

CAMERA-TRAP MONITORING REVEALS FLOWER VISITOR DIVERSITY AND DIEL ACTIVITY PATTERNS IN THE FOREST UNDERSTORY: BRAMBLE PATCHES (*RUBUS FRUTICOSUS* AGG.) AS A MODEL SYSTEM

Louise Bonneau-Chloup¹, Cécile Hignard², Baptiste Lemaire¹, Sophie Pasek³, Sylvie Meyer^{1*}, Laurence Walch^{1*}

¹Sorbonne Université, CNRS, IRD, INRAE, Université Paris Est Créteil, Université Paris Cité, Institut d'Ecologie et des Sciences Environnementales de Paris (IEES-Paris), 75005 Paris, France

²Université Paris Cité, Station d'Ecologie Forestière de Fontainebleau, 77300 Fontainebleau, France

³Sorbonne Université, Muséum d'Histoire Naturelle, CNRS, Ecole Pratique des Hautes Etudes, Université des Antilles, Institut de Systématique, Evolution, Biodiversité (ISYEB), 75005, Paris, France

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*Corresponding authors:
sylvie.meyer@sorbonne-universite.fr &
laurence.walch@sorbonne-universite.fr

Abstract—Pollinator communities in deciduous temperate forest understories remain poorly understood, particularly regarding the relative roles of temporal activity patterns and microclimatic conditions in structuring flower visitor assemblages. We developed a non-invasive video monitoring system to investigate flower visitor communities on brambles (*Rubus fruticosus* agg.) across four forest patches in the Fontainebleau forest (Île-de-France, France), recording 3,636 visits from 17 morphotype groups during 369 hours. Ants dominated visits (45%), followed by non-syrphid flies (10%), whereas bees, hoverflies, and Lepidoptera together accounted for 32%. Visitor assemblages exhibited substantial spatial and temporal variation, with evidence of temporal niche partitioning. Generalized additive mixed models (GAMMs) revealed taxon-specific diurnal activity patterns, with most taxa peaking during late morning to afternoon (10:00–18:00), though ants showed crepuscular activity and some groups including non-syrphid flies and hoverflies displayed bimodal distributions in certain patches. Nocturnal activity was observed for several taxa. Microclimatic effects on visitor occurrence were taxon-specific and limited: non-syrphid flies and ants responded negatively to light intensity. In addition, non-syrphid flies and hoverflies showed shorter visit durations under higher light intensity, and non-syrphid flies additionally showed temperature-dependent foraging behaviour, reducing visit duration by 57% per 10°C increase. Visit duration varied markedly among taxa, ranging from a few seconds in bumblebees and hoverflies to over an hour in some Coleoptera and Orthoptera. These findings reveal that forest flower visitors partition temporal niches more strongly than microclimatic niches. This non-lethal monitoring approach successfully captured complex ecological patterns, demonstrating brambles' potential as a model system for forest pollination ecology while preserving natural environmental contexts and enabling continuous day-night observations.

Keywords—floral visitor community, temperate forest, temporal niches, microclimate, video monitoring, *Rubus*

INTRODUCTION

Temperate forests provide a diverse array of essential resources that support pollinator communities throughout the growing season. Native forests offer critical nesting and overwintering habitats for ground-nesting, cavity-nesting, and wood-boring bee species through

dead wood, hollow stems, and areas of bare soil (Ulyshen et al. 2023). Forests also supply abundant and temporally diverse floral resources from understory herbaceous plants, shrubs, and canopy trees; notably, even wind-pollinated tree species such as oaks (*Quercus* spp.) provide readily accessible pollen that is heavily exploited by bees and hoverflies during early spring when other

resources are scarce (Saunders 2018; Urban-Mead et al. 2021; Mola et al. 2021; Ulyshen et al. 2023). Beyond floral resources, forests provide non-floral sugar sources such as honeydew (Ulyshen et al. 2023), and tree resins collected and used as nesting materials by bees in the families Apidae and Megachilidae (Requier & Leonhardt 2020; Ulyshen et al. 2023). Furthermore, forests may serve as climatic refugia, with canopy closure buffering flower-visiting insect communities in the understory from temperature extremes, potentially mitigating some impacts of climate change (Díaz-Calafat et al. 2026). The diversity, abundance, and phenological complementarity of these resources throughout the growing season make forests important supporting habitats for maintaining diverse and stable pollinator populations in temperate landscapes.

In return, these forest-dependent flower visitors provide essential ecological functions, especially in the reproductive success of forest plants in different layers. Understory spring-flowering herbs rely primarily on flies, solitary bees, and bumblebees for reproduction, with bumblebee-pollinated species showing particularly high interannual variability in pollination success (Motten 1986; Kudo et al. 2008). Understory shrubs, such as European bilberry (*Vaccinium myrtillus*), are pollinated by wild bees (*Andrena*, *Bombus*, *Lasioglossum*), producing fruits that constitute a critical food resource for forest fauna, including the threatened capercaillie (*Tetrao urogallus*) whose winter survival depends on this production (Eckert et al. 2019). Some overstory trees such as chestnut require insect pollination, mainly by beetles, to produce nuts (Larue et al. 2021) that also constitute an important food resource for forest fauna. These pollination roles are essential to support food web interactions and plant community regeneration, and therefore to support the forest biodiversity and ecosystem functioning (Neuschulz et al. 2016). Beyond their role within forests, forest-associated pollinators provide critical pollination functions to adjacent agricultural systems through spatial spillover (Kremen et al. 2002; Ulyshen et al. 2023). Forest edges supply early-spring floral resources from canopy trees and understory plants, supporting wild bee and hoverfly populations that subsequently move into neighbouring apple orchards fields during bloom periods (Urban-

Mead et al. 2023). This spillover effect has also been demonstrated for oilseed rape fields (Bailey et al. 2014), and other pollinator-dependent crops (Garibaldi et al. 2013), with pollinator abundance and diversity declining with increasing distance from forest edges in temperate agricultural landscapes (Bailey et al. 2014; Alison et al. 2022).

However, the mechanisms that structure pollinator communities and underlying pollination functions remain poorly understood in European forest ecosystems. As in other ecosystems, insect pollinators may enhance plant reproductive success through increased visitation rates, complementary pollination among species with differing traits, and temporal partitioning of foraging activity (Garibaldi et al. 2013; Fründ et al. 2013). Temporal complementarity, where pollinator species partition foraging activity across times of day or season, is increasingly recognized as a key mechanism underlying such benefits, reducing interspecific competition and stabilizing pollination functions (Blüthgen & Klein 2011; Fründ et al. 2013). This temporal partitioning among co-occurring pollinators has been linked to differences in circadian regulation, thermoregulatory physiology, and competitive interactions (Willmer 1983; Fründ et al. 2013; Bloch et al. 2017; Blareau et al. 2025). In forest ecosystems, microclimate heterogeneity may further modulate these temporal patterns, community composition, and pollination outcomes. Pollinator activity in forests is strongly constrained by local environmental conditions, with temperature and light availability influencing both the timing and intensity of flower visitation throughout the day (Beattie et al. 1984; Herrera 1995). Microclimate conditions also structure pollinator communities; for instance, dipterans preferentially forage in lower light intensity conditions while hymenopterans exploit the full light intensity gradient (Herrera 1997). Recent boreal studies have further demonstrated taxon-specific responses to microclimate, with local temperature acting as a primary filter controlling bumblebee occurrence and light modulating their foraging activity (Bartholomée et al. 2025), while both temperature and light influence dipteran occurrence and foraging duration (Díaz-Calafat et al. 2026). Vertical microclimate gradients may shape bee community composition and diversity in forests, as suggested by studies in edge forests

showing distinct assemblages in the warmer, sunnier canopy versus shadier understory (Urban-Mead et al. 2021). These microclimate-driven differences in pollinator communities can have consequences for plant reproductive success; for instance, long-term monitoring of bilberry (*Vaccinium myrtillus*) in Finnish Lapland revealed that reproductive success was twice as high in a forested site compared to a distant open site, which was speculated to be in part due to a larger pollinator network in the forest (Boulanger-Lapointe et al. 2017). Despite these insights into how microclimate shapes pollinator community structure, activity patterns, and reproductive outcomes, empirical tests of how temporal complementarity among forest pollinators, and its interaction with microclimate variation, ultimately affects pollination functions remain scarce, particularly in temperate deciduous forests.

Empirical investigation of these processes in forest understories has long been hampered by the cryptic nature of pollinator activity under dense canopy cover and the difficulty of continuous observation at fine temporal scales. Among emerging approaches, insect camera traps show promise for monitoring floral visitor activities at different spatiotemporal scales (Bjerger et al. 2022; Ştefan et al. 2025; Høye et al. 2025; Serra-Marin et al. 2025). Applying this method in the context of forest ecology requires targeting a suitable plant, a native, perennial, entomophilous species found across various stands, persistent at the same locations over multiple years, and whose large generalist flowers are technically accessible and visited by a diversity of taxa. While camera traps have been used to study pollination of specific plant species in forested environments (Houlihan et al. 2019), to our knowledge no study has yet combined this approach with a widespread generalist species to characterize and compare flower visitor communities across several temperate forest sites.

