habitats to provide nesting and dormancy sites and for the season-long provision of food (Cole et al., 2020). However, these habitats are under threat from agricultural intensification, and their loss is considered to be the primary cause of declines in wild bee abundance and diversity (Ollerton, 2017).

Wild pollinators tend to be more abundant and diverse at locations closer to semi-natural habitats and within landscapes with higher proportions of semi-natural habitat (Senapathi et al., 2017).

Woodlands and forests (used interchangeably here as an area of land, of any size, dominated by trees) are somewhat neglected in this field of study, but there is now increasing evidence that they can benefit wild bee communities in temperate regions (Alison et al., 2022; Ganuza et al., 2022; Ulyshen et al., 2023). For example, greater woodland cover has been shown to increase the abundance and/or diversity of wild bees in both North America (Collado et al., 2019; Pfeiffer et al., 2019; Smith et al., 2021; Watson et al., 2011) and Europe (Proesmans et al., 2019; Rivers-Moore et al., 2023; Sõber et al., 2020), while increasing proximity to forest has also been linked to higher abundance and/or richness of wild bees in crops (Bailey et al., 2014; Joshi et al., 2016). However, other landscape studies have shown forest cover and/or proximity have no effect (Mallinger et al., 2016; Schüepp et al., 2011) or even a negative effect on bee diversity and abundance (Kallioniemi et al., 2017; Winfree et al., 2007). Indeed, the composition of forests can be critical, with bee richness having a positive and negative relationship, respectively, with insect-pollinated tree diversity and the proportion of conifer trees (Traylor et al., 2024).

Experts consider that groups of trees on European farms provide some of the greatest resources for nesting bees among the habitats available (Cole et al., 2020), and bumblebee nests are frequently found in woodlands (Pugesek et al., 2024). This habitat may provide, for example, leaf litter, fallen logs and abandoned mammal burrows and other underground cavities, which can all be used for nesting (Mola et al., 2021; Pfeiffer et al., 2019; Urban-Mead et al., 2021). Although not widely considered, trees may facilitate mate-seeking for a range of bumblebee species by providing various structures favoured by scent-marking males, for example, at the base of trunks (e.g. *Bombus hortorum* L.) or in the high canopy (e.g. *B. terrestris* L. and *B. lapidarius* L.) (Bringer, 1973; Fussell & Corbet, 1992). Deciduous woodland could be a major source of forage for bees: in the United Kingdom, understory herbs and spring-flowering canopy trees, such as Sycamore (*Acer pseudoplatanus* L.), make woodlands one of the most nectar-rich habitats (Allen & Davies, 2023; Baude et al., 2016). Summer-flowering canopy trees, such as Sweet Chestnut (*Castanea sativa* Mill.), could also augment woodland nectar provision to bees (Larue et al., 2021), and there is considerable potential for improving current woodland floral resources with pollinator-friendly management (Cole et al., 2020). Finally, trees can also provide materials and substances for nesting and protection, as well as non-floral sources of nutrition, such as honeydew (Requier & Leonhardt, 2020).

The three-dimensional structure of deciduous woodlands provides a set of conditions which are unique among the semi-natural habitats of farmed landscapes. Before canopy closure, the woodland understory is exposed to sunlight (like non-woodland habitats throughout the season), but as the canopy closes in late spring/early summer, conditions become increasingly vertically stratified (Cunningham-Minnick et al., 2023). Accordingly, woodlands favour early-flowering plant communities, while open farmland habitats may provide a greater source of forage later in the season (Ammann et al., 2024; Cole et al., 2020). Furthermore, the springtime floral community of woodland understories is often different to that of non-woodland habitats (e.g. Timberlake et al., 2019), providing a distinct foraging resource for bees.

In summer, the largely shaded understory of dense woodlands provides generally unfavourable conditions for ectotherms, such as bees. Consequently, more open woodlands have been linked to higher numbers of summer-foraging bees (Hanula et al., 2016). Bees may avoid the understory of denser woodlands altogether, choosing instead to travel through or over the sunlit canopy when crossing woodlands (Ewers et al., 2013). However, bees, like other insects, may also take advantage of shaded understories to avoid overheating when foraging, patrolling, or travelling on particularly hot, sunny days (Sunday et al., 2014; Vives-Ingla et al., 2023). Thanks to their distinct physical structure, woodlands likely complement open habitats, increasing the range of available resources in both time and space. As such, we might expect bees to move frequently between open, understory and canopy habitats as supported, for example, by the gut-pollen analyses of Urban-Mead et al. (2023).

Studies that examine small-scale differences in bee activity within and between these habitats, and across the season, can help us to infer the role of each in supporting bee populations. Several have compared understory bee abundance with that of more open habitats (e.g., fields, field margins, woodland edges and woodland clearings). Considering overall abundance across the season, all sourced studies found that bee abundance was lower in the understory (Bartual et al., 2019; Ewers et al., 2013; Mandelik et al., 2012; Proctor et al., 2012; Roberts et al., 2017; Wagner et al., 2019). A similar pattern was found when considering bumblebee nest densities and nest-searching queens in Europe (Svensson et al., 2000; Osborne et al., 2008, but see O'Connor et al., 2017). However, some studies that explicitly examined springtime understory abundance found that it was equivalent to that of adjacent open habitats in spring (Allen & Davies, 2023; Mandelik et al., 2012). Studies comparing canopy with understory activity have produced mixed results, with canopy traps catching higher (Campbell et al., 2018; Ewers et al., 2013; Ulyshen et al., 2010, 2020), equal (Cunningham-Minnick & Crist, 2020; Urban-Mead et al., 2021) or lower (Allen & Davies, 2023; Bak-Badowska, 2012; Banaszak & Cierzniak, 1994) numbers of bees. Regarding temporal and spatial patterns of abundance, Urban-Mead et al. (2023) found springtime peaks in abundance in both the understory and canopy (contrasted with a summer-time peak for nearby orchards), while Allen and Davies (2023) found the canopy activity of bees was much higher when flowering *A. pseudoplatanus* trees were present.

In European studies investigating the effects of woodland on bee populations, sampling explicitly from woodland interiors, either from the understory or the canopy, is rare (for examples, see Allen & Davies, 2023; Bartual et al., 2019; Korpela et al., 2015). As such, we have little understanding of how European woodlands might function to support bees on farmland. Across all temperate regions, studies which examine changes in relative abundance between woodland understories and open habitats at different times of the year are largely lacking (for examples, see Mandelik et al., 2012; Proctor et al., 2012). To our knowledge, only a single study—on introduced *B. terrestris* in New Zealand—has investigated bee abundance in canopy, understory and open habitats (Ewers et al., 2013), and none have done so at multiple times of the year. Consequently, our understanding of how these habitats function to support bees in agricultural landscapes, and of their relative effects on bee activity, is severely limited.

Bee sampling in the canopy at scale necessarily entails the use of traps, and blue vane traps (BVTs) are particularly effective at sampling bee communities (Hall, 2018; Joshi et al., 2015). The area over which an individual trap is effective in attracting insects has not yet been studied (Mathis et al., 2024); however, the larger the potential sampling area, the more likely it is that trap catches will be biased downwards by nearby vegetational structures obscuring traps from view. Therefore, average trap catches between structurally distinct habitats cannot provide absolute measures of abundance for comparison. Rather, differences in patterns of relative abundance between different sampling periods can be informative. Additionally, locally abundant flowers reduce the relative attractiveness of traps, such that trap catches are not always proportional to local bee abundance (Mathis et al., 2024). We also consider that trap catches do not precisely reflect local abundance relating to other, non-foraging activities, such as nest searching and patrolling. Rather, traps are likely to attract travelling, forage-seeking bees that are not otherwise engaged in alternative behaviours. These considerations inform our predictions and the interpretation of results in the present study.

To gain insights into the role woodlands play in supporting wild bee activity on farmland, we sampled bees with BVTs from three distinct habitats—field margins, woodland canopies and woodland understories—within several UK agricultural landscapes, from late spring to mid-summer (before and after canopy closure). This enabled us to answer the following questions:

Q1. Is relative understory activity higher before canopy closure?
Q2. Is the activity in the two sun-exposed habitats (field margin and canopy) positively correlated?
Q3. Is understory activity higher under more open canopies?
Q4. Is canopy activity higher where nectar-producing trees are present?
Q5. Are trap catches higher closer to the woodland edge?

Additionally, we take advantage of differences in mean daily temperature between sampling events to examine the likelihood that bees respond by adjusting their relative use of open and shaded habitat. To accommodate a thorough exploration of these patterns, the present study is limited to the analysis of total bee abundance. We consider the potential mechanisms that best explain our results and what these indicate about the role of woodland habitats in supporting wild bees. We then highlight the implications for the creation and management of woodlands for farmland bee conservation.

METHODS

Sampling sites

A map-based search was conducted to identify privately owned Norfolk woodlands that are mature (majority of trees >20 m in height: Lidar maps from Norfolk Trees and Hedges (2022)), deciduous (identified from Natural England's Priority Habitat Inventory) and bordered by arable farmland. Following inspections, some were rejected as candidates as they had uniquely structured understories dense with Cherry laurel bushes (*Prunus laurocerasus*), specifically planted to provide game cover. In the remaining sites, *A. pseudoplatanus* was frequently present, and the final 12 sites were selected to ensure a near-even balance between its presence (seven sites) and absence (five sites), with each interspersed across the study area. *Castanea sativa* was less frequently present, and its presence at five sites was interspersed across the study area to a lesser degree (Figure 1). Woodlands were all managed under the UK government's English Woodland Grant Scheme, and the smallest was 1.6 ha (Table S1). Most had undergone some tree thinning and contained tracks for vehicular access. All woodlands provided understory floral resources, though their abundance and type varied considerably across sites. The following understory plants (ordered from earliest to latest flowering) were in flower in some or most of the woodlands in high abundance during sampling: *Hyacinthoides non-scripta* (L.) Chouard ex Rothm, *Glechoma hederacea* L., *Stachys sylvatica* L. and *Rubus* spp. (see Figure S1 for Family-level abundance).

