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Canopy sampling reveals hidden potential value of woodland trees for wild bee assemblages

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Abstract

1. Woodlands can play an important role in supporting bee abundance and diversity in agricultural landscapes. However, in temperate-region studies, the canopy is rarely sampled, and our understanding of its contribution is limited.
2. To explore this, we sampled bees in late spring with blue vane traps in the understory ($n = 30$) and crowns of mature *Quercus robur* ($n = 35$) at the exposed southern edges and in the interiors (ca. 25–75 m from woodland edges) of 15 woodland sites across an English agricultural landscape.
3. A significant proportion of bee abundance and diversity was found in the canopy: canopy-trap catches were estimated to be a third as large as understory-trap catches, and 23 of the 29 sampled species were present in the canopy. Of the seven most common species sampled, four were equally abundant in woodland edge and interior traps; three were more abundant in understory traps, and a single species—*Bombus lapidarius*—was more abundant in canopy traps. The sex ratio of the most abundant species, *B. pratorum*, was female-skewed in the canopy. Additionally, the presence of nearby *Acer pseudoplatanus* trees in flower greatly increased canopy-trap catches in woodland interiors.
4. These results suggest that both the woodland canopy and understory have a significant role to play in supporting farmland bee communities; they indicate the importance of nectar-producing trees in woodland interiors, opening avenues for canopy-based management; and they demonstrate that a diverse bee community has the potential to exploit canopy floral resources.

KEYWORDS
Andrena, *Bombus*, bumblebees, nectar, pollen, pollinators, solitary bees, temperate agricultural landscape, understory, wind-pollinated

INTRODUCTION

There is evidence for local, regional and national declines in wild bee abundance and diversity across multiple regions globally, and habitat loss associated with agricultural intensification is generally considered to be the most important cause (Ollerton, 2017). In agricultural landscapes, wild bees rely on non-crop semi-natural habitats for the provision of essential resources such as food, nesting sites and dormancy sites (Cole et al., 2020; Mola et al., 2021), and landscapes with higher proportions of these habitats tend to support higher wild bee abundance and diversity (Senapathi et al., 2017). Experts across Europe perceive small woodlands to be among the habitats that currently provide the greatest resource for nesting bees, while the potential for improving current woodland floral resources with pollinator-friendly management is considered to be large (Cole et al., 2020). Tree canopies can provide a greater density of nectar and pollen than is available at ground level, as suggested by Donkersley (2019), and nectar provision of the woodland understory relative to its area coverage can be disproportionately large in spring (Timberlake et al., 2019). Baude et al. (2016) identify broadleaf woodland in the United Kingdom as being among the habitats that produce the greatest amount of nectar per unit area, thanks both to its understory plants and its canopy trees, such as *Acer pseudoplatanus*. Additionally, trees offer non-floral resources, which can provide bees with extra nutrition (e.g. honeydew), nesting material, or substances to protect themselves and/or their nests (Requier & Leonhardt, 2020). Furthermore, woodlands may complement other habitats by providing temporal continuity of resources—they are perceived to be a rich source of early-season forage, with field margins perceived to provide greater forage later in the season (Cole et al., 2020).

In non-woodland contexts, studies have shown that both bumblebees and solitary bees are frequent visitors to nectar-producing woodland-tree taxa, including *Acer*, *Tilia* (Hausmann et al., 2016) and *Castanea sativa* (Larue et al., 2021), while in the United Kingdom, bumblebees have also been observed foraging on the flowers of wind-pollinated *Fagus*, *Alnus* and *Ulmus* (DoPI, 2022). However, most evidence of bees foraging from woodland canopy-tree genera comes indirectly, from pollen collection studies. In Michigan, USA, *Acer* makes up over a quarter of early-season pollen collections of solitary bees (Wood et al., 2018). *Acer* pollen forms a significant proportion of the diets of several species of UK-*Andrena*—around a quarter in at least four species (weighted averages calculated from Wood & Roberts, 2017). Regarding bumblebees, pollen loads taken from early-season *Bombus terrestris* workers returning to their nests have shown *Acer* proportions to be moderate (7%: Eckerter et al., 2020) or high (ca. 25%: Bertrand et al., 2019; 34%: Kämper et al., 2016).

Osmia bicornis, which is widespread in agricultural environments across Europe, has been shown to collect the largest proportion of its early-season diet from wind-pollinated *Quercus* (Bednarska et al., 2021; Bertrand et al., 2019; Free & Williams, 1970; Persson et al., 2018; Ruddle et al., 2018; Yourstone et al., 2021) followed, in some cases, by *Acer* (Bertrand et al., 2019; Yourstone et al., 2021). Across the northern hemisphere, several other species of *Osmia* have also been shown, on occasion at least, to collect large quantities of *Quercus* pollen (Haider et al., 2014; Kraemer & Favi, 2005; Kratschmer et al., 2020; MacIvor et al., 2014; Vicens et al., 1994; Williams & Kremen, 2007). In the United Kingdom, *Quercus* and *Fagus* form a significant proportion (6.0%–10.5%) of the diets of at least three *Andrena* species (weighted averages calculated from Wood & Roberts, 2017). One member of this genus, *A. ferox*, forages almost exclusively on *Quercus* pollen, although this species is rare in the United Kingdom and throughout its European range (Else & Edwards, 2018). Regarding bumblebees, evidence of pollen from wind-pollinated trees within pollen loads is scarce. In a global sample of 4132 bumblebee pollen loads (Wood et al., 2021), just six contained these pollens at appreciable levels (over 2%) with load proportions of up to 50%.

Several North American and European studies indicate that wild bee abundance and/or diversity can increase with increasing woodland cover within a landscape (Collado et al., 2019; Pfeiffer et al., 2019; Proesmans et al., 2019; Smith et al., 2021; Sõber et al., 2020; Watson et al., 2011) or increasing proximity to woodlands (Bailey et al., 2014; Joshi et al., 2016). Woodlands can also have benefits at the local scale, supporting greater wild bee richness and/or abundance than open habitats (Alison et al., 2022; Collado et al., 2019; Sõber et al., 2020). Additionally, woodlands and other closed-canopy habitats may support communities that are distinct from open habitats (Collado et al., 2019; Mallinger et al., 2016), suggesting they contribute to bee diversity at the landscape scale. Nonetheless, other studies do not find that woodland has positive effects on bee populations (Kallioniemi et al., 2017; Mallinger et al., 2016; Mandelik et al., 2012; Schüepp et al., 2011; Winfree et al., 2007). The causes will vary but may include reduced benefits of habitat complementarity in woodland-dominated landscapes (Kallioniemi et al., 2017; Winfree et al., 2007); and/or a lack of floral resources within the woodlands themselves (Kallioniemi et al., 2017; Mandelik et al., 2012).

The results of local scale studies will also vary according to differences in the definition of woodland (from open woody habitats to those with dense canopy cover), the location of sampling points (interiors, edges, clearings, rides etc.), and the timing of sampling (full or partial season). For example, in a large-scale study of European agricultural landscapes, Bartual et al. (2019) found that bee abundance was considerably lower in woodland interiors (just 12–13 m from the woodland edge) than at woodland edges, and some studies focus their sampling efforts solely within the latter habitat (Proesmans et al., 2019; Sõber et al., 2020).