Here, we developed a non-invasive, low-cost video-monitoring approach deployed on bramble flowers to monitor flower visitors, activity, and behaviour continuously, both during the day and at night, in forest stands. This system addresses several pressing needs in insect monitoring: (i) ethical concerns regarding lethal sampling methods (Barrett & Fischer 2024), particularly

given the well-documented long-term declines in terrestrial insect abundance and biomass (Van Klink et al. 2020); (ii) the growing interest in citizen science initiatives that require accessible, low cost and simple monitoring tools (Van Klink et al. 2022); (iii) the compatibility of this approach with the rapid development of machine learning algorithms for automated insect identification, which could substantially reduce the analytical burden of large-scale image processing in future applications (Van Klink et al. 2022); and (iv) the need to monitor multiple morphological groups including non-syrphid flies and ants that are often overlooked in traditional pollination studies (Van Klink et al. 2020). We used bramble (*Rubus fruticosus* agg.) as a model system because it is a long-lived perennial, widespread plant in temperate deciduous forests that provides both pollen and nectar as valuable foraging resources for a diverse array of long- and short-tongued flower visitors, among which bees, hoverflies and Lepidoptera are documented as effective pollinators and are hereafter referred to as “known *Rubus* pollinators” (Gyan & Woodell 1987a, 1987b; Baude et al. 2016; Wignall et al. 2020; Anderson et al. 2023). Although *Rubus fruticosus* agg. is a complex of taxa, most of which are apomictic polyploid hybrids producing seeds without fertilization, pollination is still required to trigger asexual seed development, making bramble suitable for investigating flower visitor communities and behaviour (Nyblom 1985; Sochor et al. 2015). Moreover, focusing on natural vegetation avoids the potential biases introduced by artificial attractants (Høye et al. 2025) and, should in long term, reinforce the ecological meaning of the observations.

As a proof of concept, we deployed *in situ* camera traps on bramble flowers coupled with microclimate monitoring across four temperate deciduous forest sites with contrasting microclimates, to evaluate the capacity of this approach to capture ecologically meaningful variation in flower visitor communities and behaviour. Specifically, we assessed whether this system is capable of (1) characterizing diel activity patterns of major flower visitor taxa, (2) detecting temporal partitioning of foraging activity among co-occurring taxa, and (3) examining associations between microclimate conditions and visitor occurrence. Provided the system successfully

captures known pollinator taxa and ecological processes, we expected (i) distinct diel activity peaks among taxa, consistent with known differences in foraging ecology, (ii) reduced temporal overlap among co-occurring taxa relative to random expectation, and (iii) visitation occurrence positively associated with locally favourable microclimatic conditions.

MATERIALS AND METHODS

STUDY SITES

We selected four study sites in the Fontainebleau forest (Île-de-France, France), which provides a wide range of forest stands and management types (Table 1). To secure the equipment, all sites were located within fenced areas or private parts of the forest. At each site, we selected one bramble patch (*Rubus fruticosus* agg.), referred to as P1 to P4. All patches were located within homogeneous forest stands under semi-shaded conditions (small treefall gaps). Sites selected represent oak-dominated deciduous forests. Sites P1 to P3 were located within the experimental forest plots of CEREEP–ECOTRON, adjacent to the *Forêt de la Commanderie*, while P4 was in the Réserve biologique dirigée de la Touche aux Mulets (plot 608, *Forêt de Fontainebleau*). Although the patches are geographically close, they differ in canopy openness, floral cover, and surrounding forest structure, introducing natural variability in the data. Sampling dates also varied among sites due to logistical constraints, which may represent potential sources of bias. A summary of site characteristics, including geographic coordinates, forest composition, floral cover, bramble size, habitat openness, and recording periods, is provided in Table 1. Beehives were installed at CEREEP on 22 June 2024, during the sampling period, approximately 400 m from patch P1. This installation was not part of the study design and occurred without prior notice, it represent an unplanned confounding factor modifying honeybee dynamics at and near P1. Recordings were carried out between early June and early July 2024 across all sites, during the bramble flowering season (Table 1). All times are reported in local summer time (UTC+2).

BRAMBLE PATCHES AS MODEL SYSTEMS

Bramble patches (*Rubus fruticosus* agg.) were selected as a model system for several reasons.

Bramble flowers provide a generalist floral resource (pollen and large volume of nectar) that attracts a wide diversity of pollinators, including bees, hoverflies, and Lepidoptera (Percival 1946; Wignall et al. 2020; Anderson et al. 2023). Their widespread occurrence in forest understories ensures accessibility across multiple sites. The flowering period of brambles is relatively long, with a peak from June to July, allowing for repeated observations. Additionally, brambles occur at a sufficiently high mean floral cover (Table 1), and their flowers have a relatively large corolla, which likely improves detectability and accuracy in camera-based monitoring. Individual flowers last around two days. During our recording sessions, petal loss was occasionally observed, however flower continued to receive visits through each session. Flower phenology was not experimentally controlled. Within a given bramble patch, flowers did not always close at night; some showed petal movements depending on light intensity, with partial closure under cloudy or shaded conditions and reopening within minutes when exposed to sunflecks. Finally, *Rubus fruticosus* agg. encompasses phenotypic variation among microspecies (apomictic clonal lineages), which may introduce uncontrolled variability in floral traits and visitor attraction across sites, though this has not been formally demonstrated. Bramble microspecies were not distinguished within and among patches in this study, partly due to the inherent difficulty of identifying *Rubus fruticosus* agg. microspecies (Sochor et al. 2015).

AUTOMATED CAMERA-TRAP SURVEYS OF FLOWER VISITOR

Flower visitor activity was recorded from 4 June to 5 July 2024 using trail cameras (Ceyomur 65 CY65, 4K, 40 MP, China) equipped with a macro lens (+10, 37 mm, Annadue, China). Black tape was applied over the camera's infrared LED to prevent overexposure in night-time images. Each camera was positioned approximately 10 cm from the bramble flowers, facing north, and mounted at flower height using a support arm attached to a stake in the ground (Fig. S1A). Videos were recorded at 30 frames per second with a resolution of 3840 × 2160 pixels, providing excellent image quality, as shown in Figures 1, S1B, S1C and S2. A total of seven cameras were deployed, with 3–4 cameras per bramble patch. Video recordings were conducted for 5–7 consecutive days per site under

Table 1. Characteristics of the bramble patches monitored in Fontainebleau forest (Île-de-France, France). Mean floral cover was estimated by counting the number of flowers per m² using quadrats, based on an average of five measurements per patch. Habitat openness was visually estimated from the canopy cover percentage within a 1-hectare area surrounding each bramble patch. Flowers receiving ≥ 1 visit indicates the number of distinct flowers that received at least one visit during the study period; flowers present in the camera field of view but never visited (likely senescent or unattractive) were not assigned individual identifiers and were therefore not included in the dataset.

Patch	Geolocation (WGS84)	Distance from P1	Dominant forest type	Bramble characteristics			Habitat openness (% ha)	Start/End of recording	Number of recording days	Camera- hours	Flowers visible simultaneously on a given video (median, range)	Flowers receiving ≥ 1 visit
				Area (m ²)	Average height (cm)	Mean floral cover (m ²)						
P1	48.2843° N, 2.6668° E	–	Oak–ash woodland (<i>Quercus petraea</i> – <i>Fraxinus excelsior</i>)	> 300*	~110*	18.4	42	19–27 June	6	104.5	4 (1–4)	43
P2	48.2856° N, 2.6701° E	335 m	Oak–hornbeam woodland (<i>Quercus petraea</i> – <i>Carpinus betulus</i>)	322	60	4.1	40	4–13 June	5	67	1 (1–2)	15
P3	48.2876° N, 2.6748° E	647 m	Oak–beech woodland (<i>Quercus petraea</i> – <i>Fagus sylvatica</i>)	60	60	2.3	10	26 June–5 July	6	94	4 (1–8)	61
P4	48.3907° N, 2.5944° E	12.9 km	Oak woodland (<i>Quercus pubescens</i>)	50	40	2.2	7	4–11 June	7	103.5	2 (1–2)	21

*The large size and limited accessibility made the assessment approximate.

calm weather conditions. Cameras recorded continuously, capturing sequential 3-minute videos separated by a 2-second interval between recordings (no motion-triggered detection was used, as this is unreliable for small insects on flowers). Some interruptions occurred due to camera malfunctions (technical bugs), which were sporadic and not associated with environmental conditions, and thus unlikely to introduce systematic bias. Rainy days were not sampled because videos recorded during precipitation are typically unusable. This leads to an underrepresentation of extreme microclimatic conditions (high humidity, low light), but this bias is ecologically acceptable as flower visitor activity is naturally minimal during rainfall. To account for occasional gaps in recording, all sampling periods were reconstructed from video metadata, distinguishing true absences of visitors from periods without recording. In addition, since nighttime visitor activity was lower than their daytime counterparts (representing 9.8 % of total activity; see Table S1); analyses focus on diel activity between sunrise (05:00) and sunset (22:00). Sampling coverage varied among sites and dates, with observation periods starting and ending at different times relative to sunrise (Fig. S3). Overlapping recordings from multiple cameras at the same patch and time (95 hours, 25.7% of monitoring time, affecting 24.7% of observations during the period 5h00-22h00) were accounted to standardize sampling effort across intervals with variable numbers of active cameras.