The sites clustered into two regions, 'West' and 'South-east' Norfolk, separated by 23 km (Figure 1). Within each region, sites were separated from their nearest neighbour by no less than 500 m (a compromise to ensure adequate site independence, commonly considered to be fully achieved at 1 km, under logistical considerations and limited site availability). All woodlands bordered arable land, with six additionally bordering pasture and three bordering dwellings. This land was under various management schemes, from the most common to the least: Middle Tier Countryside Stewardship, Higher Tier Countryside Stewardship, no agri-environment scheme and Entry Level plus Higher Level Environmental Stewardship.

Bee sampling regime

BanfieldBio™ BVTs were used to catch bees. These can effectively sample the bee community, especially bumblebees, and their design is well suited to canopy sampling (Allen & Davies, 2023). Traps were partially filled with water to euthanise and store specimens. Woodlands were sampled at three to five trapping locations, depending on their size and ease of traversal, for an average of four locations per woodland. For unbiased selection of canopy trap locations, areas of mature (>20 m height) deciduous woodland were searched for the first available tree with suitable crown branches for rigging, while constraining inter-trap distance to between 60 and 90 m. Additionally, locations were selected such that at canopy height, traps were surrounded by tree crowns in all directions within a 10 m radius, thereby reducing variation in long-distance visibility. Otherwise, canopy trap locations were random with respect to the surrounding tree species. A Bigshot® slingshot with a weighted throwline was used to rig rope to which traps were attached to be raised into the canopy. Traps were set towards the edge of tree crowns within the top third of the total tree height (i.e., at >13.5 m in height).

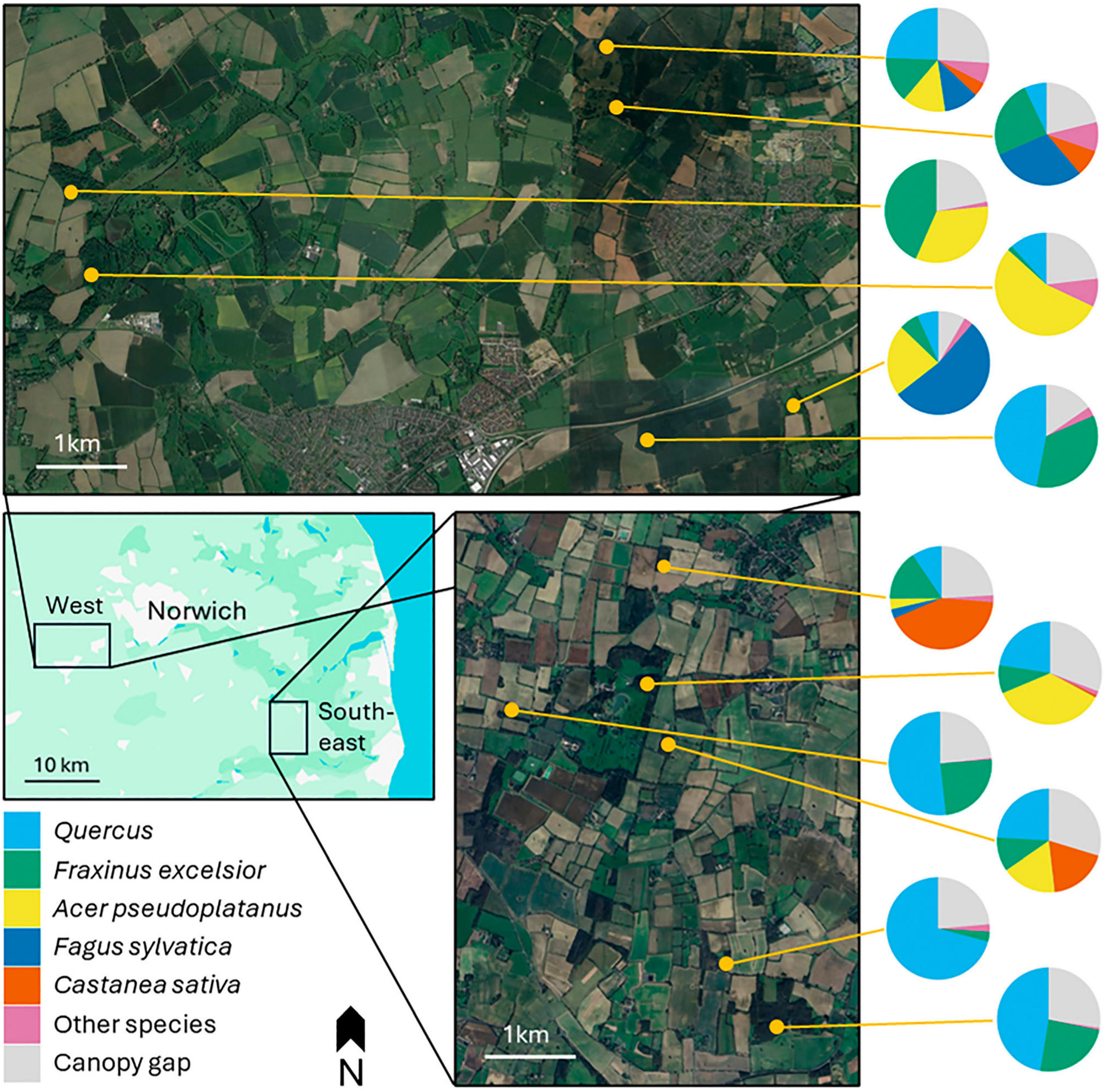

FIGURE 1 The two study regions in Norfolk, UK: 'West' and 'South-east'. The percentage areal extent of the crowns of each tree species within each woodland site (orange circles) is displayed (for further details, see Appendix S2). *Source*: Image ©2024 Google, annotations by G. Allen.

Understory traps were set in the same locations, each beneath its corresponding canopy trap. Adjacent to each woodland, two traps, separated by 60 m, were set at a nearby hedged field boundary. In both habitats, traps were set at a height of ca. 0.8 m, with field margin traps at 0.5 m distance from the boundary–hedge on its southern side. Field margin trap locations were further standardised at nine sites, sharing features of potential relevance to bees travelling to and from woodlands: (1) traps were positioned at 60 and 120 m, respectively, from the woodland (and no less than 120 m from other woodlands); (2) they were facing an arable field of a non-insect-attractive crop and (3) they were visible from the woodland edge with no hedgerows blocking potential flight paths. This standardisation was not possible for the remaining three sites, however, and so these were excluded a priori from the analysis specific to variables influencing field margin trap catches.

BVTs were set over four sampling periods in 2022: the first, 5–11 May ('early May'); the second, 26–30 May ('late May'); the third, 15–18 June ('mid-June') and the fourth, 11–16 July ('mid-July'). As such, we sampled in late spring (May) and summer (June/July) both before and after canopy closure, which occurred towards the end of May. Weather forecasts were monitored to ensure sampling periods coincided with suitable weather for bees (mostly dry and sunny; minimum daily temperature high of 14°C; maximum windspeeds of 7.5 m s^{-1}). For each sampling period, traps were set, one woodland site at a time, over 2 days (1 day per region). Because bee numbers vary temporally, depending on weather and life-cycle stage, trap deployment lengths were allowed to vary across sampling periods to ensure appropriate and approximately equal numbers (aiming for 5–10 bees at monitored ground-level traps) were caught in each period. Despite this effort, however, unexpectedly high numbers of bees were caught in late May, and bees were slightly under-sampled in mid-June. At the end of each deployment, traps were removed over a period of 2 days following the same site order in which they were set. Thus, within each sampling period, all traps were deployed for approximately the same number of hours (ca. 120, 76, 48 and 96, respectively), and traps within each site were deployed over the same period of time (and, hence, weather conditions). Note that one canopy trap and one understory trap failed in mid-June and mid-July, respectively.

Weather records were taken from the nearest available location (Norwich Weather Centre) to the sampling sites (Past Weather, Norwich, May to July, 2022). Average temperature was calculated from hourly records between 06:20 and 20:20 over the complete sampling days for each region in each period. All bee specimens were pinned and stored, with tags linking specimens to their samples. *Bombus* specimens were identified to species by the lead author using Falk (2015). To inform interpretations of total bee abundance patterns across sampling periods, the contributions of the five most common species are presented, and total bee abundance is summarised by major taxa and *Bombus*-caste.

Understory and canopy measures

During each sampling period, ground floral cover was estimated across a 100 m^2 quadrat centred on each ground-level trap (variable: *floral index*); for further details, see Appendix S1. In each woodland, the canopy tree species composition was estimated over the area (2800–5200 m^2) of bee sampling (Figure 1), and from this, the site-level presence or absence of *A. pseudoplatanus* and *C. sativa* was determined for use in analyses (factors *Sycamore* and *Chestnut*, respectively). Observations of site trees with readily visible areas of potential crown flowering indicated that during early May, most *A. pseudoplatanus* trees were in flower; in late May, relatively few *A. pseudoplatanus* trees were in flower; in mid-June, no nectar trees were in flower and in mid-July, *C. sativa* trees were flowering. For further details on canopy measurements, see Appendix S2.