In a review of pollinator conservation in North American forests, understory temperature and light levels are the abiotic factors identified as most important to bees foraging at ground level (Hanula et al., 2016). Management is necessary to maintain these factors at high levels after canopy closure; however, the upper canopy receives sunlight throughout the season regardless of woodland management and potentially represents a stable, micro-climatically favourable habitat. A canopy-tree's flowers are also concentrated where the crown is exposed to sunlight (Pires et al., 2014). As such, the upper canopy could support a significant proportion of a woodland's overall contribution to bee abundance. Additionally, given that female, but not male, bees forage for pollen, and given differing floral (Cullen et al., 2021) and temperature (Kells & Goulson, 2003) preferences among species, one might expect community-level differences between the canopy and understory.

To our knowledge, there are just five replicated, temperate-region studies that investigate full bee assemblages in the canopy, all of which were conducted in North America. These have found canopy traps to catch equal (Cunningham-Minnick & Crist, 2020; Urban-Mead et al., 2021) or higher (Campbell et al., 2018; Ulyshen et al., 2010, 2020) numbers of bees than those set in the understory. Cunningham-Minnick and Crist (2020) and Ulyshen et al. (2010) provide some evidence that communities are distinct between strata, while Urban-Mead et al. (2021) found that the canopy sex ratio was significantly female-skewed and speculate that females forage on pollen from the abundantly available wind-pollinated trees. In New Zealand, trap catches of a single non-native species, *B. terrestris*, are reported and these are found to be significantly higher in the canopy (Ewers et al., 2013). In Germany, cavity-nesting bees and wasps were sampled with trap nests, and abundance was found to be higher in canopies and positively correlated with tree diversity (Sobek et al., 2009). Otherwise, European studies may be limited to two small surveys conducted in Poland in which canopy traps were found to catch fewer wild bees than understory traps (Bak-Badowska, 2012; Banaszak & Cierzniak, 1994). However, despite the potential for the canopy to harbour bees and for trees to provide forage, evidence for tree-flower foraging in woodland canopies may be restricted to just one study from Japan: Inari et al. (2012), investigated a single woodland plot over a period of 5 years, finding links between floral production of *Acer* and *Tilia* species and worker production in three species of bumblebee.

To our knowledge, bee communities in the canopy of UK woodlands have not previously been investigated. Moreover, none of the above canopy studies have compared trap catches at sun-exposed woodland edges to those of woodland interiors, nor have these studies examined the effects of nearby flowering trees on canopy-trap catches. Consequently, our understanding of the role of woodland canopies in supporting wild bee communities is limited. To gain insight into this role, we sampled bees from the canopies and understories of woodland edges and interiors (ca. 25–75 m from edges) within an agricultural landscape in late spring, and we examined: (1) the extent to which bees were active in these habitats; (2) differences in bee community composition between these habitats; (3) differences in sex ratios between the understory and canopy; and (4) the influence of nectar-producing canopy trees on canopy activity. The findings are discussed in terms of the canopy's potential contribution to woodland bee abundance; resource provision by nectar-producing and wind-pollinated trees; the potential for canopy-based management of woodland interiors for bee conservation; and the implications for ground-level bee surveying.

METHODS

Sampling sites

The study comprised 15 sampling sites across a circa 10 km^2 area on Raveningham Estate, UK (Figure 1). Using 2017–2020 LIDAR data presented by Norfolk County Council—Norfolk Trees and Hedges (2021), sites were selected if they contained a majority of trees >15 m in height and had fully connected canopy coverage across a minimum area of 1.25 ha (the size of the smallest woodland sampled, Table S1). However, the proportion of canopy gaps varied across sites. Fourteen of the sites are part of the UK government's English Woodland Grant Scheme and are managed for timber. They have undergone tree thinning and contain tracks allowing vehicular access. Woodland interiors largely lacked shrubs and understory trees that might otherwise connect the canopy with ground flora. The most common trees were *Quercus robur* and/or *Fraxinus excelsior* (12 sites), *Acer pseudoplatanus* (two sites), and *Castanea sativa* (one site; see Table S1). At the time of bee sampling in late spring, most sites supported occasional to frequent flowering plants in the woodland interior, including *Ajuga reptans*, *Glechoma hederacea*, *Veronica* spp., *Anthriscus sylvestris* and *Geranium robertianum*. Southern woodland edges were generally populated by shorter trees with larger crowns and supported well-developed understory hedging and trees. The surrounding agricultural land is a mixture of arable and pasture. Some is under Middle Tier Countryside Stewardship (three sites) or Entry/Higher Level Environmental Stewardship (five sites); while half is under no Agri-Environmental Agreement (seven sites).

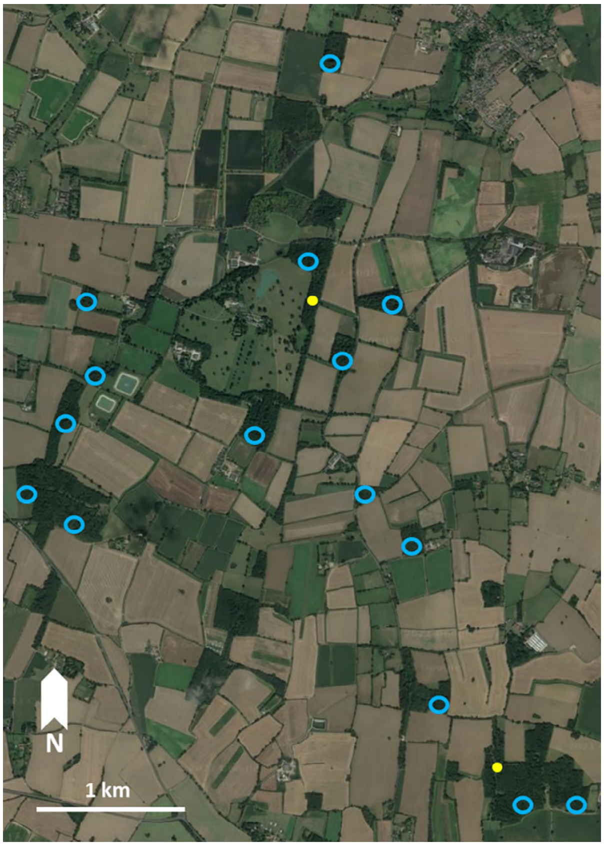

FIGURE 1 Study area (Raveningham Estate, UK). Blue circles represent the study sites in which either four or five bee traps were present ($n = 15$). Yellow circles represent additional sites in which a single canopy trap was present ($n = 2$). *Source*: Image ©2021 Google, annotations by G. Allen

Bee sampling regime

BanfieldBio™ blue vane traps (BVTs) were used to catch bees. These are effective in trapping a diversity of bee species, including larger-bodied taxa—such as bumblebees—which are underrepresented in pan traps (Prendergast et al., 2020); and of the commercially available vane colours (also including yellow), blue traps consistently catch the highest bee abundance and diversity (Acharya et al., 2022; Prendergast et al., 2020). Vane traps are also suitable for canopy sampling—they are designed to be hung, and their collecting jars offer secure storage for specimens. We recognise that BVTs, in common with other insect traps, collect a sub-set of the available bee diversity (Prendergast et al., 2020), but, in the absence of other feasible methods for high canopy sampling, we consider their use sufficient for examining patterns of abundance between woodland habitats. A mixture of 150 ml water and 150 ml propylene glycol was used to euthanise and preserve insects in the trap collection jars.