MICROCLIMATE MONITORING

Simultaneously with video recordings, microclimatic conditions were measured at flower height using data loggers (HOBO0169, Prosensor, France) positioned next to the cameras (Fig. S1A). Air temperature and light intensity were recorded at 1-minute intervals throughout the sampling period. Air temperature and light intensity were selected because both factors strongly influence pollinator activity and foraging behaviour, particularly in forest understory environments (Bartholomée et al. 2025; Díaz-Calafat et al. 2026). Relative humidity was also recorded but was not used in the analyses because it was strongly correlated with air temperature. The maximum temperature recorded across the study (43.4°C, at P1) likely reflects brief direct sun exposure of the

sensor through canopy gaps, consistent with the higher openness of this patch (42%; Table 1).

IDENTIFICATION OF FLOWER VISITORS

All videos (9472 in total) were reviewed by direct visual observation, and each flower visit was recorded manually. Visitors were classified into broad morphological categories that could be reliably identified from the video footage, each assigned a code in the data collection table. In this study, we use the terms “taxon” and “morphotype group” interchangeably to refer to these morphological categories. The following morphotype groups were used: **Diptera**: hoverflies or syrphid flies (SYR) and non-syrphid flies (NSYR); **Hymenoptera**: honeybees (AM), halictid-like bees (HAL), bumblebees (BUM), other bees (API), and ants (ANT); **Lepidoptera**: adults (LI) and caterpillars (LC); **Coleoptera**: longhorn beetles (CER) and other beetles (COL); **Orthoptera** (ORT); **Heteroptera** (HET); **Arachnida** (ARA); **Isopoda**: woodlice (WOO); **Gastropoda**: slugs (SLU); and unidentifiable insects (INS) (Fig. 1). HAL is a catch-all morphological category comprising small bees that could not be reliably distinguished to family level from video footage; this group may include Andrenidae or other morphological similar small bee taxa in addition to Halictidae. The “other bees” category (API, $N = 82$) comprised bees that could not be confidently assigned to a more specific morphotype: 69 individuals tentatively identified as honeybees but for which the forewing marginal cell was not sufficiently visible to confirm the diagnostic features, and 13 large wild bees that could not be reliably categorized. Additionally, 33 flower visits (INS) could not be identified beyond class Insecta. Overall, 115 visits (3.2% of the 3,636 total observations) could not be assigned to a specific morphotype.

VISITOR ACTIVITY AND BEHAVIOUR

For each visit, the following information was recorded: flower number (if multiple flowers appeared in the video), morphotype code, time of arrival and departure from the flower, and additional notes, including whether the visitor was still present at the end of the video to allow calculation of total visit duration. Each flower contact was treated as an independent visit event, regardless of whether the same individual may have visited multiple times, as individual tracking

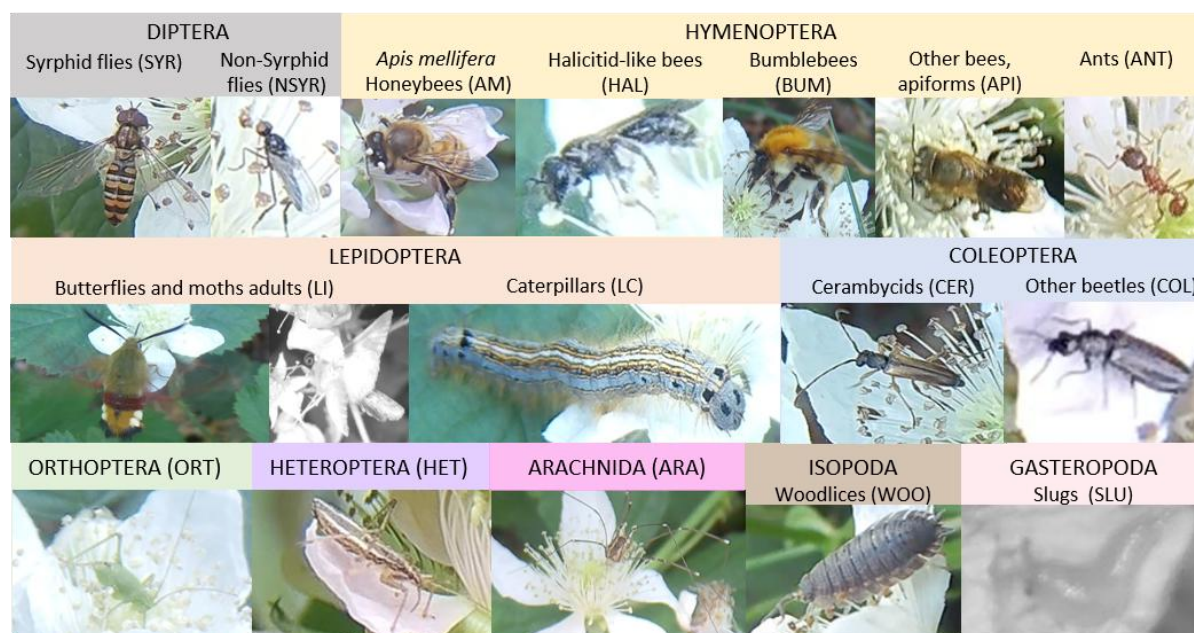


Figure 1. Illustration of the taxon categories used for video analysis. Images were extracted from video footage and are presented with zoom adapted to visitor size.

was not feasible without marking. Visitor activity was quantified as the number of visits per time interval, and total visit duration was used as a measure of foraging behaviour and/or other activities such as resting or mating.

STATISTICAL ANALYSES

All statistical analyses were performed in R version 4.2.3 (R Core Team 2023).

To explore spatial and temporal variation in flower visitor assemblages, we calculated relative abundances for each morphotype group, sampling day, and bramble patch. When multiple cameras filmed the same patch simultaneously, visit numbers were normalized by dividing by the number of active cameras to standardize sampling effort across days. Relative abundances were calculated as normalized visits per morphotype divided by total normalized visits per day. Temporal variability was visualized with boxplots and quantified using coefficients of variation ($CV = SD/mean \times 100$) for each taxon-patch combination.

To characterize diurnal activity patterns of flower visitors, Generalized Additive Mixed Models (GAMMs) were fitted separately for each taxon-patch combination, reflecting genuine ecological differences in visitor communities among patches, using the “mgcv” package (Wood

2011). The unit of replication was the hourly visit count per sampling date, with sampling date included as a random effect ($s(Date, bs = "re")$) to account for between-day variability. Cameras were positioned to film distinct floral neighbourhoods with no overlapping fields of view, ensuring independence among camera-level observations within each patch. Individual flower identity was not included as a random effect, as visits were aggregated at the patch level. Only combinations with at least 30 observations during daytime hours (5:00–22:00) were retained to ensure sufficient data for stable estimation of smooth terms. For each taxon-patch combination, Poisson, quasi-Poisson and negative binomial distributions were tested and compared by Akaike Information Criterion (AIC) comparison and residual diagnostics. The negative binomial was preferred when AIC was lower than Poisson, and quasi-Poisson was retained when overdispersion exceeded 1.5. Zero-inflated models (to account for excess zeros from non-visits) were initially tested but did not improve model fit and were excluded. The number of visits (activity) per taxon was modelled as a smooth function of hour ($s(Hour, bs = "tp", k = 8^{**})$), increased to $k = 16$ for two models where basis dimension checks indicated insufficient flexibility), where bs specifies the basis function type (thin plate regression spline) and k

determines the maximum degrees of freedom for the smooth term. Variable sampling effort when multiple cameras recorded simultaneously at the same patch and time was controlled for by including an offset term $\log(\text{nb_cameras})$ in all models. Predicted hourly activity curves ($\pm$ SE), averaged across all sampling dates, were plotted to visualize temporal niche partitioning among visitor groups. Activity peaks were identified as the hour with maximum predicted activity for each taxon-patch combination showing significant temporal patterns.

To quantify temporal niche overlap among co-occurring visitor taxa, we calculated pairwise overlap indices from individual visit timestamps using the *overlap* package (Ridout & Linkie 2009) in R. Each timestamp was converted to radians. Overlap was estimated using kernel density estimation to smooth discrete observations into a continuous distribution, with the overlap estimator *Dhat4* for sample sizes ≥ 50 and *Dhat1* for smaller samples, following the authors' recommendations. Bootstrap confidence intervals (95%, 999 replicates) were computed using the *bootCI* function. To test whether observed overlap was lower than expected by chance, a null distribution was generated by randomly permuting visit timestamps across taxa within each patch (999 permutations). A one-tailed *P*-value was computed as the proportion of permuted overlap values equal to or lower than the observed value, testing whether temporal segregation exceeded chance expectation.