The variable *canopy openness* (%) was measured before and after canopy closure, in early and late May, respectively, using a densiometer and taking the average light-gap reading from four cardinal directions at the location of each understory trap. Densiometer readings were taken again in mid-June wherever *Fraxinus excelsior* trees were present, the only species which had not fully opened its leaves by late May. Otherwise, since canopy cover varies little after canopy closure, the remaining understory locations in mid-June were assigned canopy-openness values equal to those measured in late May, while mid-July values were equal to those of mid-June. Additionally, the distance of each understory trap to the closest woodland edge (variable: *edge distance*) and to the nearest clearing (defined as canopy gaps with a minimum width of 6 m and area of 50 m^2; variable: *clearing distance*) were recorded.

Statistical analyses

Analyses were conducted in R, version 4.3.2. All modelled variables are summarised in Table 1. Models were run on four datasets: (1) all habitat traps, (2) understory traps, (3) canopy traps and (4) field margin traps (Table 2). To aid model interpretation, datasets were divided by sampling period, except for the field margin trap dataset, whose corresponding model was readily interpretable with all periods together. In all models, *site* was included as a random intercept to account for the non-independence of traps within the same site. Models were initially fitted with a Poisson distribution and, in all but one case, re-fitted with a negative binomial distribution using the function *glmmTMB* (family *nbinom2*) from the glmmTMB package (Brooks et al., 2017) after detecting significant, or near-significant, overdispersion with the *check_overdispersion* function in the package 'performance' (Lüdecke et al., 2021). All selected models were tested for diagnostic issues and spatial autocorrelation using the packages DHARMa (Hartig, 2024) and 'ncf' (Bjornstad, 2022), respectively. No model had significant diagnostic issues or spatial dependence of its residuals (see Appendix S3 for further details).

Continuous variables were log-transformed to ensure a more even spread of values across the range of each (Table 1). None were strongly inter-correlated: the maximum Pearson's correlation, between *floral index* and *canopy openness* in early May, was 0.53 (Figure S3). For the analyses of understory, canopy and field margin traps, respectively, global models were first constructed, containing all potentially influential variables (Table 2). All possible model subsets of these variables were ranked by AIC with the function *dredge* from the MuMIn package (Bartoń, 2025). Important variables were determined using summed Akaike weights (function *sw*) with a minimum threshold of 0.6. The lowest AIC model that contained all variables of importance *and* met all the diagnostic criteria outlined above was selected in each analysis (see Appendix S4 for further details and Tables S3–S5 for top-ranking models). The significance of each variable in selected models was determined with likelihood ratio tests. Pseudo R^2 values were obtained using the r2 function from the package 'performance' (Lüdecke et al., 2021).

Comparing trap catches between habitats (Q1 and Q2)

Models 1–4 (Table 2) were run to examine patterns of activity across habitats and across the season. An interaction with *region* was included to account for the potentially distinct effect of a given habitat under distinct weather conditions. Post hoc Tukey tests were performed (package emmeans: Lenth, 2025) to identify pair-wise differences between habitats within each region. To aid visual

TABLE 1 Summary of all variables modelled.

Variable	Description	Number of levels (categorical variables/ grouping factors)	Transformations (continuous variables)
region	Geographical/temporal clustering of sites/sampling.	2 (West, South-east)	
site	Discrete areas which include woodland and field margin traps.	12 (9 for field margin model)	
habitat	Distinct habitats in which traps were placed.	3 (field margin, understory, canopy)	
floral index	Floral cover at each ground-level trap.		$\text{Log}_{10} + 1$
Sycamore	Presence of *Acer pseudoplatanus* in woodland canopy.	2 (present, absent)	
Chestnut	Presence of *Castanea sativa* in woodland canopy.	2 (present, absent)	
canopy openness	% canopy openness at each understory trap.		Log_{10}
edge distance	Distance to the nearest woodland edge from each understory trap.		Log_{10}
clearing distance	Distance to nearest woodland clearing from each understory trap.		Log_{10}
wood proximity	Distance of field margin traps to the woodland edge.	2 (60 m, 120 m)	
trap location	Field margin trap location.	18	
period	Sampling period.	4 (early May, late May, mid-June, mid-July)	

TABLE 2 Summary of dataset groups and their corresponding global models. PI, PII, PIII and PIV represent the sampling periods in early May, late May, mid-June and mid-July, respectively.

Grp no.	Dataset	Mod no.	Global model equation (R notation)	*n*
1	PI:all habitat traps	1	Trap catch ~ *region*habitat* + (1 | *site*)	120
	PII:all habitat traps	2	As above	120
	PIII:all habitat traps	3	As above	119
	PIV:all habitat traps	4	As above	119
2	PI:understory traps	5	Trap catch ~ *region* + *canopy openness* + *edge distance* + *clearing distance* + *floral index* + (1 | *site*)	48
	PII:understory traps	6	As above	48
	PIII:understory traps	7	As above	48
	PIV:understory traps	8	As above	47
3	PI:canopy traps	9	Trap catch ~ *region* + *canopy openness* + *edge distance* + *clearing distance* + *Sycamore* + (1 | *site*)	48
	PII:canopy traps	10	As above	48
	PIII:canopy traps	11	Trap catch ~ *region* + *canopy openness* + *edge distance* + *clearing distance* + (1 | *site*)	47
	PIV:canopy traps	12	Trap catch ~ *region* + *canopy openness* + *edge distance* + *clearing distance* + *Chestnut* + (1 | *site*)	48
4	PI–PIV:field margin traps	13	Trap catch ~ *period*region* + *period*wood proximity* + *floral index* + (1 | *site* / *trap location*)	72

comparison of relative activity patterns between region–period pairings, model-estimated means were plotted relative to understory estimates (which were set to zero). Finally, the relationship, relative to understory estimates, between field margin and canopy estimates after canopy closure (from late May, $n = 6$) was tested using Spearman's rank correlation.

Variables influencing woodland understory and canopy activity (Q3, Q4 and Q5)

Models 5–8 and 9–12 (Table 2) were run to examine influences on activity within woodland understories and canopies, respectively. For the canopy-trap models, *canopy openness* was included to control

TABLE 3 Summary of catches in each sampling period of the five most common species sampled across the season.

Period	*Bombus pratorum* L.	*Bombus pascuorum* Scop.	*Bombus hortorum* L.	*Bombus terrestris* L.	*Bombus lapidarius* L.	Total bee specimens
Early May	119 (**24**)	95 (19)	23 (4.7)	23 (4.7)	39 (7.9)	493
Late May	614 (**42**)	103 (7.1)	199 (14)	91 (6.2)	70 (4.8)	1457
Mid-June	130 (**39**)	49 (15)	34 (10)	21 (6.3)	23 (6.8)	336
Mid-July	33 (6)	57 (10)	38 (6.9)	84 (15)	86 (**16**)	547
Total	896 (**32**)	304 (11)	294 (10)	219 (7.7)	218 (7.7)	2833

Note: Percentages of total bee specimens are in parentheses, with the largest for each period in bold.

for sampling bias related to the visibility of canopy traps to bees flying in or over the canopy, rather than as a variable of biological interest. *Sycamore* and *Chestnut* were additionally included in canopy models only during periods which coincided with their flowering (i.e., early and late May for *Sycamore* and mid-July for *Chestnut*). Finally, to rule out the potential (but unlikely: Allen & Davies, 2023) scenario that canopy traps merely attract a random subset of bees from the understory, understory trap catches were added post hoc as a predictor to all selected canopy models. No evidence of understory influence was found (minimum p ($>|z|$) value returned was 0.23).

Variables influencing field margin trap catches (Q5)

Model 13 (Table 2) was run to examine influences on field margin trap catches. A *period* × *wood proximity* interaction was included to account for potential differences in woodland influence throughout the season and a *period* × *region* interaction was included to account for the potentially inconsistent effect of a region depending on the weather it experiences in a given period. Finally, *trap location* was included as a random intercept (nested within *site*) to account for the repeated measures.

RESULTS

A total of 2833 bees were caught across the four sampling periods. Mean trap catch was 5.9 (±SE 0.47) with a minimum of zero and a maximum of 126. *Bombus pratorum* L. was the most abundant species from early May to mid-June (Table 3), while *Apis mellifera* L. was most abundant in July (Table 4). Preliminary examinations of solitary bee specimens indicate they belong to a large range of species with no single species dominating.

Habitat trap catches in each sampling period (Q1 and Q2)

In early May, before canopy closure, understory catches were equivalent to field margin and canopy catches in both regions (Figure 2A). From late May, after canopy closure (Figure 2B–D), field margin catches were significantly higher than understory catches in four of the six region–period pairings, and canopy catches were significantly lower than understory catches in five of the pairings. After canopy closure, field margin and canopy estimates, relative to the understory, have a strong and significant positive correlation ($r_{s4} = 0.89$, $p < 0.05$, Figure 3). Additionally, within each of these three periods, relative field margin and canopy estimates are consistently highest in the region with the lowest temperature (Figure 3). Most notably, the lowest field margin estimate relative to the understory occurs in the hottest region–period pairing (Figure 2C, South-east: 5+°C higher than the others).

Variables influencing understory activity (Q3 and Q5)

In early May, understory catches significantly decrease as canopy openness increases (Table 5; Figure 4A). In late May and mid-July, however, understory catches significantly increase with increasing canopy openness (Table 5: Figure 4B,D), while in mid-June, there is no evidence for an effect of canopy openness (Table 5; Figure 4C). There is some evidence, later in the sampling season, that understory catches are higher closer to the woodland edge, although this effect is only significant in mid-July. However, there was no evidence for an effect of floral availability or for an effect of clearing proximity during any sampling period (Table 5).