At each of the 15 woodland sites, two pairs of traps were set: one pair at the exposed southern woodland edge and the other in the woodland interior (ca. 25–75 m from the nearest woodland edge). Each pair comprised an understory trap and, approximately above this, a canopy trap. Hereafter, when discussing results and unless otherwise specified, we use the word ‘habitat’ to refer to all four trap positions: edge-understory (EG), edge-canopy (EC), interior-understory (IG) and interior-canopy (IC). Our purpose was not to assess woodland site characteristics, but rather to sample replicates of these habitats, and, given the efficacy of BVTs (Prendergast et al., 2020), we consider that a single trap per habitat in each woodland site is sufficient for this purpose. Woodland-edge traps were limited to the southern edge in order to maximise and standardise the solar regime for bee activity sampling between sites. Canopy traps were hung exclusively in *Q. robur* to standardise any effects of the immediate canopy environment. As such, sampling points at woodland sites were largely dictated by the availability of *Q. robur* trees. Six additional IC traps were set to increase replication with regard to nearby nectar-producing trees, and one EC trap was removed for safety reasons. Accordingly, the total number of traps, hereafter referred to as ‘primary traps’, was 65 (14 EC, 15 EG, 15 IG and 21 IC) (Table S1).

To ensure sufficient canopy specimens were caught for sex-ratio analyses (described later), a further seven canopy traps were set: five were added to existing sites and two to new sites (Figure 1, Table S1). These additional traps did not meet the criteria to be classified as either IC (too close to woodland edge) or EC (not at southern edge). The maximum number of traps in any one site was five. Within sites, canopy traps were separated by >30 m with the exception of one site with a 21 m separation. Traps from different sites were separated by a minimum distance of 200 m (mean 425 m ± SE 62.1) (Figure 1), and potential impacts of spatial non-independence on model residuals were tested for (see Statistical analyses).

Understory traps were hung where access and the availability of branches allowed at a height of 1.5–2 m and at a mean horizontal distance of 8 m (minimum 0 m and maximum 29 m) from their corresponding canopy traps (Table S1). To set canopy traps, 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 hung as high as possible and within 3 m of the sun-exposed tree crown edge—that is, on the south side of the crown and/or towards the top— in order to maximise and standardise canopy-trap catches, while limiting long-distance visibility. Otherwise, trap position in the crown was dictated by the availability of suitable branches for rope rigging. Mean EC-trap height, as estimated with a clinometer, was 10.2 m (minimum 7 m, maximum 12.5 m) and mean IC-trap height was 15.4 m (minimum 9.5 m, maximum 21.5 m)—Table S1.

Trap setting coincided with a period of unusually cold weather (23–27 May: daily mean of 11.3°C—Past weather, Beccles, 2021) during which very few bees were caught. This was followed by a marked increase in temperatures (and much higher catch rates) over the 5–6 remaining days of deployment (28 May to 2 June: daily mean of 16.5°C), such that the effective trapping time for all traps corresponded to this latter period. Traps within each site shared the same effective trapping period, and the time difference of ca. 1 day between some sites was controlled for statistically (see Statistical analyses). The timing of trap deployment was planned to coincide with the predicted peak pollen production by *Q. robur*, as judged in early/mid-May, as well as with *A. pseudoplatanus* flowering. However, during deployment, only a minority of *Q. robur* trees—both those containing traps and those across each site—appeared to have live catkins that contained fresh pollen. The remaining *Q. robur* trees contained seemingly moribund catkins, often with stunted growth, possibly as a consequence of an unusually cold and wet May (Met Office, 2021), although pollen production may have also been low in response to a probable mast event the previous year (Bogdziewicz, 2021; Whittle, 2021).

Bee taxonomy

All bee specimens were rinsed in ethanol, dried, pinned where necessary, and sexed. All individuals of *Bombus* were identified to species by the lead author using Falk (2015). Relevant features were examined under ×45 magnification to confirm the sex and species. Solitary bees were identified by local taxonomic authority Nick Owens. All bees were stored at University of East Anglia. With the exception of the abundant *B. pratorum* specimens—which were stored together for each sample—all specimens were pinned with individual tags allowing cross-reference to the identifications made for each sample.

Surveying nearby nectar-producing trees and ground flora

A single layer of trees that formed the visible canopy surrounding the *Q. robur* trees with traps, and up to 15 m from the *Q. robur* crown edge, was identified. Within this layer, the species of nectar-producing trees in flower at the time of trap deployment were noted as present or absent. These comprised *A. pseudoplatanus*, *A. campestre* and *Crataegus monogyna*. Ground floral cover and a proxy for understory trap shading were also estimated—details, including their analysis and interpretation, are presented in Appendix S1.

Statistical analyses

All analyses were conducted in R studio, version 3.6.1. To facilitate analysis and interpretation, three configurations of the dataset were used, which are summarised with their corresponding analyses in Table 1. Moran's I tests were performed on the residuals of all univariate models using the *testSpatialAutocorrelation* function in the package DHARMa (Hartig, 2019) and no significant spatial autocorrelations were detected (Table S2).

Univariate count models—Construction and fit

Univariate analyses of count data (i.e. of bee abundance within each trap—hereafter referred to as trap catches) were all fitted with negative binomial distributions following tests of Poisson models using the *check_overdispersion* function in the package 'performance' (Lüdecke et al., 2021) and tests of fit of both distributions using the *plot* function in the package DHARMa (Hartig, 2019). Negative binomial fits were superior in all cases and presented no diagnostic issues.

To account for the non-independence of traps within the same site (thereby accounting for site characteristics), and differences in deployment length between sites, *woodland site* was always included as a random intercept (with 15 levels) for initial model fitting and only removed if it explained a non-significant ($p > 0.05$) proportion of variation according to the likelihood ratio test. For mixed effects models, the function *glmmTMB* (family *nbinom2*) from the glmmTMB package (Brooks et al., 2017) was used; and for fixed effects models the function *glm.nb* from the MASS package (Venables & Ripley, 2002) was used. Using likelihood ratio tests, fixed factors and interaction terms were excluded if non-significant and the significance of remaining terms was confirmed. Only one model (the effect of *sycamore* and *position* on canopy-trap catches) retained an interaction term. Pseudo R^2 values were obtained using the *r*2 function from the package 'performance' (Lüdecke et al., 2021).