To identify microclimatic drivers of visitor occurrence independently of diel temporal patterns, occurrence probability was modelled per 15-minute interval using GAMMs (binomial distribution, logit link) fitted with the "mgcv" package (Wood 2011). The unit of replication was the 15-minute interval per patch per sampling date. Taxa with at least 100 visits were retained to ensure sufficient data for reliable parameter estimation; all taxa included in the analysis had at least 160 visits during the observation period (06:00–20:00, when light intensity was sufficient for measurement). Cameras were positioned to film distinct floral neighbourhoods with no overlapping fields of view. Individual flower identity was not included as a random effect, as visits were aggregated at the patch level. An offset

for the logarithm of the number of active cameras per interval was included to account for variable sampling effort. Sampling date and bramble patch were included as random effects ($s(\text{Date}, \text{bs} = \text{"re"})$ and $s(\text{Roncier}, \text{bs} = \text{"re"})$) to account for temporal and spatial variability unrelated to microclimate. To account for the strong diel covariation between temperature, light intensity and visitor activity, time of day was included as a smooth term ($s(\text{Hour}, \text{bs} = \text{"tp"}, k = 8)$) in all models. Temperature and log-transformed light intensity (to account for variation over several orders of magnitude) were moderately correlated (Pearson's $r = 0.61$, $P < 0.001$; VIF = 2.09), indicating acceptable collinearity levels. For each taxon, three models were fitted and compared by AIC: temperature only, log-transformed light intensity only, and a combined model including both predictors as fixed effects. Residual diagnostics were assessed via simulation (500 iterations) using the "DHARMa" package (Hartig 2024). All models passed dispersion and zero-inflation tests ($P > 0.05$).

To assess microclimate effects on visit duration, we fitted linear mixed models (LMMs) with log-transformed visit duration as the response variable, using the "lme4" package (Bates et al. 2015). Only visits recorded between 06:00 and 20:00 were included and analyses were restricted to five taxa with sufficient sample sizes (AM, ANT, BUM, NSYR, SYR; $N = 2,465$ observations). Temperature (centred) and log-transformed light intensity were tested as fixed effects. To test whether microclimate effects varied among taxa, we included taxon $\times$ microclimate interactions as fixed effects, with site (bramble patch) and sampling date as random intercepts to account for spatial and temporal correlation in the data. The logarithm of the number of active flowers per video was included as an offset to control for sampling effort. Model selection was performed using likelihood ratio tests to assess the significance of interaction terms. Residual diagnostics (QQ plots and residual vs. fitted plots) revealed slight deviations from normality and homoscedasticity, which were considered acceptable given the large sample size ($N = 2,465$). When significant interactions were detected, taxon-specific temperature effects were calculated from the model coefficients (main effect + interaction term for each taxon).

RESULTS

We recorded 3,636 flower visits on 140 flowers across four bramble patches during 369 hours of video monitoring (254.5h during the day, between 05:00–22:00, and 114.5h at night; Table 1 and Table S1). Seventeen morphotype groups were observed, with ants dominating the entire dataset (1,651 visits, 45.4%; Table S1). Known *Rubus* pollinators (bees, hoverflies, and Lepidoptera) accounted for 1,189 visits, representing 32.7% of the total. Bees and hoverflies were exclusively diurnal, whereas Lepidoptera were mostly nocturnal (moths represented 67.6% of the LI visits; Table S1). Beyond this day-night activity pattern, visitor assemblages varied considerably across both bramble patches and sampling dates.

SPATIAL AND TEMPORAL VARIATION IN FLOWER VISITOR ASSEMBLAGES

Floral visitation activity was concentrated during daytime (12.9 visits/h) compared to night (3.1 visits/h), with most taxa operating exclusively or predominantly during the day (Table S1). Nocturnal visitor assemblages were dominated by

ants, with adult moths recorded exclusively at bramble patch P3, and Coleoptera and Orthoptera present at P2 and P4 (Fig. S4A). Nocturnal visit durations varied markedly among taxa, with adult moths showing short visits (median: ~8s) compared to ANT, Coleoptera and Orthoptera which remained in flowers for up to several hours (Fig. S4B). Given the low nocturnal visitation rates, subsequent spatial and temporal analyses focused on the diurnal period. Ants dominated at all sites (median proportion of total daily visits: 0.46–0.70), followed by non-syrphid flies which were particularly abundant at P3 (0.17) and P4 (0.30) (Fig. 2). Bumblebees peaked at P2 (median 0.29) compared to other sites (≤ 0.07), while hoverflies showed moderate abundances across all patches (0.07–0.13). Other visitor groups showed lower abundances, including halictid-like bees (median 0.02–0.06, highest at P4), Lepidoptera (0.01–0.02, which were present only at P3 and P4). Honeybees were recorded at P1 (0.14), P2 (0.40), and P3 (0.22) following beehive installation during the study period. Longhorn beetles were rare visitors

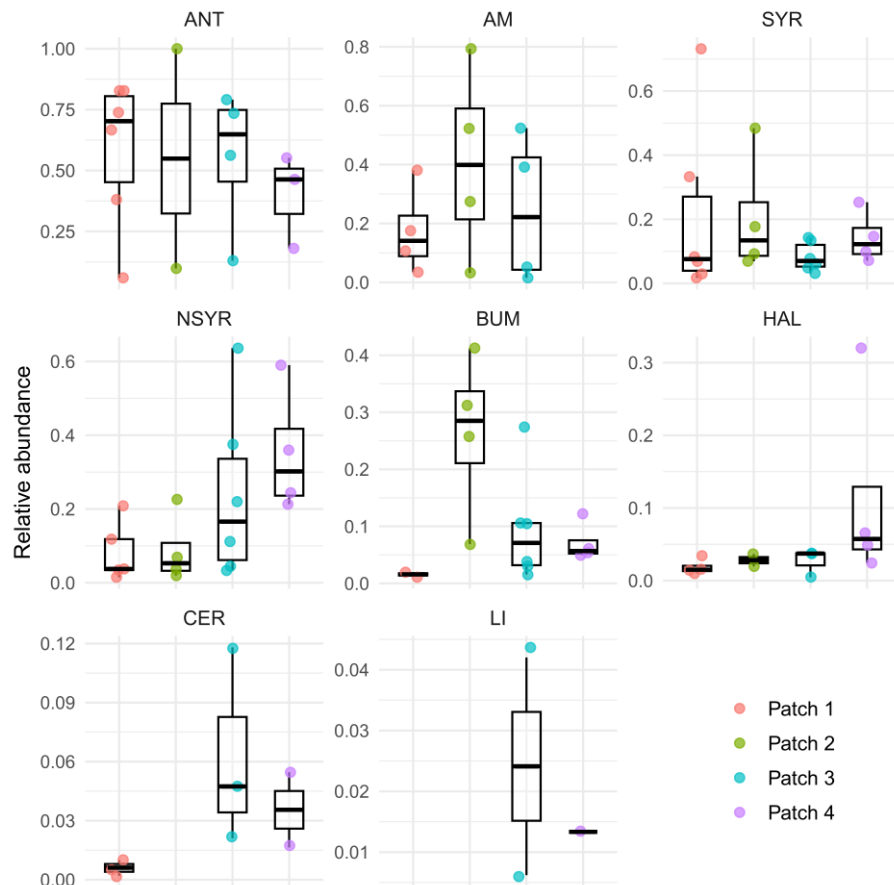


Figure 2. Relative abundance (proportion of total visits) of main visitor groups during daytime (05:00–22:00) across four bramble patches. Each point represents one sampling date. Taxa shown include known *Rubus* pollinators (AM: honeybees, BUM: bumblebees, LI: adult Lepidoptera, SYR: hoverflies), as well as halictid-like bees (HAL), ants (ANT), longhorn beetles (CER), and non-syrphid flies (NSYR). Note that scales differ among panels to improve readability; panels are ordered by decreasing y-axis scale.

(median < 0.05), with occasional presence limited to P3 and P4. Substantial temporal variability within sites was evident for all taxa (Fig. 2), as quantified by coefficients of variation exceeding 50% in 79% of cases (mean CV ranged from 60 to 105% across taxa). As bramble patches P1 and P3 were monitored later in the flowering season than P2 and P4 (Table 1), differences in visitor assemblages among patches may partly reflect temporal variation in flower visitor phenology and weather conditions rather than habitat-specific effects alone.

TEMPORAL NICHE PARTITIONING ACROSS BRAMBLE PATCHES

Temporal niche analysis revealed distinct activity patterns among visitor taxa. Despite spatio-temporal variability in visitor communities, GAMMs fitted for taxon-patch combinations with

≥30 observations during daytime hours (5:00–22:00) showed significant temporal preferences for 13 of 17 combinations (Fig. 3). Four combinations (P2-SYR, P3-CER, P4-ANT, P4-HAL) did not show significant temporal patterns ($P > 0.05$). Most taxa exhibited an activity concentrated during the late morning to afternoon (10:00–18:00), including honeybees, bumblebees, and most hoverflies. However, notable exceptions were observed: ants at P1 and P3 exhibited predominantly crepuscular behaviour, with activity peaks at dusk (21:00). Some taxa exhibited unimodal activity patterns with a single daily peak, such as honeybees with peaks ranging from 13:30 to 16:30 across three patches. However, peak activity times varied considerably among patches for some taxa, suggesting temporal niche flexibility. For example, non-syrphid flies showed early morning activity