Variables influencing canopy activity (Q4)

In early May, when most *A. pseudoplatanus* trees were flowering (see the 'Methods' section), canopy catches were significantly (1.95×) higher in woodlands in which this species was present (Table 6; Figure 5). However, there was no evidence for this effect in late May (when fewer trees were flowering) (Table 6). Similarly, there was no evidence for an effect of *C. sativa* presence during its period of flowering in mid-July (Table 6). Increasing canopy openness significantly increased canopy catches in early May (Table 6; Figure 5) and mid-July (Table 6). However, there was no evidence for this effect in late May or mid-June (note that low catches in mid-June may have precluded the detection of significant effects: Table 6). Finally, there was no evidence for an effect of proximity to the woodland edge or to clearings in any sampling period (Table 6).

TABLE 4 Summary of all catches in each sampling period according to taxonomic group and bumblebee caste.

Period	*Bombus* queens	Social *Bombus* males	*Bombus* workers	Parasitic *Bombus*	Solitary bees	*Apis mellifera* L.	Total bee specimens
Early May	148 (**30**)	5 (**1.0**)	160 (**32**)	4 (**0.8**)	174 (**35**)	2 (**0.4**)	493
Late May	83 (**5.7**)	330 (**23**)	752 (**52**)	82 (**5.6**)	180 (**12**)	30 (**2.1**)	1457
Mid-June[a]	20 (**6.0**)	44 (**13**)	215 (**64**)	15 (**4.5**)	32 (**9.5**)	9 (**2.7**)	336
Mid-July	19 (**3.5**)	84 (**15**)	207 (**38**)	24 (**4.4**)	112 (**20**)	101 (**18**)	547

Note: Percentages are in bold and in parentheses.

[a] The caste of one female *Bombus* specimen in mid-June could not be determined.

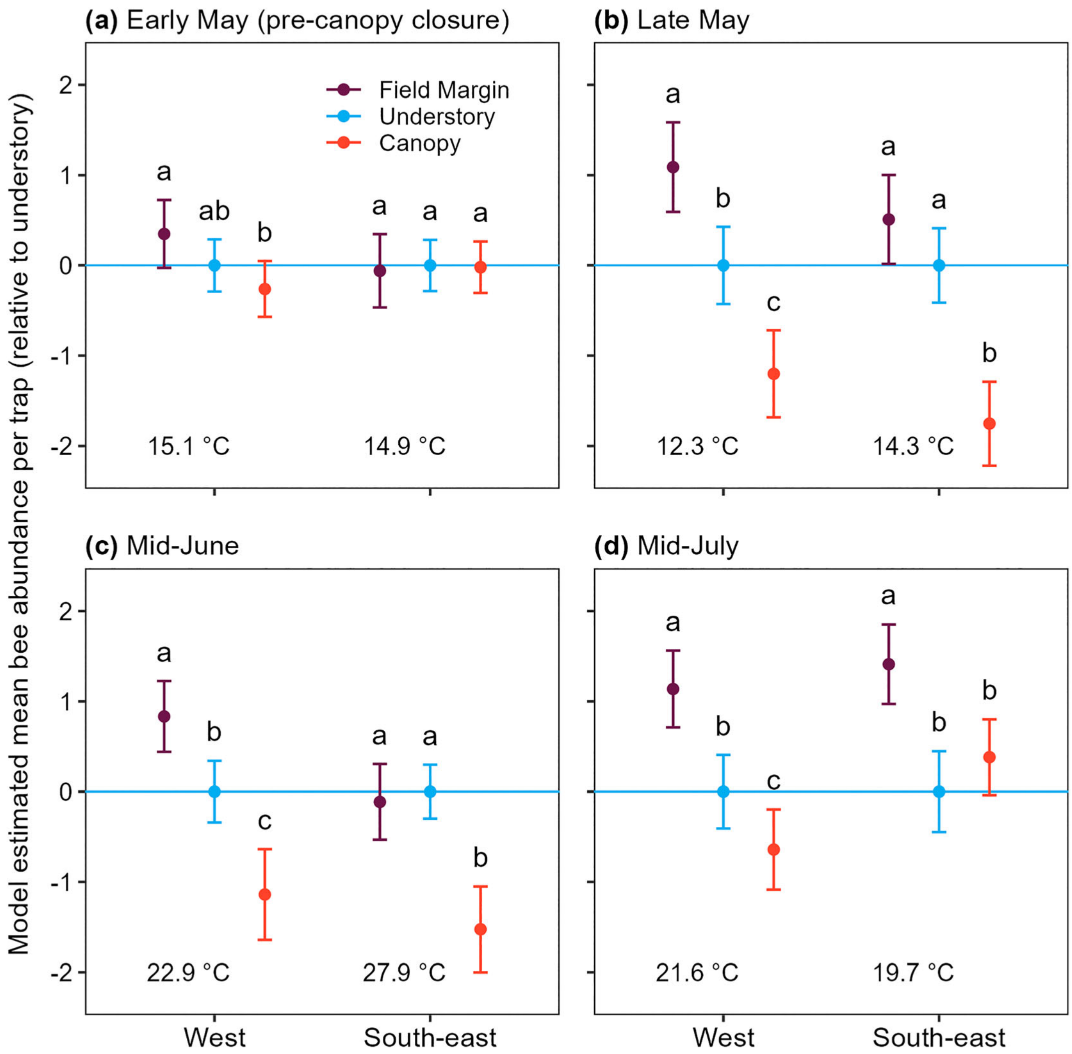

FIGURE 2 Relative model estimated mean bee abundance per trap (log scale) in field margin, understory and canopy habitats at sites across two regions (West and South-east Norfolk, UK) over four sampling periods (A–D). Model estimated means are plotted relative to the understory to aid comparisons of relative activity patterns between pairings of region and period. Error bars represent 95% confidence intervals. Letters (a–c) denote significant ($p < 0.05$) differences between estimated trap catches *within* region–period pairings according to post hoc Tukey testing. Average temperature over full sampling days for each region–period pairing is displayed.

Variables influencing field margin trap catches (Q5)

Bee catches were significantly (1.80×) higher in traps placed closer (60 m) to woodlands than those placed further away (120 m) (Table 7). There was no significant *period* × *wood proximity* interaction; that is, the proximity effect was consistent across the sampling periods (Figure 6A–D). There was also no evidence for an effect of floral availability (Table 7).

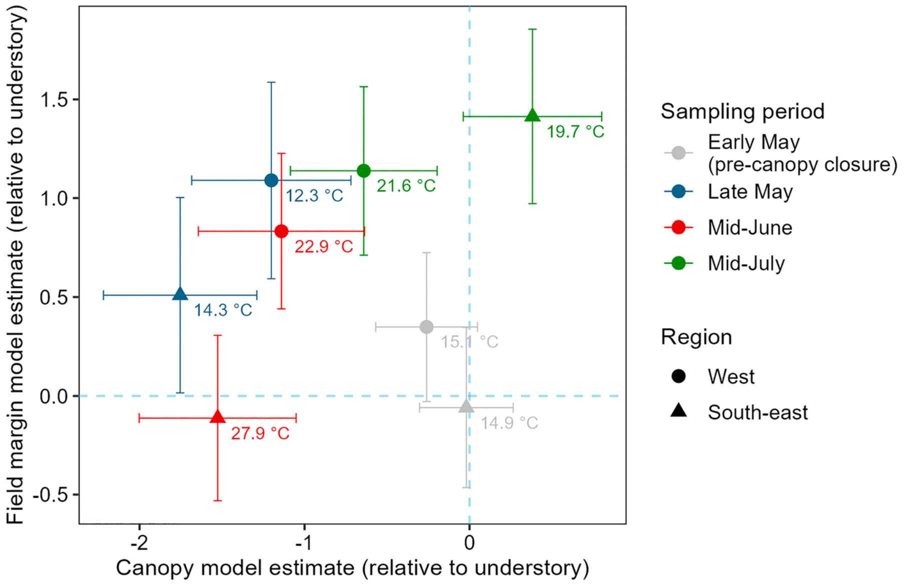

FIGURE 3 The relationship between field margin and canopy model estimated mean bee abundance per trap (log scale), relative to the understory, before and after canopy closure (grey and coloured circles, respectively). Equal abundance per trap across all habitats is represented where the dashed lines cross. Estimates are from two regions (West and South-east) in Norfolk, UK, and average temperature over full sampling days for each is displayed. Error bars represent 95% confidence intervals of model estimates.

TABLE 5 Variables included in global models of understory trap catches of bees in each sampling period prior to model selection.

		Variable in understory global model					
	Total bee count	*region*	*canopy openness*	*edge distance*	*clearing distance*	*floral index*	Marginal R^2
Early May	200	0.31	−0.60*				0.15
Late May	625	0.65**	0.96**				0.51
Mid-June	172	0.40		−0.85			0.22
Mid-July	149	−1.05***	0.79**	−0.96*			0.43

Note: Variables in selected models (see the 'Methods' section for selection procedure) are represented by their parameter estimate, with significance levels according to likelihood ratio tests: ***$p < 0.001$, **$p < 0.01$ and *$p < 0.05$.

DISCUSSION

In this study, we found that relative activity in woodlands was generally highest before canopy closure, while woodlands continued to attract bees throughout the season. Woodlands with nectar-producing trees attracted more bees to the canopy in spring, but patterns of abundance across all habitats after canopy closure suggest that subsequent canopy activity was largely the result of bees avoiding the shaded understory. Additionally, while our results indicate that conditions are improved for bees under more open canopies, they also suggest that shaded understories may provide protection from hot weather.