The effect of habitat on total and individual species' trap catches

The 65 primary traps were used to investigate the effects of habitat on trap catches (Table 1). First, trap catches of all bees were modelled as a function of *position* (two levels: Edge and Interior) and *stratum* (two levels: Understory and Canopy). Second, community- and species-level effects of *position* and *stratum* were examined using the *manyglm* function in the mvabund package (Wang et al., 2012), which, by pooling the effects of separate generalised linear models (GLMs) for each species, has considerable power to detect community responses. Species caught in fewer than eight traps were excluded from this analysis. Following a Dunn–Smyth residual plot check and a non-significant community-level factor interaction, each species was fitted with a negative binomial GLM, with *woodland site* controlled for as a fixed factor, and no interaction. Community-level *p*-values for the factors *position* and *stratum* were calculated by resampling the data 1000 times with the PIT-trap method; using a likelihood ratio test (LRT) statistic; and assuming independence between species response variables (all default methods). Separate *p* values for each species were also returned, controlling for family-wise error rates ($p.uni =$ '*adjusted*') (Wang et al., 2012).

The manyglm univariate results revealed a single species, *B. lapidarius*, whose response to *stratum* was in opposition to that of the other species. To provide robust evidence of this effect, *B. lapidarius* trap catches were modelled as a function of *stratum* and *position* following the full diagnostic testing and term-deletion procedures outlined earlier for univariate count models.

Differences in sex ratio between understory and canopy

All 72 traps (30 understory, 42 canopy) across all woodland sites ($n = 17$) were used to investigate the effect of canopy versus understory on sex ratios in bees (Table 1). However, only species in which numbers of both females and males were sufficient (minimum of 15 for each sex) to allow for statistical analyses were included (Table S3). With sex ratios varying considerably between species (reflecting differing phenologies), a clearer interpretation of results is achieved with single-species analyses. Only *B. pratorum* had sufficient numbers of both sexes for a robust analysis, while *B. hortorum* numbers permitted an analysis with a reduced degree of confidence.

The trap catches of *B. pratorum* and *B. hortorum* were each pooled across the understory traps and canopy traps, respectively, within

TABLE 1 Summary of dataset configurations and their corresponding analyses

Dataset (number of traps)	Sites (*n*)	Response variables	Predictors of interest (*factor labels*)	Controlling for (*factor labels*)
Primary traps (65)	15	Total trap catch and species' trap catch	Habitat (*position*—Edge or Interior; *stratum*—Understory or Canopy)	Site effects (*woodland site*)
All traps (72)	17	Trap catches by species and sex pooled across each site stratum	Stratum (*stratum*—Understory or Canopy)	Site effects (*woodland site*)
Primary canopy traps (35)	15	Canopy-trap catch	Flowering *Acer pseudoplatanus* (*sycamore*—Present or Absent)	Site effects (*woodland site*), trap position (*position*— Edge or Interior) and trap height

Note: 'Primary traps' refer to those placed in one of four habitats (in the understory or canopy at the woodland edge or interior). 'Trap catch' refers to the abundance of bees within an individual blue vane trap.

TABLE 2 A summary of the 12 most abundant bee species caught in the 65 primary traps used for habitat analyses across 15 sites

Species	Abundance	Percentage of total bees	Number of sites in which present
Bombus pratorum (Linnaeus, 1761)	1032	67.36	15
B. lapidarius (Linnaeus, 1758)	82	5.35	15
B. hortorum (Linnaeus, 1761)	63	4.11	15
B. hypnorum (Linnaeus, 1758)	60	3.92	11
B. pascuorum (Scopoli, 1763)	59	3.85	14
B. terrestris spp. *audax* (Harris, 1776)	54	3.52	15
Andrena nitida (Müller, 1776)	50	3.26	13
A. haemorrhoa (Fabricius, 1781)	31	2.02	12
B. sylvestris (Lepeletier, 1832)	16	1.04	7
Lasioglossum calceatum (Scopoli, 1763)	14	0.91	8
A. scotica (Perkins, R.C.L., 1916)	12	0.78	6
B. vestalis (Geoffroy, 1785)	10	0.65	8
Remaining 16 species	49	3.20	
Total	1532	100.00	

each woodland site. This resulted in 32 samples (15 from the understory and 17 from the canopy) for *B. pratorum* and 25 samples (14 from the understory and 11 from the canopy) for *B. hortorum*. The log odds ratio of females versus males was modelled for each species, as a function of *stratum* (Canopy or Understory) using a binomial error distribution with logit link. For each model, *woodland site* was included as a random intercept, but removed for the *B. hortorum* model as it explained no variation. DHARMa diagnostic tests (from the *plot* function) indicated no issues with model fits. For the *B. pratorum* model, pseudo R^2 values were obtained using the *r.squaredGLMM* function from the MuMIn package (Bartoń, 2020), and the *delta* values are reported.

The influence of flowering trees on canopy activity

While controlling for trap position (edge or interior) and height, modelling the nearby presence or absence of either flowering nectar-trees of all species or solely flowering *A. pseudoplatanus* (*sycamore*) produced near-identical canopy responses ($n = 35$) (Tables S9 and S11). This indicated the relative importance of *A. pseudoplatanus* in the context of our survey—it comprised six out of the seven nectar-trees in flower within woodland interiors—and as such, only the latter model is presented (Table 1). To explore the nature of the revealed *position*–*sycamore* interaction, canopy-trap catch model estimates were plotted against the four combinations of each factor-level, and post hoc Tukey tests were performed (package emmeans—Lenth, 2021) to identify pair-wise differences.

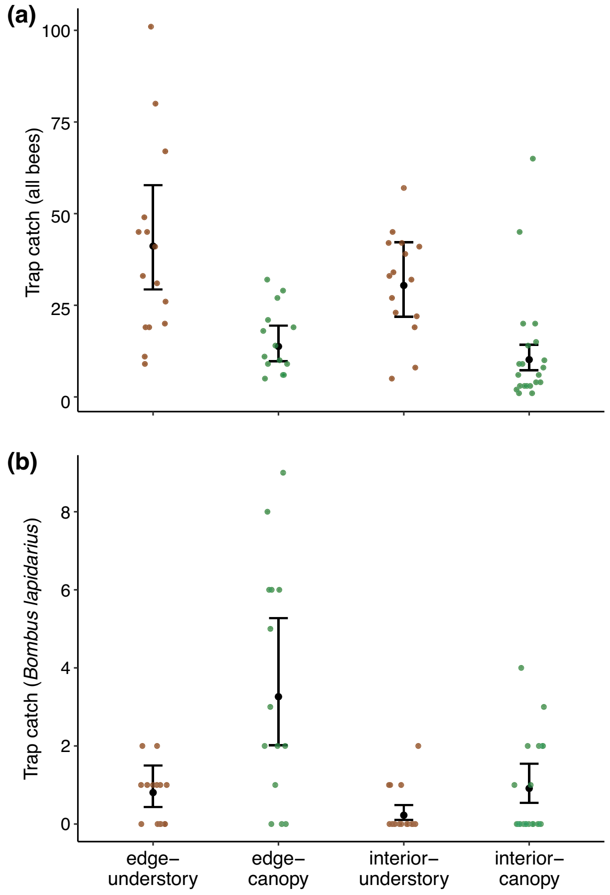

FIGURE 2 Trap catches ($n = 65$) of (a) all bees and (b) *Bombus lapidarius* in each of four habitats across 15 woodland sites on Raveningham Estate, UK. Habitats combine the woodland edge or interior with the understory or canopy. Model estimates (black circles) and 95% CIs are superimposed. Model estimates and tests of significance are summarised in Tables S4 and S6.