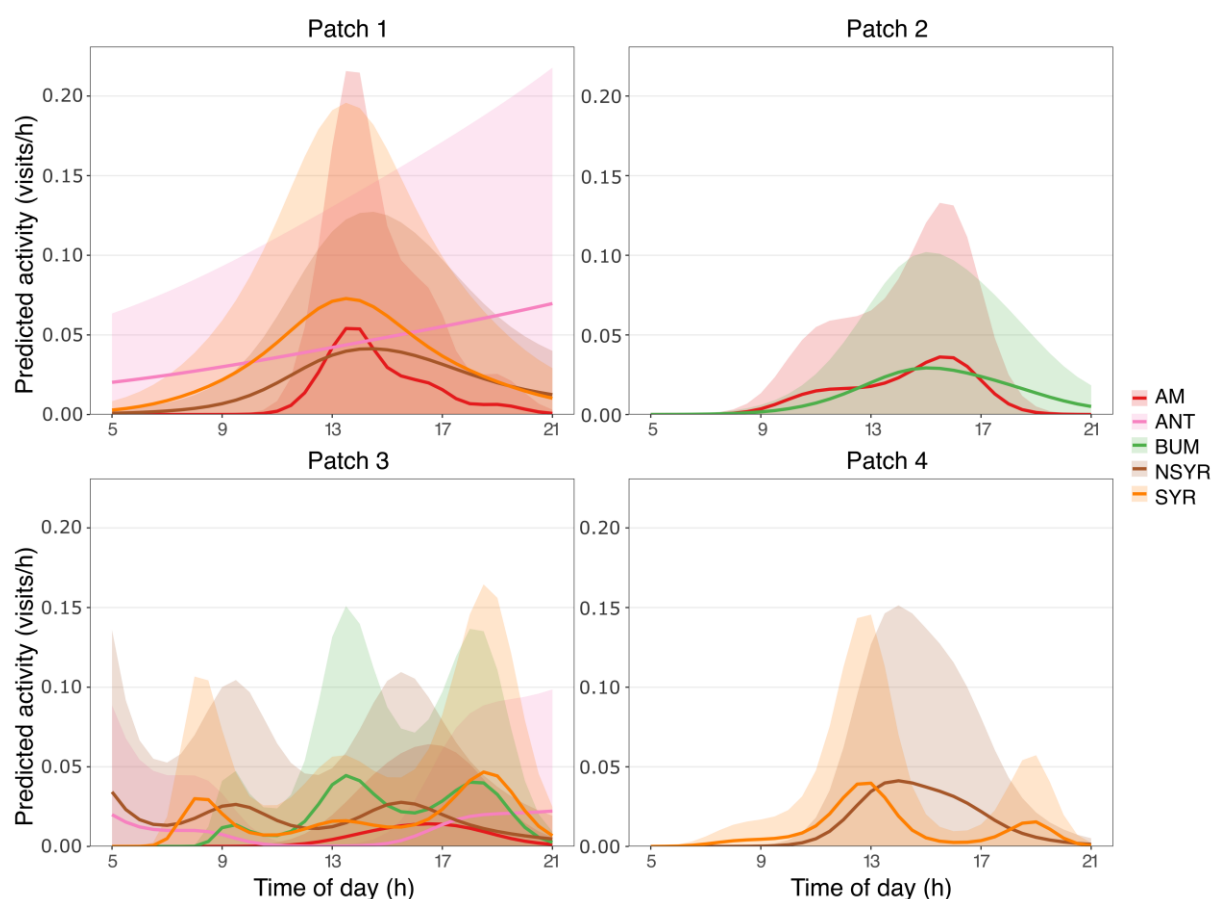


Figure 3. Temporal niches of main flower visitor taxa across four bramble patches. Predicted activity (visits per hour) as a function of time of day for pollinator groups with ≥30 observations per patch during daytime hours (5:00–22:00). Predictions were obtained from Generalized Additive Mixed Models (GAMMs) with Poisson or Negative Binomial distributions, including a random effect for date and an offset for sampling effort (number of cameras). Predictions were averaged across all dates. Ribbons indicate prediction uncertainty ($\pm$ standard error). Taxa without significant temporal preferences ($P > 0.05$) were excluded. AM: honeybees, ANT: ants, BUM: bumblebees, NSYR: non-syrphid flies, SYR: syrphid flies.

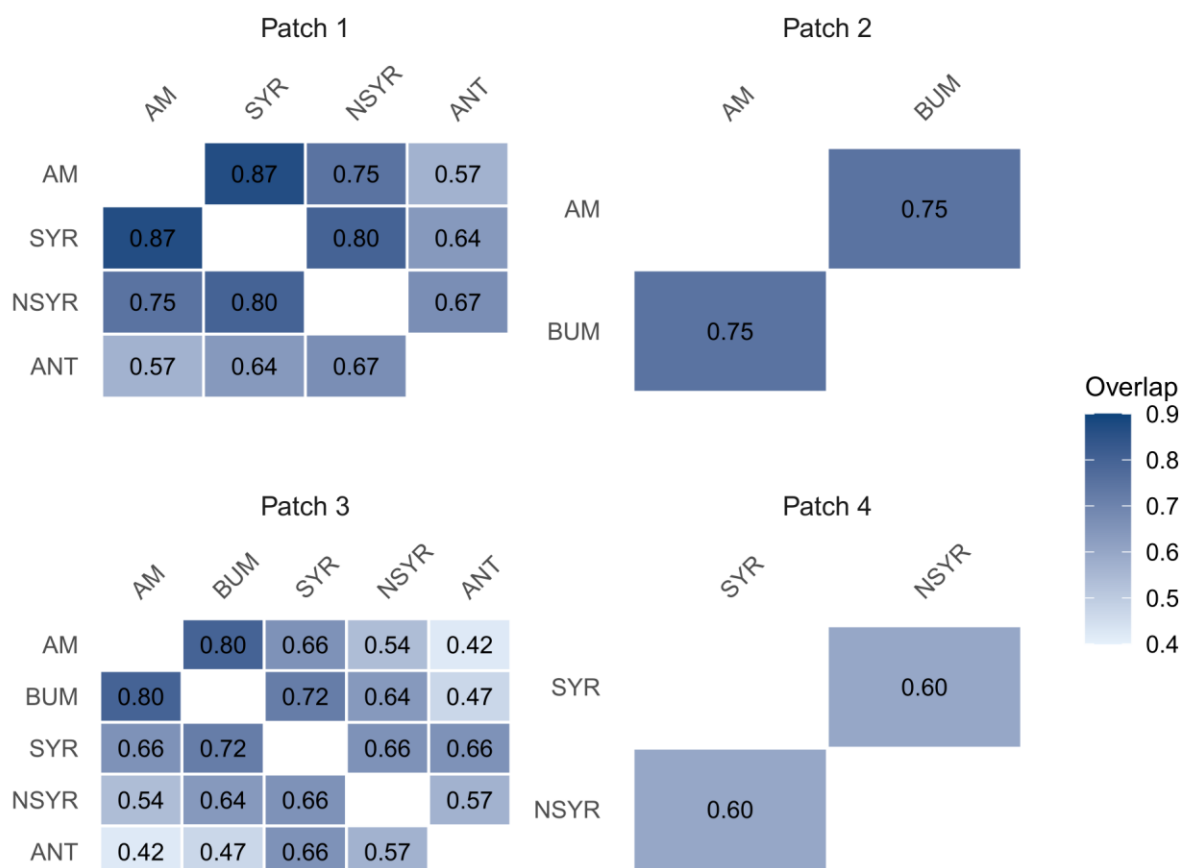


Figure 4. Pairwise temporal niche overlap (Dhat) among co-occurring floral visitor taxa within each bramble patch during daytime hours. Darker cells indicate higher temporal overlap (lower temporal segregation). Values correspond to those reported in Table S2. Abbreviations: AM: honeybees, ANT: ants, BUM: bumblebees, NSYR: non-syrphid flies (Diptera), SYR: hoverflies (Syrphidae).

at P3 (5:00) but afternoon peaks at P1 and P4 (14:00–14:30). Similarly, hoverflies peaked in early afternoon at P1 and P4 (13:00–13:30) but showed a late afternoon peak at P3 (18:30). Bumblebees peaked between 13:30 and 15:00 at P2 and P3, with a secondary peak observed in late afternoon at P3.

Pairwise temporal niche overlap was significantly lower than random expectation in 19 of 20 taxon pairs tested across patches (permutation test, $P < 0.05$; Table S2, Fig. 4 and S5), indicating that temporal segregation among co-occurring taxa was higher than expected by chance. The single exception was the AM–SYR pair at Patch 1 ($P = 0.0501$). However, overlap values varied considerably among pairs (overlap range: 0.42–0.87), indicating that the degree of temporal segregation was not uniform across taxa. In patches with sufficient pairwise comparison among co-occurring taxa (Patches 1 and 3), pairs involving ants consistently showed the lowest

overlap values with other taxa (AM–ANT: overlap = 0.57 at Patch 1, 0.42 at Patch 3; ANT–BUM: overlap = 0.47 at Patch 3), consistent with their crepuscular activity pattern. In contrast, pairs of dipteran taxa showed higher overlap values (NSYR–SYR: overlap = 0.80 at Patch 1, 0.66 at Patch 3), reflecting their broadly similar diurnal activity windows.