Bombus pratorum was the most abundant species from May to June (Table 3) and likely had the most influence of any one species on patterns of total abundance over this period. However, it was outnumbered by solitary bees during the period of *A. pseudoplatanus* flowering in early May, while *A. mellifera* and four other *Bombus* species were more common in July (Tables 3 and 4). Moreover, we present patterns that remain constant despite changes in *B. pratorum* relative abundance (Figures 4B,D and 6A–D), in addition to contrasting patterns when its relative abundance changes little (Figure 4B,C). Given this, findings cannot be explained solely in terms of this species' relative abundance, and we believe they could apply to a variety of generalist, *Bombus*-dominated bee communities across similar study systems, that is, across temperate, arable farmland that incorporates discrete areas of deciduous woodland.

Early season woodland activity

Before canopy closure, we found that bee catches in woodland understories were equivalent to those of field margins (Figure 2A), while after this, understory relative abundance tended to decrease (Figure 2B–D). Similarly, Mandelik et al. (2012) found understory abundance to be only marginally lower than that of open fields in spring but not summer, while Allen and Davies (2023) found trap

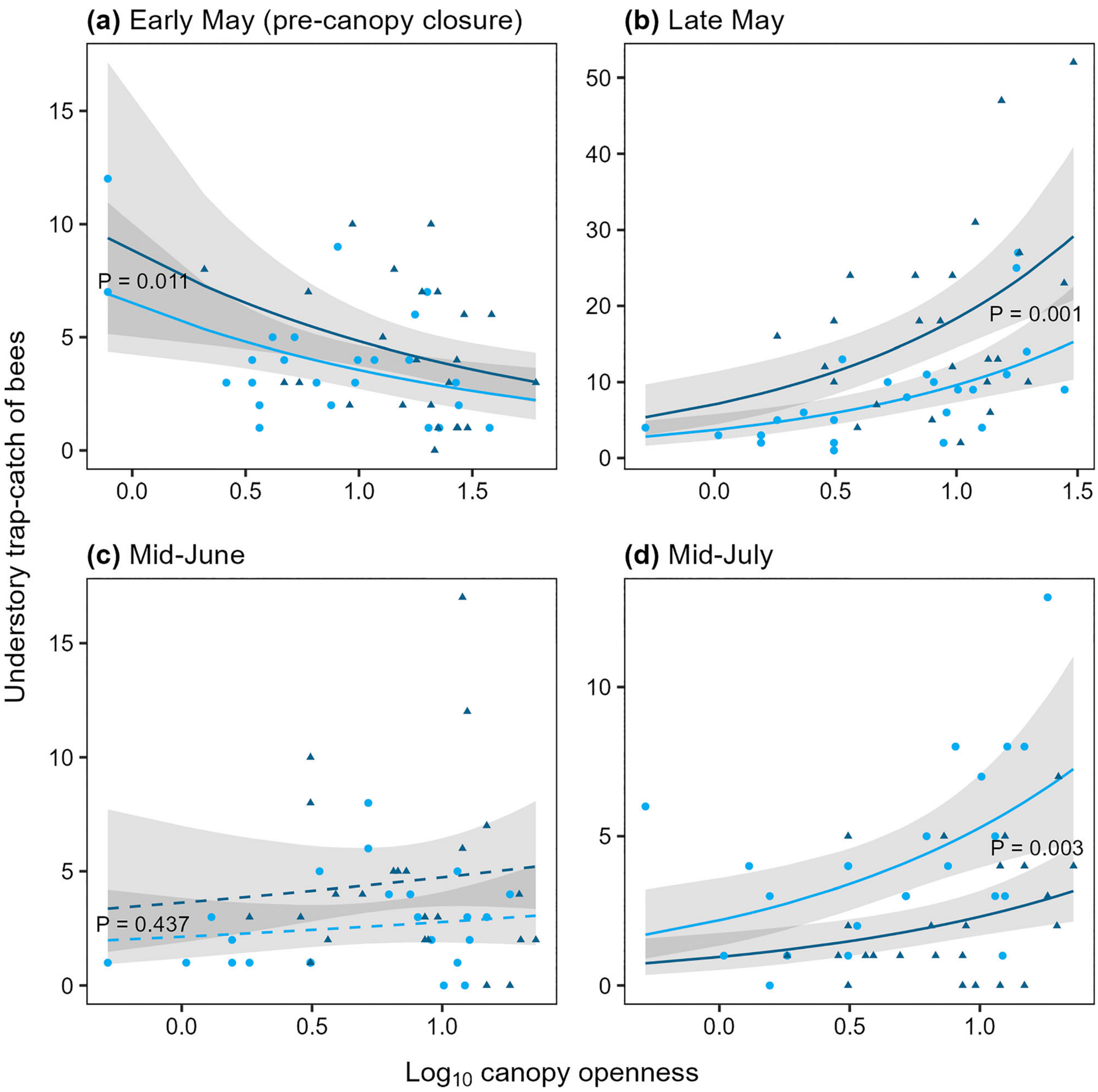

FIGURE 4 Understory trap catches of bees against canopy openness in two regions (West: Light blue circles and South-east: Dark blue triangles) over four sampling periods (A–D). Estimates from GLMMs comprising these two variables (with no interaction) are displayed: Solid lines represent a significant relationship with canopy openness and dotted lines represent a non-significant relationship, with the corresponding likelihood ratio test *p* values also displayed. Grey bands represent 95% confidence intervals.

catches of bees to be equivalent at exposed woodland edges and interior understories in late spring. The lower shading of understories, pre-canopy closure, can provide more favourable conditions for the activity of foraging ectotherms, such as bees (Hanula et al., 2016). However, at this point in our study, understory shading was still considerably higher than that of field margins; mean canopy openness was just 16% (see Figure 4A for log$_{10}$ values), while field margins and their surrounds were generally unshaded. This would imply a potential energetic cost to activity in the understory, even before full canopy closure.

Woodlands can provide distinct and abundant understory floral resources in spring (Ulyshen et al., 2023), and in the present study, Lamiaceae, Asparagaceae and Amaryllidaceae were abundant in some woodlands in early May (Figure S1). Such floral resources can provide significant quantities of nectar (Baude et al., 2016) and may attract bees despite the potential energetic cost of foraging in the shade. Woodlands can also provide ample nesting opportunities for spring-emerging bumblebee queens (Mola et al., 2021). In our study, queens were proportionally much more common in early May than in subsequent periods (Table 1), which, if they were nest-searching in

TABLE 6 Variables included in global models of canopy trap-catches of bees in each sampling period prior to model selection.

		Variable in canopy global model						
	Total bee count	*region*	*canopy openness*	*edge distance*	*clearing distance*	*Sycamore* (present/absent)	*Chestnut* (present/absent)	Marginal R^2
Early May	176		0.74**			0.67** (present)	*n/a*	0.34
Late May	140						*n/a*	
Mid-June	43					*n/a*	*n/a*	
Mid-July	133		1.18**		−0.86	*n/a*		0.39

Note: *Sycamore* and *Chestnut* were only included during the species' corresponding flowering periods (otherwise, they are denoted *n/a* not applicable). Variables in selected models (see 'Methods' for selection procedure) are represented by their parameter estimate, with significance levels according to likelihood ratio tests: ***p < 0.001, **p < 0.01 and *p < 0.05.

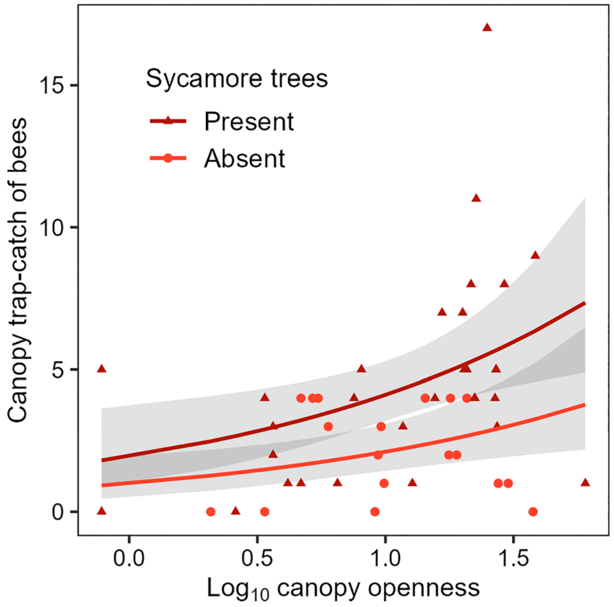

FIGURE 5 Canopy trap-catches of bees against canopy openness in woodlands in which *Acer pseudoplatanus trees* were either present (dark red triangles) or absent (light red circles) in early May. Model estimates are displayed (solid lines) with 95% confidence intervals in grey.

woodlands to a significant degree, could partly explain the relatively high understory abundance of bees at this time. Furthermore, being larger than other castes, queens are better able to retain heat under cooler conditions. As such, they may have contributed to the lack of a positive relationship between canopy openness and understory bee abundance (Figure 4A). We do not, however, have a satisfactory explanation for the significant negative relationship found between these variables at this time.