RESULTS

A total of 1532 bees were caught with the 65 primary traps (Table 2). Mean trap catch was 23.6, with a minimum of 1 and a maximum of 101. The most common species caught, comprising 67.4% of all individuals, was *B. pratorum* (Table 2). Considering all 72 traps, 29 species were caught (Table S3); 23 of these were present in the canopy—the remaining six were at low abundance (maximum of three individuals each). There were 22 non-parasitic species in which females were sampled; of these, 21 were present in the canopy.

TABLE 3 Results from the individual generalised linear models that comprise the community analysis (Table S5), summarising the effect of habitat (the understory or canopy at the woodland edge or interior) on trap catches by species, which are listed by descending abundance

		Coefficient (log scale)	Likelihood ratio test	*p* value
Bombus pratorum	*stratum* (Understory)	**+1.45**	19.08	**0.003**
	position (Interior)	−0.10	0.01	1.000
B. lapidarius	*stratum* (Understory)	**−1.46**	10.36	**0.024**
	position (Interior)	**−1.27**	12.31	**0.005**
B. hortorum	*stratum* (Understory)	**+1.39**	17.87	**0.003**
	position (Interior)	+0.03	0.02	1.000
B. hypnorum	*stratum* (Understory)	+1.23	7.58	0.064
	position (Interior)	−0.09	0.19	0.998
B. pascuorum	*stratum* (Understory)	**+2.06**	21.79	**0.001**
	position (Interior)	−0.47	2.26	0.617
B. terrestris	*stratum* (Understory)	+0.56	3.41	0.337
	position (Interior)	**−1.13**	9.91	**0.023**
Andrena nitida	*stratum* (Understory)	+0.88	5.36	0.176
	position (Interior)	+0.10	0.03	1.000
A. haemorrhoa	*stratum* (Understory)	+0.63	1.80	0.190
	position (Interior)	−0.41	0.53	0.955
B. sylvestris	*stratum* (Understory)	+1.49	4.49	0.248
	position (Interior)	−1.49	4.08	0.340
Lasioglossum calceatum	*stratum* (Understory)	+0.67	1.41	0.610
	position (Interior)	−1.02	2.83	0.544
A. scotica	*stratum* (Understory)	−0.05	0.05	0.847
	position (Interior)	−0.34	0.01	1.000
B. vestalis	*stratum* (Understory)	+0.42	0.74	0.683
	position (Interior)	−1.42	4.89	0.262

Note: Trap catches ($n = 65$) were modelled as a function of *position* (Edge/Interior) + *stratum* (Understory/Canopy) + *woodland site* (15 levels). *Woodland site* effects are omitted. *p* values < 0.05, and their corresponding coefficients, are in bold.

The effect of habitat on total trap catches and individual bee species' abundance

Bee catches were significantly higher in the understory than in the canopy ($X_1^2 = 30.61$, $p < 0.001$; Figure 2a). However, canopy-trap catches were relatively high—estimated to be a third (33.5%) as large as understory-trap catches. Within each stratum, bee catches were higher in woodland-edge traps (Figure 2a), but the significance of this is marginal ($X_1^2 = 3.32$, $p = 0.068$). Overall, habitat type explains 42% of the variation (marginal $R^2 = 0.42$ [fixed effects]).

While no significant difference in the overall trap catches of bees between woodland edge and interior was detected, a multivariate analysis (Wang et al., 2012) detected a significant effect at the community-level (LRT $= 37.06$, $p = 0.003$, Table S5). This is primarily driven by two species—*B. lapidarius* and *B. terrestris*—which were significantly more abundant at woodland edges (Table 3). However, for four of the remaining five abundant species (>49 individuals, see Table 2), there was little evidence for differences in abundance between woodland edges and interiors (Table 3: excluding *B. pascuorum*, coefficients are small, between −0.11 and +0.11, and *p* values > 0.997). Differences between understory and canopy, and between woodland sites, were also significant at the community-level (LRT $= 93.94$, $p < 0.001$; Table S5). Catches of three bumblebee species were significantly higher in understory traps, while that of one (*B. hypnorum*) was marginally higher (Table 3). One species, *B. lapidarius*, showed a unique trend: it was significantly more abundant in canopy traps. Among the other abundant species (>49 individuals), *B. terrestris* had the weakest association with the understory relative to the canopy (Table 3: smallest positive coefficient). The *B. lapidarius* results are supported by a separate fixed effects model (*stratum*: $X_1^2 = 13.12$, $p < 0.001$; *position*: $X_1^2 = 12.31$, $p < 0.001$; Figure 2b) which explains 50% of the variation (Nagelkerke's $R^2 = 0.50$).

Sex-ratio differences between the understory and canopy

The sex ratio of *B. pratorum* in the canopy was significantly female-skewed compared to the understory ($X_1^2 = 49.59$, $p < 0.001$; Figure 3a). Females in the canopy are estimated to make up 95% of the population compared to 77% in the understory. The understory–canopy contrast explains 43% of the variation in sex ratio (marginal $R^2 = 0.43$ [fixed effects]). The sex ratio of *B. hortorum* also appears to be female-skewed in the canopy ($X_1^2 = 4.69$, $p = 0.030$; Figure 3b).

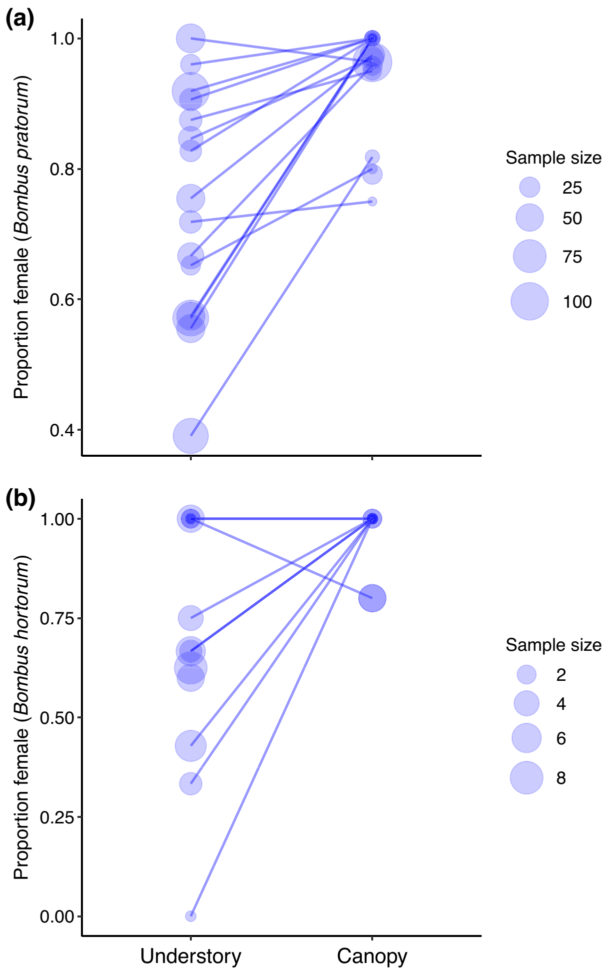

FIGURE 3 The proportion of female individuals of two bumblebee species caught in the understory and canopy of woodland sites on Raveningham Estate, UK. Samples are the pooled catches of understory traps and canopy traps, respectively, within each site. Lines connect samples from the same site. (a) *Bombus pratorum*: 17 sites, 32 samples; (b) *Bombus hortorum*: 16 sites, 25 samples. See Tables S7 and S8 for the corresponding model estimates and tests of significance.