MICROCLIMATIC DRIVERS OF VISITOR OCCURRENCE

To examine whether microclimatic conditions influenced visitor occurrence independently of diurnal temporal patterns, we modelled occurrence probability using GAMMs including a smooth term for time of day alongside temperature and light intensity as predictors. Temperature ranged from 7.4 to 43.6°C (mean $\pm$ SD: 19.3 $\pm$ 4.9°C, median: 19.3°C) and light intensity from 0 to 160,742 lux (median: 4,581 lux) during the observation period (Fig. S6). For each

taxon, the single-predictor model with the lowest AIC was retained as the final model, except for ANT where the combined model outperformed both single-predictor models (Table S3). For most taxa (AM, BUM, SYR), neither temperature nor light intensity significantly predicted occurrence probability ($P > 0.14$; Table 2). Two taxa showed significant responses to light intensity, with occurrence decreasing under higher luminosity conditions for both non-syrphid flies and ants (Table 2 and Fig. 5). For ants, the combined model

revealed a significant positive effect of temperature (Table 2), though of modest magnitude.

FLOWER VISIT DURATION AND MICROCLIMATIC INFLUENCE

Visit durations differed markedly between functional groups of flower visitors (Fig. 6). Among known *Rubus* pollinators, bumblebees and honeybees exhibited the shortest visits (medians < 5 s), while among other visitors, beetles, orthopterans, and true bugs showed the longest

Table 2. Effects of microclimatic variables on floral visitor occurrence probability, after accounting for diurnal temporal patterns. Models were fitted to 928 observation intervals (15 minutes) per taxon collected between 06:00 and 20:00, using Generalized Additive Mixed Models (GAMMs; binomial distribution) with a smooth term for time of day ($s(\text{Hour}, \text{bs}='tp', k=8)$), random effects for sampling date and bramble patch, and an offset for the number of active cameras. For each taxon, temperature-only, light intensity-only, and combined models were compared by AIC (see Table S3); the retained model is indicated. β : standardized coefficient; SE: standard error. Significant effects ($P < 0.05$) are shown in bold. All models passed dispersion and zero-inflation tests (DHARMA; $P > 0.05$ for all taxa).

Taxon	N visits	N intervals with occurrence	Retained model	Temperature			Light intensity		
				β	SE	P	β	SE	P
AM	547	150	Temperature	0.211	0.201	0.294	-	-	-
ANT	973	195	Combined	0.541	0.251	0.031	-0.642	0.253	0.011
BUM	165	90	Temperature	0.414	0.282	0.142	-	-	-
NSYR	293	149	Light intensity	-	-	-	-0.495	0.206	0.016
SYR	212	115	Temperature	-0.014	0.172	0.933	-	-	-

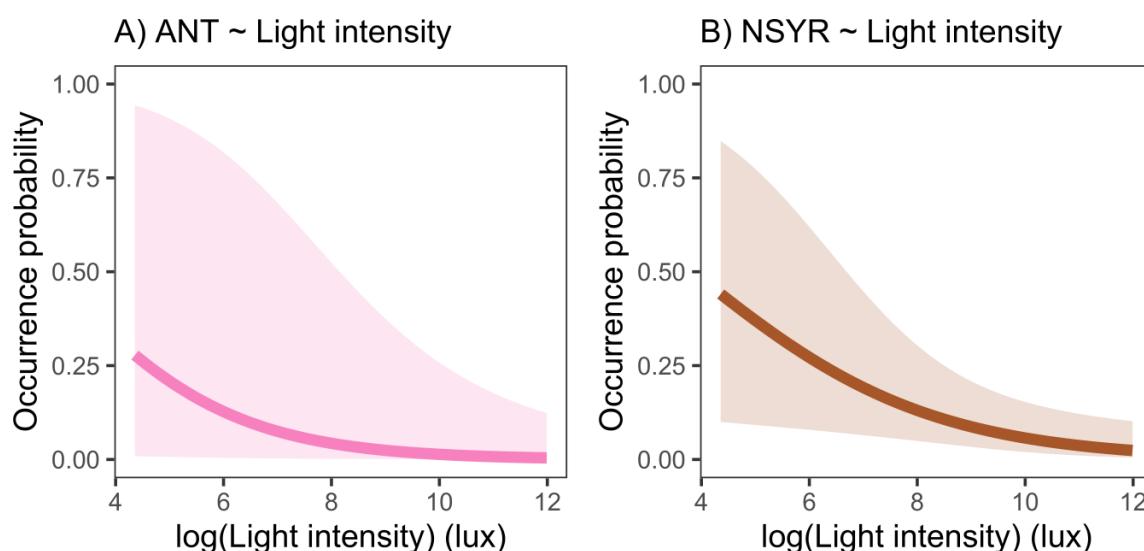


Figure 5. Effect of light intensity on the occurrence probability of ants (ANT) and non-syrphid flies (NSYR) during daytime hours (06:00–20:00) across all four patches combined. Predicted occurrence probabilities ($\pm$ 95% confidence interval) were obtained from Generalized Additive Mixed Models (GAMMs) including log-transformed light intensity, a smooth term for time of day ($s(\text{Hour})$) to account for the nonlinear diel pattern, and random effects for sampling date and bramble patch. Predictions are shown across the observed range of light intensity, with temperature held at its mean value. ANT: ants, NSYR: non-syrphid flies.

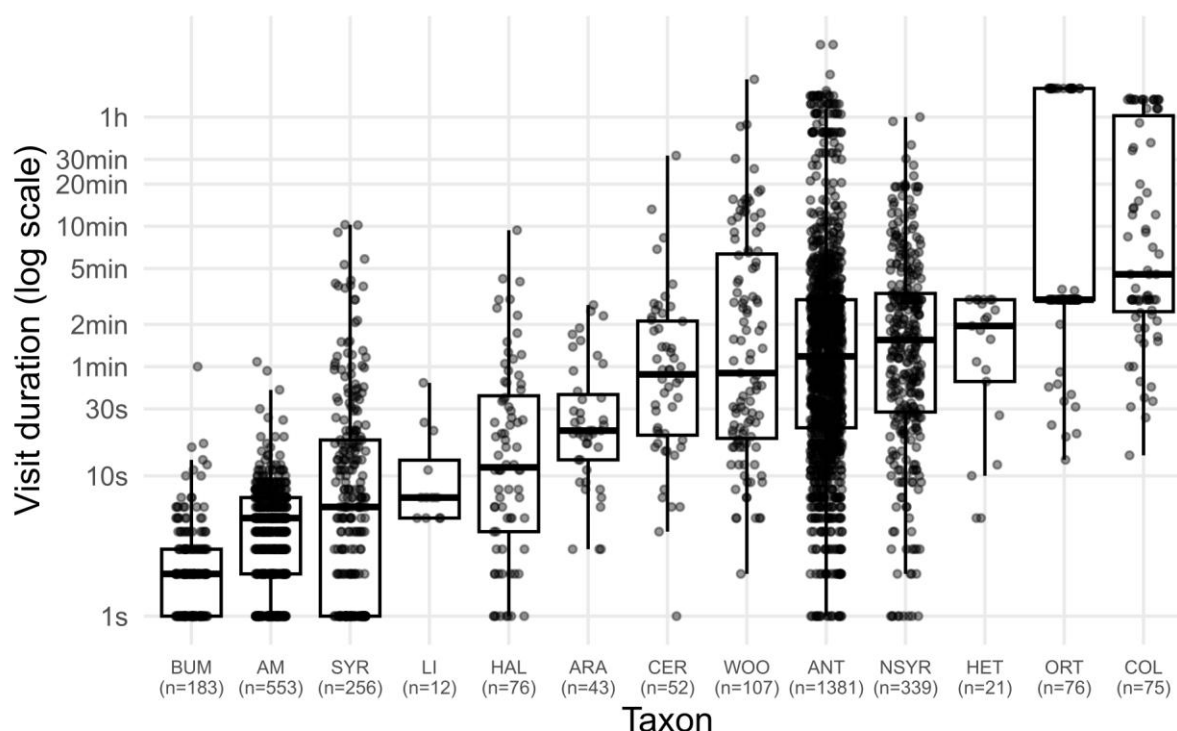


Figure 6. Visit duration by flower visitor taxon during daytime hours (5:00–22:00), pooled across all four bramble patches. Sample sizes are shown in parentheses for each taxon. Abbreviations: AM: honeybees, ANT: ants, ARA: Arachnida, BUM: bumblebees, CER: longhorn beetles (Cerambycidae), COL: other beetles (Coleoptera), HAL: Halictid-like bees, HET: Heteroptera, LI: Lepidoptera (diurnal Lepidoptera imago), NSYR: non-syrphid flies (Diptera), ORT: Orthoptera, SYR: hoverflies, WOO: woodlice (Isopoda).

durations, with medians exceeding 2 minutes. Some of them spent the night inside the flower (orthopterans, beetles).

To test whether microclimatic conditions affected the duration of flower visits differently among insect taxa, we fitted linear mixed-effects models with taxon $\times$ microclimate interactions on visit-specific temperature and light intensity measurements. A significant interaction was detected for temperature ($\chi^2 = 21.39$; $df = 4$, $P < 0.001$), with the interaction model showing substantial improvement over the additive model ($\Delta AIC = 13.4$), indicating that taxa differed in how their visit duration responded to temperature. Specifically, NSYR showed a strong negative response to temperature ($\beta = -0.085 \pm 0.020$ SE, $P < 0.001$), with visit durations decreasing by approximately 57% for every 10°C increase. This effect was taxon-specific, as the temperature $\times$ NSYR interaction term was highly significant ($\beta = -0.094$, $P < 0.001$). Other taxa showed weaker or non-significant responses to temperature. Only

ants showed a marginally significant negative trend (interaction term: $\beta = -0.021$, $P = 0.058$).