We found that canopy trap-catches, relative to those of the other habitats, were generally higher in early May than in later periods (Figure 2). Although decreasing trap visibility after canopy closure may contribute to this pattern, it seems likely that bees were actively exploring the canopy in the earliest sampling period. Indeed, we found that canopy abundance was significantly higher in woodlands that had *A. pseudoplatanus* crowns in the canopy layer (Figure 5). This species provides quality forage for bees (Somme et al., 2016); its pollen can comprise up to a third of the diet of *B. terrestris* in spring (Kämper et al., 2016); and it has previously been shown to increase bee abundance in interior woodland canopies (Allen & Davies, 2023). Additionally, *Quercus* and *Fagus* produce pollen at this time, which is collected by several common UK solitary bee species (Saunders, 2018). Together, these trees were present in the canopies of 11 of the 12 sampled woodlands (Figure 1), while solitary bees made up 35% of the early May bee sample (Table 1); foraging from wind-pollinated trees could, therefore, partly explain the relatively high canopy activity at this time.

Woodland activity after canopy closure

By late May, canopy closure was nearly complete, understory shading had increased, and understory floral availability had decreased, while that of field margins remained high (Figure S2). Additionally, the bee community had become more forage-focused, with bumblebee workers making up a larger proportion of total bees after canopy closure (Table 1). These factors likely explain the general decrease in understory abundance relative to that around field margins between early May and the subsequent periods. Other temperate-region studies have compared understory bee abundance with that of more open habitats by pooling data across the season. In these, understory abundance was found to be much lower than that of woodland edges (Bartual et al., 2019), adjacent grasslands (Ewers et al., 2013) and forest clearings (Wagner et al., 2019).

After canopy closure and relative to the understory, abundance in the two more sun-exposed habitats—canopy and field margin—was significantly and positively correlated (Figure 3). This suggests that, after canopy closure, canopy activity may have largely been a function of understory avoidance. Similarly, Ewers et al. (2013) found that *B. terrestris* abundance was high in both open grasslands and resource-poor forest canopies but low in the understory, concluding that bees

TABLE 7 Variables included in global models of field margin trap catches of bees across all sampling periods prior to model selection.

	Variable in field margin global model						
Total bee count	*period* × *region*	*period* × *wood proximity*	*period*	*region*	*wood proximity* (60 m/120 m)	*floral index*	Marginal R^2
920			X***		−0.59** (120 m)		0.67

Note: Variables in the selected model (see 'Methods' for selection procedure) are represented by their parameter estimate where possible (otherwise an *X*), with significance levels according to likelihood ratio tests: ***p < 0.001 and **p < 0.01.

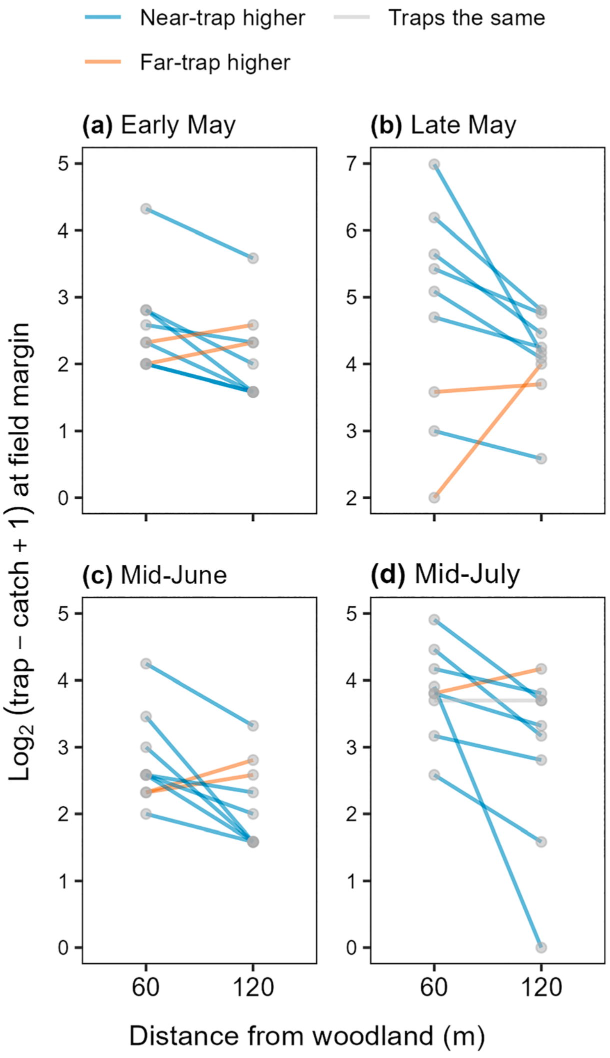

FIGURE 6 Field margin trap catches at two distances from woodland over four sampling periods (A–D). Lines connect traps from the same site and are coloured according to which trap—near or far from woodland—has the highest catch.

took advantage of the higher light levels in the canopy while commuting between non-forest food resources. Considering whole bee communities, the choice to fly in/over the canopy could be influenced by the degree of understory shading and floral resource availability, the ambient temperature, and the bee species or caste in question, leading to a range in the likelihood of canopy activity across the season (Figure 3).

Despite decreases in relative woodland activity after canopy closure, our results indicate that woodlands continued to be utilised by bees throughout the season: field margin traps placed closer (60 m) to woodlands consistently caught more bees than those placed further away (120 m) (Figure 6A–D). If bees commute back and forth from woodlands, the density of individuals in the surrounding open habitat will be highest at locations closest to woodland. This, combined with traps that may attract bees over several tens of metres, could lead to the observed patterns. Similarly, previous temperate-region studies have found that the abundance of wild bees in crops increases with proximity to forests within 200 m (Bailey et al., 2014; Joshi et al., 2016).

After canopy closure, understory flowers were available in some woodlands (and utilised by bees: observations by GA), albeit at low and declining abundances (Figure S2). However, the consistency of the woodland proximity effect suggests that it was driven by more stable resources than these. Nesting in woodlands could be one such driver: nests of European bumblebees are frequently found in this habitat (Pugesek et al., 2024), although other studies indicate nesting is less common within woodlands than at woodland edges and field margins (Osborne et al., 2008; Svensson et al., 2000). The utilisation of woodlands by mate-seeking bumblebee males is another potential driver. *Bombus lapidarius and B. terrestris* are known to patrol tree tops and hedges, while *B. pratorum* patrols vegetation closer to the ground, and *B. hortorum* visits the bases of tree trunks (Bringer, 1973; Fussell & Corbet, 1992). Indeed, in a previous study, the woodland sex ratios of these latter two species were found to be skewed towards males in the understory relative to the canopy (Allen & Davies, 2023).

If woodlands attract bees from open habitats, understory traps placed closer to the woodland edge would be more likely to catch bees commuting between these habitats. However, we only observed a significant effect of this in the final sampling period (Table 2). Alternatively, in order to efficiently exploit both woodland and open habitats, we might expect woodland foraging, patrolling and nesting activities to be more concentrated towards the woodland edge. Besides being where bees switch between ground-level habitats, the exposed woodland edge may itself provide a unique and beneficial habitat for both bumblebees (Kells & Goulson, 2003) and solitary bees (Proesmans et al., 2019), which could contribute to the patterns observed, both in the understory and at field margins.

In common with North American studies (Chase et al., 2023; Urban-Mead et al., 2021), we found that understory abundance increased with canopy openness (in two out of the three sampling periods after canopy closure: Figure 4). A review of pollinator conservation in North American forests found that more open forests are linked to higher understory temperatures, light levels, floral resources and, hence, bee abundance (Hanula et al., 2016). In our study, floral availability was significantly correlated to canopy openness in all sampling periods (Figure S3); however, it had no relationship with understory (or field margin) trap catches (Tables 5 and 7). The distracting effect of flowers may preclude such a relationship from occurring (Mathis et al., 2024); indeed, on several occasions during sampling, GA observed multiple bees foraging in close proximity to traps with low catches. However, considering the relationships among floral availability, canopy openness and understory trap catches together, our results indicate the summer-foraging potential of woodlands with more open canopies, which favour both increased floral resources and increased bee activity.

In the canopy, we found no effect of flowering *C. sativa* on bee abundance in mid-July. This species has been studied outside woodlands and is known to attract bumblebees and solitary bees (Larue et al., 2021). Given that bees were active in the canopy in mid-July (Table 3), foraging at *C. sativa* flowers could be expected. However, only two of the five sites in which *C. sativa* was present had it in appreciable quantities (>10% canopy coverage) compared to six out of the seven sites with *A. pseudoplatanus* (Figure 1); thus, replication was probably only sufficient to detect an effect of the latter species.

Temperature effects

Exposure to sunshine greatly increases the operative body temperatures of insects (Sunday et al., 2014), and flying insects can easily move between shaded and exposed habitats to maintain optimum operative temperatures as ambient temperatures change (Shreeve, 1984; Slamova et al., 2011; Vives-Ingla et al., 2023). Such dynamics could explain a pattern in our data: within each period after canopy closure, understory abundance, relative to the more sun-exposed habitats, was highest in the region with the highest temperature (Figure 3). Additionally, insects are insufficiently tolerant of high temperatures to survive in exposed habitats during the warmest weather without, for example, seeking shade (Sunday et al., 2014). This could explain two findings during the mid-June spike in temperatures: the lack of canopy openness–understory abundance relationship (Figure 4C) and the maximal abundance in the understory relative to the field margins (Figure 3). Indeed, the potential protective role of woodlands under a warming climate is now receiving increased attention (Ulyshen et al., 2023). During hot weather, bees may select more shaded environments for their usual activities. Alternatively, more open habitat-associated members of the community may become less active overall. The former is feasible if resources available in shaded and unshaded environments are interchangeable: for example, *Rubus* spp. are utilised by a broad range of bee species and grow both inside and outside woodlands. Otherwise, the protective shade of woodlands may only benefit those members who are already inclined to use them.