However, with males numbering just 18 out of the 70 individuals caught across 16 sites, caution is needed in interpreting this result.

The influence of flowering *A. pseudoplatanus* on canopy activity

Controlling for *position* and *sycamore*, there was no evidence that canopy trap height had an influence on catches ($X_1^2 = 0.33$, $p = 0.56$). There was a significant interaction between the factors *position* and *sycamore* ($X_1^2 = 10.19$, $p < 0.01$) and post hoc Tukey testing indicates that canopy-trap catches in woodland interiors—but not at the woodland edge—were significantly increased, by an estimated 297.0%, in the presence of adjacent *A. pseudoplatanus* trees in flower (Figure 4). The presence of nearby *A. pseudoplatanus* and the woodland edge–interior contrast explain 46% of variation (marginal $R^2 = 0.46$ [fixed effects]).

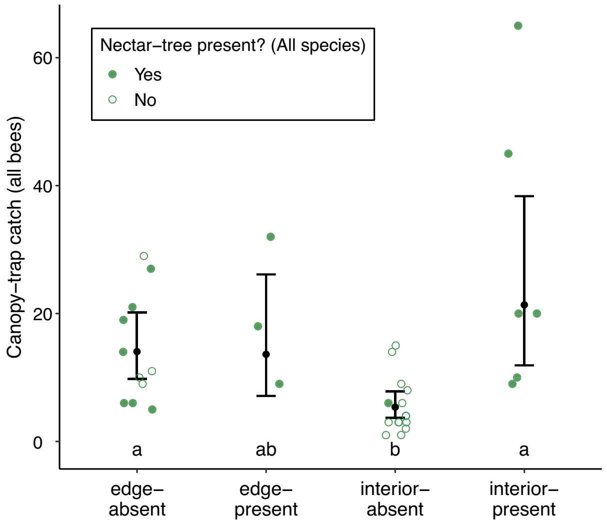

FIGURE 4 Canopy-trap catches ($n = 35$) of bees across 15 woodland sites on Raveningham Estate, UK. The left-two categories represent the woodland edge when flowering *Acer pseudoplatanus* trees are absent or present, and the right-two categories represent the same for the woodland interior. The presence of nearby nectar-producing canopy trees in flower belonging to all species (additionally including *A. campestre* and *Crataegus monogyna*) is shown with filled circles. Model estimates (black circles) with 95% CIs are superimposed. Different letters denote significant ($p < 0.01$) differences between estimated trap catches according to post hoc Tukey testing. Model estimates and tests of significance are summarised in Tables S9 and S10.

DISCUSSION

In this study, a non-negligible proportion of bee abundance originated from woodland canopies: model estimates show that canopy-trap catches of bees were on average a third as large as understory-trap catches (Figure 2a). While three out of the seven most common species were significantly more abundant in understory traps, one of these—*B. lapidarius*—was significantly more abundant in canopy traps; four—including *B. pratorum*, which was intensively sampled—were equally abundant in woodland edge and interior traps, while two—*B. lapidarius* and *B. terrestris*—were significantly more abundant in woodland edge traps (Table 3). Between strata, a further community-level difference was represented by a significant female-skew in the sex ratio of *B. pratorum* in the canopy (Figure 3a). Finally, the presence of *A. pseudoplatanus* trees flowering in the vicinity of canopy traps significantly increased bee catches in the woodland interior (by an estimated 297.0%) but not at the woodland edge (Figure 4).

Canopy and understory bee abundance

Trap catches of bees in the understory were significantly higher than those in the canopy (Figure 2a). However, this pattern does not necessarily translate to overall bee abundance in the canopy versus understory habitats if we consider habitat volume. In the understory, as defined here by the 1.5–2 m height at which we set our traps, bees are concentrated in a relatively two-dimensional plane closely bounded by the ground, whereas in the canopy bees disperse through a greater volume of habitat. Thanks to the three-dimensionally varied structure of the canopy, its volume is likely greater even if we limit the definition of suitable canopy habitat to a 3 m depth from the sun-exposed crown edges, as is implied by trap placement in the present study. Consequently, equal per-area sampling in the canopy and understory habitats will likely lead to under-sampling of the canopy. Nonetheless, other studies have also employed equal per-area sampling effort, allowing for between-study comparisons to be made.

The results of this study are in contrast to the five conducted in North America, in which canopy-trap catches were found to be significantly higher (Campbell et al., 2018; Ulyshen et al., 2010, 2020) or at least equal (Cunningham-Minnick & Crist, 2020; Urban-Mead et al., 2021) to understory-trap catches. However, in agreement with our study, two surveys in Polish woodlands found that canopy traps caught fewer wild bees with catches being on average 46.8% (Banaszak & Cierzniak, 1994) and 10.5% (Bak-Badowska, 2012) the size of understory catches, respectively. Interpreting differences remains challenging given differences among studies in the woodland systems; trap type; period of deployment; trap positions relative to the canopy exterior; and biogeographical context.

In this study, the interior understory abundance of woodlands may have been unusually high—we found that interior-trap catches were only slightly lower than edge-trap catches (Figure 2a) with little evidence that interior trap catches were any lower for four common species (Table 3). This is in contrast to the prevailing pattern in Europe—Bartual et al. (2019) investigated 62 agricultural landscapes in four countries and found that bee abundance was considerably lower in woodland interiors (just 12–13 m from the woodland edge) than at woodland edges. Four of the five North American canopy–understory studies were conducted in woodland interiors—if understory abundance is low in these studies, as might be expected (Bartual et al., 2019), then this may partially explain differing canopy–understory contrasts. Rather than canopy abundance being lower in our study, it may be that understory abundance is higher. Nonetheless, in the remaining North American study, woodland edges were sampled—with the same traps used in the present study—and bee catches were found to be equal between the canopy and understory (Cunningham-Minnick & Crist, 2020).

We suspect the high interior understory abundance in our study is a consequence of the woodlands' management for timber production. They generally had a low tree density and relatively open canopy—even at the point of canopy closure in late May—allowing for microclimatic conditions favoured by bees and their floral food sources (Hanula et al., 2016). That said, no relationship was found between ground floral resources and understory trap catches (Appendix S1) and there were examples of high understory catches in shaded locations with little or no ground flora (Table S1). Regarding the survey design, nearby flowers may draw bees away from traps despite boosting activity locally, but biological explanations could also be relevant, such as the tendency of bees to nest in or commute through woodland understories regardless of floral resources. Whatever the explanation, the equivalence of edge and interior abundance has implications for the value of managed woodlands, given that woodland edges are considered good bee habitat (Bartual et al., 2019; Proesmans et al., 2019; Sõber et al., 2020) and that woodland interiors provide a greater habitat area.