A significant interaction was also detected for light intensity ($\chi^2 = 35.85$, $df = 4$, $P < 0.001$; $\Delta AIC = 27.9$), indicating taxon-specific responses. Non-syrphid flies ($\beta = -0.327$, $P < 0.001$) and hoverflies ($\beta = -0.292$, $P < 0.001$) both showed significant negative responses, with shorter visit durations under higher luminosity conditions. Honeybees, bumblebees and ants showed no significant response to light intensity.

DISCUSSION

In this study, we developed and tested a low-cost camera monitoring system deployed on bramble flowers to investigate flower visitor communities in the forest understory. Our non-invasive method successfully documented 3,636 flower visits across seventeen morphotypes, revealing consistent ecological patterns, including distinct diurnal activity peaks, significant temporal niche partitioning among co-occurring taxa, and taxon-specific microclimatic associations.

Among known *Rubus* pollinators, hoverflies emerged as the most active wild visitor group across all bramble patches, while bumblebees showed lower overall presence. Microclimatic effects were detected for three taxa: non-syrphid flies showed a negative response to light intensity on occurrence probability and a strong negative effect of temperature on visit duration, hoverflies also showed shorter visit durations under higher light intensity, and ants showed modest but significant responses to both light intensity and temperature on occurrence probability. These findings demonstrate that adapted camera traps can effectively capture complex ecological patterns in forest flower visitor communities, which remain understudied in temperate forest understories, while avoiding the ecological impact of lethal sampling methods.

FLOWER VISITOR COMMUNITIES

Brambles were visited by diverse flower visitor morphotype groups including bees (*Bombus*, halictid-like bees), flies (Syrphidae and other Diptera), butterflies and moths (Lepidoptera), and beetles (Cerambycidae and other Coleoptera). These morphotype groups represent distinct functional types varying in body size, tongue length, and foraging behaviour, including floral resource use (pollen and/or nectar) and non-foraging activities. This diversity of potential pollinators is consistent with the large actinomorphic bowl floral morphology characteristic of generalist pollination systems with nectar and pollen production (Fenster et al. 2004). These findings align with previous studies on pollination (Wignall et al. 2020) and confirm that brambles function as generalist resources in forest.

The composition of these visitor assemblages varied spatially and between sampling days, indicating that brambles were likely visited by itinerant opportunist visitors (Beattie 1971). Among them, ants (flightless workers) were the most frequent and stable group across most of the patches. The role of ants as pollinators in temperate climates appears highly context-dependent and remains unknown in European forests. While exclusion experiments have demonstrated that ants can increase seed set in some grassland species (Schürch et al. 2000; Carvalheiro et al. 2008), seed germination may be

reduced due to decreased pollen viability on ant cuticles, probably due to metapleural gland secretions of antibiotics (Beattie et al. 1984; Rostás et al. 2018). Moreover, ants tend to forage on the same individual, promoting geitonogamy rather than outcrossing. Given the complex reproductive system of brambles, facultative pseudogamous apomixis and variable self-compatibility, geitonogamous pollen deposited by ants may facilitate the stimulus needed for endosperm development in apomictic seeds and facilitate self-fertilization in sexual reproduction. While ants likely contributed little to bramble outcrossing and genetic diversity, they may contribute to maintaining locally adapted apomictic clones.

In contrast to ants, flying visitors showed greater variation in their distributions. *Apis mellifera*, bumblebees, and hoverflies were the most frequent known *Rubus* pollinators. However, *Apis mellifera* was recorded only in patches P1, P2, and P3 located near the managed hives installed by external beekeepers during the study (see Methods). Bumblebees displayed strong spatial heterogeneity with 5-fold variation in relative abundance across patches but temporal stability within sites (narrow boxplots). Hoverflies (SYR) and non-syrphid flies (NSYR) displayed contrasting spatial patterns, with SYR more abundant in P1-P2 and NSYR more abundant in P3-P4. These spatial differences may reflect habitat-driven distribution, differences in bramble patch characteristics, or spatial partitioning among visitor groups, but could also reflect temporal variation in community composition given the non-overlapping monitoring periods across patches. While flies are often considered less efficient pollinators than bees, they may play a more substantial role in pollination than previously recognized (Raguso 2020). Studies on *Rubus chamaemorus* support this view, showing that dipterans, particularly muscids, represented a substantial proportion of flower visitors and contributed significantly to pollination success (Brown & McNeil 2009).

Beyond these dominant groups, brambles were also visited by less abundant taxa including solitary bees (halictid-like-bees), butterflies, and longhorn beetles (Cerambycidae). While these groups contributed minimally to overall visitation rates, their consistent presence across certain

patches suggests they may provide functional insurance, maintaining pollination functions when dominant groups fluctuate. Notably, halictid-like bees showed an opposite spatial trend to Syrphidae, increasing toward patches P3-P4, reinforcing the pattern of spatial complementarity observed among flying visitors, though temporal confounding cannot be excluded. While beetles have traditionally been considered relatively unimportant pollinators in temperate climates (Proctor et al. 1996), recent findings of longhorn beetles carrying substantial chestnut pollen loads suggest their role may be underestimated for some plant species (Jacobson & Pilkey 2024). Finally, adult Lepidoptera were recorded exclusively during nocturnal hours at patch P3. Given that Anderson et al. (2023) demonstrated that moths can achieve higher pollen deposition rates on *Rubus* at night than diurnal visitors during the day, moths may represent an underappreciated component of the bramble pollination system in temperate forest, at least in certain sites and time periods. The factors driving their patch-specific distribution and the effectiveness of these minor visitor groups as bramble pollinators remains to be determined.

DAILY ACTIVITY PATTERNS

Bramble visitors exhibited a general peak in activity approximately between 10:00 and 18:00. However, visitor groups showed distinct daily activity patterns that varied among patches. Patches differed both in the degree of temporal overlap among groups and in the shape of activity distributions in the same morphotype group. Some groups showed unimodal patterns, characterized by a single midday peak (particularly AM and SYR in P1), whereas others displayed bimodal patterns with morning and afternoon peaks, most notably NSYR and SYR in P3. Such within-community temporal partitioning is increasingly recognized as a key mechanism reducing interspecific competition and contributing to the stability of pollination functions (Blüthgen & Klein 2011; Fründ et al. 2013). Temporal complementarity among co-occurring pollinators has been linked to differences in circadian regulation, thermoregulatory physiology, and foraging competition (Willmer 1983; Fründ et al. 2013; Bloch et al. 2017; Blareau et al. 2025).

Ants exhibited continuous activity throughout the diel cycle, with almost 30% of visits occurring at night. This pattern is likely to be consistent with their social organization, which enables colony-level foraging across all hours. In the nectar-feeding ant *Camponotus rufipes*, under laboratory conditions, task allocation and division of labour allow foragers and nurses workers to maintain activity around the clock to meet colony needs regardless of external temporal cues (Mildner & Roces 2017). The near 24-hour visitation pattern observed at the community level may also reflect the coexistence of multiple ant species with complementary temporal niches. In temperate European forests, the coexistence of ant taxa with contrasting diel activity, such as predominantly diurnal *Formica* spp. and more nocturnal *Myrmica* spp., has previously been documented, particularly in open or disturbed habitats (Žmihorski & Ślipiński 2016). The constant presence of ants and their exploitation of nectar may shape the temporal dynamics of floral rewards and influence pollinator visitation patterns, although such ant-pollinator competition has been primarily documented in tropical and subtropical systems or with aggressive invasive ants (Schaffer et al. 1983; Miner & Wilson Rankin 2025).

The other flying visitors, by contrast, displayed more restricted and patch-dependent activity windows. Bees were strictly diurnal, in agreement with their well-established circadian entrainment and thermal sensitivity (Bloch et al. 2017). In the most open and flower-rich patch (P1; Table 1), all major flying visitor groups converged on a pronounced midday peak, and temporal overlap involving dipteran taxa was generally high (NSYR-SYR: overlap = 0.80; AM-SYR: overlap = 0.87), consistent with relaxed temporal partitioning under abundant floral resources. In contrast, patches with lower floral density and reduced openness (P3 and P4) exhibited clearer temporal segregation among visitors, though differences in monitoring periods across patches preclude firm conclusions about habitat effects. In P3, the lowest overlap values consistently involved ants (AM-ANT: overlap = 0.42; ANT-BUM: overlap = 0.47), which is more parsimoniously explained by their intrinsic crepuscular activity pattern than by competitive exclusion. In P4, syrphid and non-syrphid flies minimized temporal overlap, while

P3 showed the most fragmented temporal structure, with multiple groups displaying bimodal activity patterns. For non-ants pairs, differences in thermal or light preferences and competitive interactions are both plausible explanations but cannot be distinguished with the present data. Similar variation in temporal structuring across environmental gradients has been documented in urban flower visitor communities, where the degree of temporal niche partitioning differed markedly between sites with contrasting resource availability and anthropogenic pressure (Blareau et al. 2025). As noted by these authors, such shifts could be partly explained by the categorization of flower visitors into morphotype groups, which pool multiple species together. Environmental filtering, driven by microclimate, floral density, or competitive pressure, may select for species with specific temporal preferences within each morphotype group. In our system, the transition from unimodal to bimodal activity patterns in certain groups between patches could therefore reflect species turnover within morphotype groups rather than solely behavioural responses to local conditions.