Conclusions and implications for conservation management

By sampling at field margins and in both the woodland understory and canopy across the season, we have revealed patterns of bee activity which suggest that deciduous woodlands (1) play a significant role in supporting foraging bees in springtime; (2) continue to provide suitable foraging conditions where canopies are more open; (3) provide other resources, such as nesting and patrolling sites, throughout the season and (4) potentially provide refuge to bees during hot weather.

Our findings suggest that the conservation and creation of woodlands on farmland has an important role, which could increase with climate warming, in supporting generalist, wild bee communities. Although woodlands across our study regions were generally closely connected to one another, over half of the woodlands sampled in this study were small (under 6.5 ha: Table S1), and we show that bees may move regularly between these and open habitats. This suggests that even small parcels of woodland, which could be readily incorporated into farmland, could benefit bee communities. Additionally, the foraging potential of woodlands can likely be increased by including nectar-producing trees, such as *A. pseudoplatanus*, and by maintaining more open canopies, via, for example, tree thinning. Other management activities, such as deer culling and vegetation clearance, which were widely practised across our study sites, may be important in maintaining understory flora.

Future research should examine any differences in patterns of abundance between the habitats studied here according to species and caste, to reveal their potentially complementary roles in supporting bee populations and diversity. Observational methods could be used to establish the relative frequency of nesting, foraging and patrolling behaviours, linking these to small-scale and short-term environmental differences, in order to better understand how woodland understories and field margins co-function to support bee communities.

AUTHOR CONTRIBUTIONS

Guthrie Allen: Conceptualization; methodology; investigation; formal analysis; visualization; writing – original draft; writing – review and editing; data curation. **Lynn V. Dicks:** Writing – review and editing; methodology; supervision. **Martin I. Taylor:** Writing – review and editing; methodology; supervision. **Daniel Hewitt:** Writing – review and editing; supervision. **Richard G. Davies:** Conceptualization; methodology; supervision; writing – review and editing; funding acquisition; project administration.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to declare.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Dryad at https://doi.org/10.5061/dryad.5dv41nshm.

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REFERENCES

Alison, J., Botham, M., Maskell, L.C., Garbutt, A., Seaton, F.M., Skates, J. et al. (2022) Woodland, cropland and hedgerows promote pollinator abundance in intensive grassland landscapes, with saturating benefits of flower cover. *Journal of Applied Ecology*, 59, 342–354.

Allen, G. & Davies, R.G. (2023) Canopy sampling reveals hidden potential value of woodland trees for wild bee assemblages. *Insect Conservation and Diversity*, 16, 33–46.

Ammann, L., Bosem-Baillod, A., Herzog, F., Frey, D., Entling, M.H. & Albrecht, M. (2024) Spatio-temporal complementarity of floral resources sustains wild bee pollinators in agricultural landscapes. *Agriculture, Ecosystems & Environment*, 359, 108754.

Bailey, S., Requier, F., Nusillard, B., Roberts, S.P., Potts, S.G. & Bouget, C. (2014) Distance from forest edge affects bee pollinators in oilseed rape fields. *Ecology and Evolution*, 4, 370–380.

Bak-Badowska, J. (2012) Spatial diversification of bee (Hymenoptera: Apoidea: Apiformes) assemblages in forest communities of the Suchedniów-Oblegorek Landscape Park. *Journal of Apicultural Science*, 56, 89–106.

Banaszak, J. & Cierzniak, T. (1994) Spatial and temporal differentiation of bees (Apoidea) in the forests of Wielkopolski National Park, Western Poland. *Acta Universitatis Lodziensis, Folia Zoologica*, 2, 3–28.

Bartoń, K. (2025) *MuMIn: multi-model inference. R package version 1.48.11*. Available from: https://CRAN.R-project.org/package=MuMIn

Bartual, A.M., Sutter, L., Bocci, G., Moonen, A.C., Cresswell, J., Entling, M. et al. (2019) The potential of different semi-natural habitats to sustain pollinators and natural enemies in European agricultural landscapes. *Agriculture, Ecosystems & Environment*, 279, 43–52.

Baude, M., Kunin, W.E., Boatman, N.D., Conyers, S., Davies, N., Gillespie, M.A.K. et al. (2016) Historical nectar assessment reveals the fall and rise of floral resources in Britain. *Nature*, 530, 85–88.

Bjornstad, O.N. (2022) *ncf: spatial covariance functions. R package version 1.3–2*. Available from: https://CRAN.R-project.org/package=ncf

Bringer, B. (1973) Territorial flight of bumble-bee males in coniferous forest on the northernmost part of the Island of Öland. *Zoon*, 1, 15–22.

Brooks, M.E., Kristensen, K., Van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A. et al. (2017) glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal*, 9, 378–400.

Campbell, J.W., Vigueira, P.A., Viguiera, C.C. & Greenberg, C.H. (2018) The effects of repeated prescribed fire and thinning on bees, wasps, and other flower visitors in the understory and midstory of a temperate forest in North Carolina. *Forest Science*, 64, 299–306.

Chase, M.H., Fraterrigo, J.M., Charles, B. & Harmon-Threatt, A. (2023) Wild bee response to forest management varies seasonally and is mediated by resource availability. *Forest Ecology and Management*, 548, 121426.

Cole, L.J., Kleijn, D., Dicks, L.V., Stout, J.C., Potts, S.G., Albrecht, M. et al. (2020) A critical analysis of the potential for EU common agricultural policy measures to support wild pollinators on farmland. *Journal of Applied Ecology*, 57, 681–694.

Collado, M.Á., Sol, D. & Bartomeus, I. (2019) Bees use anthropogenic habitats despite strong natural habitat preferences. *Diversity and Distributions*, 25, 924–935.

Cunningham-Minnick, M.J. & Crist, T.O. (2020) Floral resources of an invasive shrub alter native bee communities at different vertical strata in forest-edge habitat. *Biological Invasions*, 22, 2283–2298.

Cunningham-Minnick, M.J., Milam, J., Kane, B., Roberts, H.P. & King, D.I. (2023) Abundant, distinct, and seasonally dynamic bee community in the canopy-aerosphere interface above a temperate forest. *Ecology and Evolution*, 13, e9739.

Ewers, R.M., Bartlam, S. & Didham, R.K. (2013) Altered species interactions at forest edges: contrasting edge effects on bumble bees and their phoretic mite loads in temperate forest remnants. *Insect Conservation and Diversity*, 6, 598–606.

Falk, S. (2015) *A field guide to the bees of Great Britain and Ireland*. London, UK: Bloomsbury Wildlife.

Fussell, M. & Corbet, S.A. (1992) Observations on the patrolling behaviour of male bumblebees (Hym.). *Entomologist's Monthly Magazine*, 128, 229–235.

Ganuza, C., Redlich, S., Uhler, J., Tobisch, C., Rojas-Botero, S., Peters, M.K. et al. (2022) Interactive effects of climate and land use on pollinator diversity differ among taxa and scales. *Science Advances*, 8, eabm9359.

Hall, M. (2018) Blue and yellow vane traps differ in their sampling effectiveness for wild bees in both open and wooded habitats. *Agricultural and Forest Entomology*, 20, 487–495.

Hanula, J.L., Ulyshen, M.D. & Horn, S. (2016) Conserving pollinators in north American forests: a review. *Natural Areas Journal*, 36, 427–439.

Hartig, F. (2024) *DHARMa: residual diagnostics for hierarchical (multi-level/-mixed) regression models. R package version 0.4.7*. Available from: https://CRAN.R-project.org/package=DHARMa

Joshi, N.K., Leslie, T., Rajotte, E.G., Kammerer, M.A., Otieno, M. & Biddinger, D.J. (2015) Comparative trapping efficiency to characterize bee abundance, diversity, and community composition in apple orchards. *Annals of the Entomological Society of America*, 108, 785–799.

Joshi, N.K., Otieno, M., Rajotte, E.G., Fleischer, S.J. & Biddinger, D.J. (2016) Proximity to woodland and landscape structure drives pollinator visitation in apple orchard ecosystem. *Frontiers in Ecology and Evolution*, 4, 38.

Kallioniemi, E., Åström, J., Rusch, G.M., Dahle, S., Åström, S. & Gjershaug, J.O. (2017) Local resources, linear elements and mass-flowering crops determine bumblebee occurrences in moderately intensified farmlands. *Agriculture, Ecosystems & Environment*, 239, 90–100.

Kämper, W., Werner, P.K., Hilpert, A., Westphal, C., Blüthgen, N., Eltz, T. et al. (2016) How landscape, pollen intake and pollen quality affect colony growth in *Bombus terrestris*. *Landscape Ecology*, 31, 2245–2258.

Kells, A.R. & Goulson, D. (2003) Preferred nesting sites of bumblebee queens (Hymenoptera: Apidae) in agroecosystems in the UK. *Biological Conservation*, 109, 165–174.

Korpela, E.L., Hyvönen, T. & Kuussaari, M. (2015) Logging in boreal field-forest ecotones promotes flower-visiting insect diversity and modifies insect community composition. *Insect Conservation and Diversity*, 8, 152–162.

Larue, C., Austruy, E., Basset, G. & Petit, R.J. (2021) Revisiting pollination mode in chestnut (*Castanea* spp.): an integrated approach. *Botany Letters*, 168, 348–372.

Lenth, R. (2025) *emmeans: estimated marginal means, aka least-squares means. R package version 1.11.1*. Available from: https://CRAN.R-project.org/package=emmeans

Lüdecke, D., Ben-Shachar, M.S., Patil, I., Waggoner, P. & Makowski, D. (2021) Performance: an R package for assessment, comparison and testing of statistical models. *Journal of Open Source Software*, 6, 3139.