Even when understory conditions become unfavourable to bees, canopy conditions may remain constant: Campbell et al. (2018) and Ulyshen et al. (2020) found that understory bee abundance responded positively to prescribed fire and scrub removal, respectively, while canopy abundance was unaffected; and Urban-Mead et al. (2021) found that increasing canopy cover decreased understory catches, but not those of the canopy. These findings indicate that the canopy potentially has longer lasting seasonal benefits, and that these may persist even when understory management is lacking.

The use of BVTs for canopy sampling could risk merely attracting a random subset of bees from the understory, in which case catches would not be reflective of the canopy's biological significance. Given the patterns we have found between the strata (relating to species' relative abundances and sex ratios) and within the canopy (relating to the presence of *A. pseudoplatanus*) this would seem to be an unlikely scenario. Furthermore, when controlling for woodland site, trap position (edge or interior), and the presence/absence of flowering *A. pseudoplatanus*, trap height had no significant effect on canopy catches ($X^2_1 = 0.33$, $p = 0.56$), suggesting that potential trap visibility from the understory was not a relevant factor.

The influence of flowering *A. pseudoplatanus* on canopy activity

We found evidence that nearby *A. pseudoplatanus* trees in flower greatly increase interior canopy activity (Figure 4). The six trees driving this effect came from the three woodlands with the highest proportion of *A. pseudoplatanus* (Table S1). This correlation between the nearby presence of *A. pseudoplatanus* and woodland proportion of *A. pseudoplatanus* makes it difficult to infer, for example, what the influence of a single adjacent *A. pseudoplatanus* tree would be in a woodland, which otherwise lacked them. Notwithstanding this uncertainty, our results indicate that bees abundantly forage on *A. pseudoplatanus* in the canopy layer of woodland interiors. To our knowledge, canopy foraging within temperate woodland interiors has been demonstrated by only one other study: taking a different approach, Inari et al. (2012) demonstrated a link between changes in *Acer* and *Tilia* floral production over 5 years and worker production of three bumblebee species in a single woodland plot. Both solitary bees and bumblebees have been shown to forage on *Acer* (Hausmann et al., 2016) and collect large quantities of its pollen (Bertrand et al., 2019; Kämper et al., 2016; Wood et al., 2018; Wood & Roberts, 2017), while the spatially dense flowers of *A. pseudoplatanus* contain sucrose-rich nectar and protein-rich pollen—quality forage for bees (Somme et al., 2016). As such, this species—growing within woodland interiors—could represent a significant resource for wild bees in farmed landscapes.

In the absence of *A. pseudoplatanus*, edge-canopy trap catches were higher than interior-canopy trap catches and the presence of *A. pseudoplatanus* appeared to have no effect at the woodland edge, although the sample size for the latter was small ($n = 3$) (Figure 4). The nature of the woodland edge habitat may explain why canopy-trap catches were generally higher. Nectar-producing trees were likely more frequent at woodland edges than interiors (as evidenced by the number of edge traps vs. interior traps with adjacent nectar-trees—Figure 4). Edge-tree crowns tended to be larger and extend lower, while the distinction between the understory and canopy was less clear-cut, with hedges and understory trees extending towards the canopy, providing foraging habitat that might facilitate vertical movement. Additionally, the southern-edge habitat receives more sunlight and is exposed to non-woodland agricultural habitats from which bees may be recruited.

The effect of habitat on species' abundance

While the 11 most abundant species were present in all four habitats (*B. vestalis* was absent from IG traps), we found evidence for significant community-level effects of the understory–canopy contrast and of the woodland edge–interior contrast (Table S5). Two species in particular, *B. lapidarius* and *B. terrestris*, contributed to community-level differences. Both species were significantly more numerous in woodland-edge traps, while the remaining species had no significant associations with the woodland edge or interior (Table 3). *Bombus lapidarius* was significantly more numerous in canopy traps (Table 3), while of the remaining six abundant species (>49 individuals), *B. terrestris* had the weakest association with the understory relative to the canopy. *Bombus terrestris* is thought to have a particularly strong preference for open habitats (Eckerter et al., 2020)—for example, in a study comparing its movements with *B. pascuorum*, *B. terrestris* was less likely to enter forested areas and was suspected of flying over them during foraging commutes (Kreyer et al., 2004). *Bombus lapidarius* males are known to patrol tree tops and it is assumed that this is part of mating behaviour (Ayasse et al., 2001). However, the 82 bees contributing to the pattern in this study were all female, and 85% of these were workers. As such, it appears that *B. lapidarius* has an additional canopy association, at least for the limited time covered by the study period, that is not connected to mating behaviour—a novel finding to our knowledge.

In their synthesis, Kells & Goulson (2003) consider *B. lapidarius* to be more thermophilic than other common European bumblebees, highlighting that *B. lapidarius* workers begin their daily forage later and finish earlier; that they have a higher temperature threshold; and that *B. lapidarius* nests are more commonly found in sun-exposed locations. This might partly explain the high abundance of this species at the sunlit woodland-edge canopy and low abundance in the interior understory (Figure 2b). Similarly, in New Zealand, significantly higher numbers of non-native *B. terrestris* were caught in the canopy than in the understory, an effect possibly facilitated by higher canopy light levels (Ewers et al., 2013).

Interpreting the purpose of canopy activity can be challenging, however. In our study, most woodlands lacked abundant nectar-producing trees (Table S1) and canopy floral resources were probably very low during trap deployment. *Quercus robur* and *F. excelsior* were dominant across most sites (Table S1), but the catkins of the former appeared not to contain live pollen and the latter species was no longer in flower. In New Zealand, Ewers et al. (2013) report that floral resources were low in their sampled woodlands and suggest canopy traps caught *B. terrestris* commuting between non-forest food resources. They used non-attractive intercept traps, set at three-quarters of canopy height in woodland interiors. This would suggest that if bees were commuting, they were doing so *within* rather than above the canopy. Similarly, the attractive vane traps used in our study were generally well-concealed, especially from above, and we consider it more likely that captured bees were active within the canopy rather than outside it.

Ewers et al. (2013) also anecdotally report much greater canopy abundance of *B. terrestris* in a woodland infested with a honeydew-producing scale insect, while Ulyshen et al. (2010) found bees to be abundant in the canopy even when trees were not producing pollen or nectar—in both studies, the authors suggest a role for non-floral resources, which could be critical for some species (Requier & Leonhardt, 2020). Further complicating matters, an absence of resources, whether floral or non-floral, may not preclude active searching behaviour within canopies. Bees may have, as yet unstudied, hard-wired tendencies to visit canopies, perhaps according to the time of year, and/or canopy exploration may be reinforced by prior foraging success (Lihoreau et al., 2012). In this study, *B. lapidarius* may have had prior success foraging on *Q. robur* catkins, which were live and developing in the weeks before sampling took place.