MICROCLIMATE EFFECT

Forests generate a mosaic of heterogeneous microclimates that structure floral visitor communities. Early studies showed that in deeply shaded forests, visitor activity occurs exclusively during sunfleck events when both light and temperature temporarily increase at the local scale (Beattie 1971). Along broader spatial light intensity gradients in more open forests, taxa partition the light mosaic, with dipterans preferring lower-light areas and hymenopterans exploiting the entire gradient (Herrera 1995, 1997). The importance of canopy gaps in creating favourable microhabitat for pollinators was further supported by studies in hardwood forests (Ontario, Canada), where group-selection silviculture increased pollinator abundance: wild raspberry (*Rubus strigosus*) and soil-nesting bees particularly benefitted from canopy openings, likely due to the combination of increased light, warmer bare soils, and abundant nectar resources (Proctor et al. 2012). More recently, boreal studies have proposed that local temperature acts as the primary microclimate filter, controlling bumblebee occurrence with light modulating their abundance (Bartholomée et al.

2025), and influencing both the occurrence and foraging duration of dipterans (Díaz-Calafat et al. 2026).

In contrast to these boreal findings, our results suggest that microclimatic effects on visitor occurrence are taxon-specific and more limited than previously reported. Only two taxa showed significant microclimatic responses. NSYR showed a negative response to light intensity, with occurrence decreasing under higher luminosity conditions. Several non-exclusive mechanisms could explain this pattern. First, this may reflect a direct avoidance of high-radiation environments, consistent with the preference of dipterans for lower-light microhabitats reported by Herrera (1995, 1997), possibly mediated by visual constraints or behavioural shade-seeking. Second, light intensity may act as a proxy cue for thermally unfavourable conditions, as sunfleck events in forest understories rapidly elevate local temperatures (Beattie 1971), and dipterans may reduce visitation anticipatorily before heat stress thresholds are reached.

Beyond occurrence patterns, NSYR exhibited behavioural thermoregulation at the individual flower visit scale, reducing visit duration by 57% per 10°C increase. Additionally, visit durations were shorter under higher light intensity, suggesting that both temperature and light intensity constrain foraging time at the flower level. This fine-scale adjustment complements boreal findings showing that higher microclimatic temperatures reduce overall foraging activity duration in dipterans (Díaz-Calafat et al. 2026). This suggests a multi-scale behavioural response to thermal stress: dipterans may adjust both the duration of each flower visit and their total foraging time to limit heat and radiation exposure. Such behavioural plasticity may extend their effective thermal niche beyond what occurrence patterns alone would predict. Hoverflies also showed shorter visit durations under higher light intensity, which may reflect their strong reliance on visual cues for flight stabilization and flower recognition (Goulard et al. 2015; Barragán-Fonseca et al. 2020), high luminosity potentially disrupting visual contrast at the flower level.

Ants showed a significant negative response to light intensity, with higher occurrence probability under low-light conditions. This is consistent with

experimental evidence that some ant species directly measure ambient light levels to regulate foraging activity onset, independently of temperature or internal rhythms (Narendra et al. 2010), suggesting that light intensity may act as a primary behavioural cue in this taxon. This pattern is also coherent with their broader activity rhythm, which extends well into nocturnal hours (Fig. S4), with diurnal activity peaking during morning and evening periods of low luminosity (Fig. 3). A weak positive effect of temperature was also detected in the combined model (Table 2), but its biological interpretation remains unclear given the modest effect size and the complex activity pattern of ants across the diel cycle.

For honeybees, bumblebees and hoverflies, no significant microclimatic effects were detected once temporal patterns were accounted for. This suggests that for these taxa, diurnal activity rhythms are the primary driver of occurrence in forest understories, with instantaneous microclimate playing a secondary role. This is perhaps unsurprising given that the temperature range recorded during the study (7.4–43.6°C) largely exceeds the minimum flight thresholds typically reported for bumblebees (6–11°C) and honeybees (12–15°C) (Corbet et al. 1995; Vicens & Bosch 2000), suggesting that temperature rarely acted as a limiting factor for these taxa in this temperate forest context during the flowering season. This contrasts with boreal findings where temperature acts as a primary constraint for bumblebees (Bartholomée et al. 2025), and may reflect the generally more favourable thermal conditions of temperate forests compared to boreal systems, where temperature more frequently falls below activity thresholds for hymenopteran foraging.

The taxon-specific microclimatic sensitivities documented here, with non-syrphid flies and ants responding to light intensity, and non-syrphid flies and hoverflies additionally showing behavioural thermoregulation at the visit scale, complement the temporal partitioning patterns observed among floral visitor groups. Together, these results suggest that forest understory visitors partition both temporal and microclimatic niches, albeit in more subtle and taxon-specific ways than previously reported, with potential implications

for the resilience of floral visitation functions under environmental change.

LIMITATIONS AND CONCLUSION

This study demonstrates the potential of bramble (*Rubus fruticosus* agg.) as a model system for investigating flower visitor communities in forest understories using non-invasive continuous video monitoring combined with microclimate measurements. Brambles present several advantages: extended mass flowering, a long flowering period, accessibility for camera placement, attractiveness to diverse visitor guilds (great volume of nectar and sugar production, generalist flowers), widespread occurrence in temperate forests, and a long lifespan allowing monitoring at the same location over several consecutive years. Future studies could explore other widespread species as complementary indicators in specific forest contexts, such as *Cytisus scoparius* (broom), which flowers abundantly earlier in the season (April–May) and would be particularly suitable for monitoring bee communities in pioneer and early-regeneration forest habitats.

Our design faced limitations inherent to field studies. Spatiotemporal coverage was restricted to four patches monitored over variable and partially non-overlapping periods notably due to asynchronous flowering phenology among sites. Heterogeneity in patch size and flowering density likely affected detection probability independently of insect abundance. Additional constraints included camera autonomy issues, and weather-related interruptions, limiting joint inference. For some taxa, these factors resulted in insufficient occurrences for robust model estimation. Moreover, the composition of visitor assemblages may partly reflect taxon-specific attraction to bramble flowers rather than relative abundance in the surrounding forest. Furthermore, bramble microspecies were not distinguished among patches, which may have introduced uncontrolled variability in floral traits and visitor assemblages across sites. From a statistical standpoint, the microclimatic models were based on 15 min observation intervals, which may have retained some residual temporal autocorrelation. Finally, given the proximity of some patches (335–647 m) and typical foraging ranges reported for *Apis mellifera* in temperate deciduous forests (600 m–2.3

km) and bumblebees in open landscapes (up to 1–2 km), but not small solitary bees (~150 m in urban gardens), the same individuals may potentially have been recorded at multiple sites, which could introduce non-independence among patch-level observations (Visscher & Seeley 1982; Walther-Hellwig & Frankl 2000; Osborne et al. 2008; Hofmann et al. 2020). However, this risk is primarily relevant between P1 and P3 during their brief overlap period (26–27 June). To our knowledge, for other visitor taxa, foraging range data in temperate forest or other contexts are lacking to assess this risk quantitatively.

Nevertheless, this approach offers significant advantages. Recent studies have used automated camera systems to monitor pollinator visits on standardized experimental units such as artificial flowers or potted plants grown under controlled conditions (Blareau et al. 2025; Díaz-Calafat et al. 2026). While such designs provide strong experimental control, they partly decouple plant–pollinator interactions from their local environmental context. By contrast, our study relied exclusively on naturally occurring bramble patches, integrating fine-scale variation in microclimate, flowering phenology and vegetation structure, while retaining the non-invasive and continuous nature of automated video monitoring.

The protocol preserved both insects and flowers and enabled simultaneous day- and night-time monitoring across sites of insect–flower interactions relevant to pollination. Archived footage allowed post-hoc validation of taxonomic identifications and behavioural quantification (e.g. visit duration and flower contact patterns), data largely inaccessible through transect surveys or lethal sampling. Despite modest replication, we detected biologically meaningful patterns, including taxon-specific responses to microclimate and evidence of taxon-specific behavioural responses to temperature and light intensity.

Future work would benefit from increased temporal replication, standardized sampling windows aligned with flowering phenology, and the integration of automated image analysis or artificial intelligence to reduce video processing time. These improvements would further strengthen brambles as a tractable and ecologically realistic model system for forest pollinator ecology.

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AUTHOR CONTRIBUTION

Concept and design CH, SM & LW, Technical development CH & BL, Field work CH, SM & LW, Video annotations LBC, CH, SM & LW, Data curation LBC & LW, Data analysis LW, Writing LBC, SM & LW, Reviewing and editing LBC, SP, SM & LW.

DISCLOSURE STATEMENT

The authors declare no conflict of interest.

GENERATIVE AI DISCLOSURE STATEMENT

Generative AI (Claude, Anthropic) was used to assist in the development of R analysis scripts. All AI-generated code was reviewed, tested, and validated by the authors.

DATA AVAILABILITY STATEMENT

The data used to write this article are available at <https://nmnkjb.org/> as supporting information.

APPENDICES

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

Appendix I. Flower visitations and microclimate datasets with metadata.

Appendix II. Additional figures supporting the results.

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