Mallinger, R.E., Gibbs, J. & Gratton, C. (2016) Diverse landscapes have a higher abundance and species richness of spring wild bees by providing complementary floral resources over bees' foraging periods. *Landscape Ecology*, 31, 1523–1535.

Mandelik, Y., Winfree, R., Neeson, T. & Kremen, C. (2012) Complementary habitat use by wild bees in agro-natural landscapes. *Ecological Applications*, 22, 1535–1546.

Mathis, C.L., McNeil, D.J., Jr., Kammerer, M., Larkin, J.L. & Skvarla, M.J. (2024) Distance models reveal biases associated with passive trapping methods for measuring wild bee abundance. *Frontiers in Ecology and Evolution*, 12, 1380622.

Mola, J.M., Hemberger, J., Kochanski, J., Richardson, L.L. & Pearse, I.S. (2021) The importance of forests in bumble bee biology and conservation. *Bioscience*, 71, 1234–1248.

Norfolk County Council - Norfolk Trees and Hedges (2022). Available from: https://norfolkcc.maps.arcgis.com/apps/webappviewer/index.html?id=bc454c4b70bc481fbcd7bf11adeea099 [Accessed March 2022].

O'Connor, S., Park, K.J. & Goulson, D. (2017) Location of bumblebee nests is predicted by counts of nest-searching queens. *Ecological Entomology*, 42, 731–736.

Ollerton, J. (2017) Pollinator diversity: distribution, ecological function, and conservation. *Annual Review of Ecology, Evolution, and Systematics*, 48, 353–376.

Osborne, J.L., Martin, A.P., Shortall, C.R., Todd, A.D., Goulson, D., Knight, M.E. et al. (2008) Quantifying and comparing bumblebee nest densities in gardens and countryside habitats. *Journal of Applied Ecology*, 45, 784–792.

Past Weather, Norwich, England, United Kingdom (2022). Available from: https://www.timeanddate.com/weather/uk/norwich/historic?month=5&year=2022 [Accessed July 2023].

Pfeiffer, V., Silbernagel, J., Guédot, C. & Zalapa, J. (2019) Woodland and floral richness boost bumble bee density in cranberry resource pulse landscapes. *Landscape Ecology*, 34, 979–996.

Potts, S.G., Imperatriz-Fonseca, V., Ngo, H.T., Aizen, M.A., Biesmeijer, J.C., Breeze, T.D. et al. (2016) Safeguarding pollinators and their values to human well-being. *Nature*, 540, 220–229.

Proctor, E., Nol, E., Burke, D. & Crins, W.J. (2012) Responses of insect pollinators and understory plants to silviculture in northern hardwood forests. *Biodiversity and Conservation*, 21, 1703–1740.

Proesmans, W., Bonte, D., Smagghe, G., Meeus, I., Decocq, G., Spicher, F. et al. (2019) Small forest patches as pollinator habitat: oases in an agricultural desert? *Landscape Ecology*, 34, 487–501.

Pugesek, G., Müller, U., Williams, N.M. & Crone, E.E. (2024) Resurrecting historical observations to characterize species-specific nesting traits of bumblebees. *The American Naturalist*, 204, 165–180.

Requier, F. & Leonhardt, S.D. (2020) Beyond flowers: including non-floral resources in bee conservation schemes. *Journal of Insect Conservation*, 24, 5–16.

Rivers-Moore, J., Ouin, A., Vialatte, A., Carrié, R., Ladet, S. & Andrieu, E. (2023) Contrasting effects of wooded and herbaceous semi-natural habitats on supporting wild bee diversity. *Agriculture, Ecosystems & Environment*, 356, 108644.

Roberts, H.P., King, D.I. & Milam, J. (2017) Factors affecting bee communities in forest openings and adjacent mature forest. *Forest Ecology and Management*, 394, 111–122.

Saunders, M.E. (2018) Insect pollinators collect pollen from wind-pollinated plants: implications for pollination ecology and sustainable agriculture. *Insect Conservation and Diversity*, 11, 13–31.

Schüepp, C., Herrmann, J.D., Herzog, F. & Schmidt-Entling, M.H. (2011) Differential effects of habitat isolation and landscape composition on wasps, bees, and their enemies. *Oecologia*, 165, 713–721.

Senapathi, D., Goddard, M.A., Kunin, W.E. & Baldock, K.C. (2017) Landscape impacts on pollinator communities in temperate systems: evidence and knowledge gaps. *Functional Ecology*, 31, 26–37.

Shreeve, T.G. (1984) Habitat selection, mate location, and microclimatic constraints on the activity of the speckled wood butterfly *Pararge aegeria*. *Oikos*, 42, 371–377.

Siopa, C., Carvalheiro, L.G., Castro, H., Loureiro, J. & Castro, S. (2024) Animal-pollinated crops and cultivars—a quantitative assessment of pollinator dependence values and evaluation of methodological approaches. *Journal of Applied Ecology*, 61, 1279–1288.

Slamova, I., Klecka, J. & Konvicka, M. (2011) Diurnal behavior and habitat preferences of *Erebia aethiops*, an aberrant lowland species of a mountain butterfly clade. *Journal of Insect Behavior*, 24, 230–246.

Smith, C., Harrison, T., Gardner, J. & Winfree, R. (2021) Forest-associated bee species persist amid forest loss and regrowth in eastern North America. *Biological Conservation*, 260, 109202.

Sõber, V., Leps, M., Kaasik, A., Mänd, M. & Teder, T. (2020) Forest proximity supports bumblebee species richness and abundance in hemi-boreal agricultural landscape. *Agriculture, Ecosystems & Environment*, 298, 106961.

Somme, L., Moquet, L., Quinet, M., Vanderplanck, M., Michez, D., Lognay, G. et al. (2016) Food in a row: urban trees offer valuable floral resources to pollinating insects. *Urban Ecosystems*, 19, 1149–1161.

Sunday, J.M., Bates, A.E., Kearney, M.R., Colwell, R.K., Dulvy, N.K., Longino, J.T. et al. (2014) Thermal-safety margins and the necessity of thermoregulatory behavior across latitude and elevation. *Proceedings of the National Academy of Sciences*, 111, 5610–5615.

Svensson, B., Lagerlöf, J. & Svensson, B.G. (2000) Habitat preferences of nest-seeking bumble bees (Hymenoptera: Apidae) in an agricultural landscape. *Agriculture, Ecosystems & Environment*, 77, 247–255.

Timberlake, T.P., Vaughan, I.P. & Memmott, J. (2019) Phenology of farmland floral resources reveals seasonal gaps in nectar availability for bumblebees. *Journal of Applied Ecology*, 56, 1585–1596.

Traylor, C.R., Ulyshen, M.D., Bragg, D.C. & McHugh, J.V. (2024) Forest bees benefit from compositionally diverse broadleaf canopies. *Forest Ecology and Management*, 566, 122051.

Ulyshen, M., Urban-Mead, K.R., Dorey, J.B. & Rivers, J.W. (2023) Forests are critically important to global pollinator diversity and enhance pollination in adjacent crops. *Biological Reviews*, 98, 1118–1141.

Ulyshen, M.D., Horn, S. & Hanula, J.L. (2020) Effects of Chinese privet on bees and their vertical distribution in riparian forests. *Forest Science*, 66, 416–423.

Ulyshen, M.D., Soon, V. & Hanula, J.L. (2010) On the vertical distribution of bees in a temperate deciduous forest. *Insect Conservation and Diversity*, 3, 222–228.

Urban-Mead, K.R., Muñiz, P., Gillung, J., Espinoza, A., Fordyce, R., van Dyke, M. et al. (2021) Bees in the trees: diverse spring fauna in temperate forest edge canopies. *Forest Ecology and Management*, 482, 118903.

Urban-Mead, K.R., Van Dyke, M., Muñiz, P., Young, A.D., Danforth, B.N. & McArt, S.H. (2023) Early spring orchard pollinators spill over from resource-rich adjacent forest patches. *Journal of Applied Ecology*, 60, 553–564.

Vives-Ingla, M., Sala-Garcia, J., Stefanescu, C., Casadó-Tortosa, A., Garcia, M., Peñuelas, J. et al. (2023) Interspecific differences in microhabitat use expose insects to contrasting thermal mortality. *Ecological Monographs*, 93, e1561.

Wagner, D.L., Metzler, K.J. & Frye, H. (2019) Importance of transmission line corridors for conservation of native bees and other wildlife. *Biological Conservation*, 235, 147–156.

Watson, J.C., Wolf, A.T. & Ascher, J.S. (2011) Forested landscapes promote richness and abundance of native bees (Hymenoptera: Apoidea: Anthophila) in Wisconsin apple orchards. *Environmental Entomology*, 40, 621–632.

Winfree, R., Griswold, T. & Kremen, C. (2007) Effect of human disturbance on bee communities in a forested ecosystem. *Conservation Biology*, 21, 213–223.

SUPPORTING INFORMATION

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

Appendix S1 Ground floral surveys.

Appendix S2 Tree surveys.

Appendix S3 Model diagnostics.

Appendix S4 Model selection.

Figure S1 Floral abundance of the six most common plant families across sampling periods.

Figure S2 Combined floral abundance of plant families across sampling periods.

Figure S3 Correlation matrix charts of continuous variables included in global models.

Table S1 Size of study-site woodlands.

Table S2 Summary of tests for spatial autocorrelation in model residuals.

Table S3 to S5 Top 3 ranked AIC models produced from the global models of understory, canopy and field margin trap catches, respectively.

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