Canopy sex ratios

We found that the sex ratio of *B. pratorum* was significantly skewed towards females in the canopy (Figure 3a), and we detected a similar, marginally significant pattern in *B. hortorum* (Figure 3b). In northeastern United States, Urban-Mead et al. (2021) also found a significantly female-skewed sex ratio in the canopy, which was driven by solitary bees. Our study may be the first in a temperate region to show a vertically stratified sex-ratio difference in a native social bee. Urban-Mead et al. (2021) speculate that their observed sex ratio is the consequence of female bees foraging in the pollen-rich canopy of woodlands dominated by wind-pollinated trees, while males, which do not forage for pollen, would have less reason to enter the canopy. However, there are other, non-mutually exclusive, potential reasons for our observed sex ratios. First, while males have been shown to avoid flowers that do not produce nectar, even within nectar-producing species, differences have been found in the preferences of male and female bees (Roswell et al., 2019). Observed sex ratios, therefore, have the potential to relate to varying preferences in nectar-producing species between the canopy and understory. Second, males may avoid the canopy, not because it lacks nectar per se but because they are constrained to the understory by their mating behaviour. *Bombus pratorum* (Ayasse et al., 2001) and *B. hortorum* (Goulson, 2010) males are known to patrol and scent mark at ground level, which may partly explain their relatively high understory abundance in our study.

Canopy communities and foraging potential

Quercus pollen is rich in protein (Roulston et al., 2000) and can represent an abundant and high-quality food resource for bees (Bertrand et al., 2019). During trap deployment in our study, a single bumblebee—species not identified—was observed (by GA) foraging on *Quercus* catkins, while, in the United Kingdom, bumblebees have been observed foraging on the flowers of other wind-pollinated tree genera (DoPI, 2022). However, while evidence for *Quercus* pollen collection among solitary bees is extensive (Saunders, 2018), it is scarce among bumblebees (Wood et al., 2021). This could be due, in part, to the biases inherent from sampling foraging worker bees—particularly the paucity of early-season sampling—alternatively, it could be a reasonable reflection of evolved differences in pollen diets between the major bee taxa (which are present within these taxa—Haider et al., 2014; Wood et al., 2021). If the latter is true, it may be unlikely that pollen collection from wind-pollinated trees drives the patterns of bumblebee canopy activity observed in our study.

Nonetheless, the potential for woodland canopy foraging, and pollen collection specifically, is evident: 21 out of 22 non-parasitic species in which females were sampled were found in canopy traps (Table S3), and 9 out of the 10 sampled *Andrena* species were present within interior canopies. It seems likely that many species could take advantage of nectar-producing trees in temperate woodlands, while *Osmia* and *Andrena* could additionally exploit *Quercus* and *Fagus*. The three most abundant *Andrena* species in our study collect, on average, 20.4% of their pollen from *Acer*, *Fagus*, *Quercus* and *Castanea* (in order of pollen-abundance, calculated from Wood & Roberts, 2017). Bees may also be more likely to forage from wind-pollinated trees when nectar-sources are present, producing potential synergies when they co-occur: our observation of *Quercus*-foraging by a bumblebee was made within metres of a flowering *Sorbus aucuparia* tree on which many bumblebees were feeding; observations by Raw (1974) using cut flowers, indicate that *O. bicornis* will take nectar from other plants during bouts of *Quercus*-pollen collection, and Coudrain et al. (2016) found that more *Quercus* pollen was collected when (nectar-producing) *Salix* stands were nearby.

Future directions

In order to make inferences of pollen collection by female bumblebees in the canopy, a better characterisation of early-season pollen diets of different species is needed. In Europe, only the early-season diet of *B. terrestris* has been well-characterised (Bertrand et al., 2019; Eckerter et al., 2020; Kämper et al., 2016), with high levels of *Acer* pollen-collection demonstrated. Bumblebees are much less numerous early in the season, and greater effort is required to collect their pollens in an unbiased manner. However, the few individuals active early in the season could be vital to colony establishment and success (Mola et al., 2021). Accordingly, significant early-season pollen collection from canopy-tree taxa in additional bumblebee species would indicate an important role for the woodlands that contain these trees in supporting bumblebee populations.

To achieve more accurate representations of bee communities in the canopy, and increase sampling of solitary bees relative to bumblebees, pan traps could be used in conjunction with BVTs. Given that pollen collection from wind-pollinated trees is widespread among solitary bees (Saunders, 2018), vertically stratified patterns of abundance in this group could be particularly well developed. Future studies will benefit from canopy sampling throughout the season to investigate potential responses in bee activity as different canopy-tree species, such as *Tilia cordata* and *Castanea sativa*, come into flower later in the season. It would be informative to sample woodlands of higher tree density, which may be more representative of those found in most European agricultural landscapes (Bartual et al., 2019). The independence of canopy and understory processes demonstrated in North American studies (Campbell et al., 2018; Ulyshen et al., 2020; Urban-Mead et al., 2021) would suggest that the canopies of these woodlands would still harbour bees, but this needs direct investigation.

Although extensively addressed in North America, the factors affecting a woodland understory's capacity to support bees is an area of investigation largely neglected in Europe (though see Korpela et al., 2015 for an example). Given the relatively high understory abundance of bees in woodland interiors demonstrated in the present study, it would seem to be an important area of investigation—managed woodlands could be highly beneficial to farmland bee communities. Observational methods, comparing bee activity between woodlands and open farmland through the season, could be used to establish the relative frequency of nesting, foraging and commuting behaviours within these habitats, while avoiding the potential problem of high floral resources reducing trap-catch rates.

CONCLUSIONS AND IMPLICATIONS FOR CONSERVATION

To our knowledge, this is the first UK study to sample bees of the woodland canopy, and, as such, novel discoveries have been made. We have shown that the canopy of mature woodlands is visited by a diversity of bee species in late spring; that it can harbour a potentially significant proportion of a woodland's overall bee abundance; and that, relative to the understory, at least one common bumblebee species is more abundant here. We have also shown that canopy activity in woodland interiors is greatly increased when nearby *A. pseudoplatanus* trees are in flower. Finally, and in contrast to the prevailing evidence in Europe, we have demonstrated that several species are as abundant in woodland interiors as they are at woodland edges. These findings suggest a more significant role for woodlands in European bee conservation than may currently be supposed; they indicate that ground-level woodland surveys may not be enough to characterise the full abundance and diversity of bees; and they open avenues for the management of woodland interior canopies to support bee populations.

AUTHOR CONTRIBUTIONS

Guthrie Allen: Conceptualization (equal); data curation (lead); formal analysis (lead); investigation (lead); methodology (equal); visualization (lead); writing – original draft (lead); writing – review and editing (lead). **Richard Davies:** Conceptualization (equal); methodology (equal); supervision (lead); writing – review and editing (supporting).

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CONFLICT OF INTEREST

There are no conflicts of interest to be declared among the authors of the manuscript.

DATA AVAILABILITY STATEMENT

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

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SUPPORTING INFORMATION

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

Table S1. Summary of woodland site locations and characteristics; trap positions; ground flora and shading estimates; nearby nectar-producing trees; and trap catches.

Table S2. Summary of tests for spatial autocorrelation on univariate model residuals.

Table S3. Summary of abundance by sex, and canopy/understory presence, for all species caught in all traps.

Tables S4 to S11. Summaries of statistical models.

Appendix S1. Understory floral resources and shading—methods, results, and interpretation.

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