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FIT for purpose? Sampling Bees in Flowering Canopies with Flight Interception Traps (FITs)

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Abstract—Depending on species and season, tree canopies can provide floral resources in abundance. However, researchers often do not consider these resources when sampling bee communities, because they are difficult to access. While observer-based methods, such as hand-netting along transects, are often used for collecting bees from near-ground resources like wildflower strips, flight interception traps (FITs), such as aerial Malaise traps (AMTs) and window interception traps (WITs), can be used for collecting bees from elevated resources like flowering canopies. We assessed the suitability of WITs and AMTs for sampling bees from flowering canopies. We sampled canopies of four different tree taxa (*Salix*, *Malus*, *Robinia*, *Tilia*) in Braunschweig, Germany, between March and June 2024. In total, we collected 395 bee individuals, including 247 honeybees. Sampled communities comprised ten genera and showed marked differences in the ratio of honeybee and wild bee individuals. In *Salix* trees, wild bees were more abundant than honeybees, whereas in *Tilia* trees and especially *Robinia* trees, honeybees outnumbered wild bees. The collectors above the interception surface of both WITs and AMTs collected no bees. This came as a surprise, because we expected bees to move upwards upon flight interception, as they do in ground-based Malaise traps. We conducted a systematic literature search in the Web of Science to compare our findings to previous studies using WITs and AMTs for sampling bees. To our knowledge, our study is the first to show that collectors above the interception surface are generally inefficient when sampling bees with WITs and AMTs. Our study provides methodological advice for future researchers seeking to sample pollinators in tree canopies.

Keywords—Apoidea (Hymenoptera: Aculeata), tree canopy, window trap, aerial Malaise trap

INTRODUCTION

Tree flowers provide important nutritional resources to honeybees (Lau et al. 2019) and wild bees (Kay et al. 2020; Urban-Mead et al. 2023). While bee samplings have been generally conducted at ground-level, for example in the vast majority of pan trap studies (Krahner et al. 2024), bee resources in elevated strata have been largely overlooked in the past, likely because they are more difficult to access. Due to vertical stratification of bee communities (Ulyshen et al. 2010), disregarding certain floral resources when sampling bees risks missing a large part of the local bee fauna, even in cases of a long sampling history (Dorey et al. 2024). Tree canopies are also important for investigating food resources for bees, which play a pivotal role in bee conservation. We are not aware of any study on bee species partitioning nectar and pollen collection between canopies and ground-based floral resources. For the study of most wild bee taxa, determination of the relative importance of a pollen resource depends on in-situ data collection, i.e., collection of the bee and its pollen load close to the host plant inflorescences, although a reliable discrimination between foraging for nectar and pollen requires data on foraging behaviour. This is because pollen storages are often inaccessible to researchers, particularly in ground-nesting bee species. In the absence of pollen load samples, floral resource use is often derived from sampled activity density.

Thus, further research on the behaviour and food resources of bees in canopies can close an important knowledge gap in bee ecology (Urban-Mead et al. 2021).

In the past, researchers have sampled bees in tree canopies using a variety of methods, including pan traps (Nuttman et al. 2011; Li et al. 2021; Simon et al. 2021), trap nests (Sobek et al. 2009), blue vane traps (Gibbs et al. 2017) and hand netting with canopy nets (Dorey et al. 2024). In comparison to observer-dependent sampling methods, trapping methods have the advantage of sampling at multiple locations simultaneously over longer periods. In this way, multiple bee communities can be sampled under similar conditions (e.g., weather, season), and with a standardised sampling effort (e.g., no observer bias). In addition, the majority of bee species cannot be identified reliably at species level in the field. Thus, while trapping methods are often lethal, produce bycatch and are therefore subject to ethical concerns (Barrett et al. 2023), lethal trapping methods are justifiable for sampling bee communities. Among trapping methods, trap nest results may be driven by landscape-level factors rather than by the local-scale environment (e.g., Uzman et al. 2020; Krahner et al. 2021). Therefore, trap nests are less suitable for sampling local insect-flower associations. Likewise, samples from blue vane traps do not represent the bee fauna that is associated to surrounding flowers, and these traps pose the risk of affecting sampled bee populations through oversampling (Gibbs et al. 2017). Pan traps are used for sampling bees in various environments in a standardised manner (Krahner et al. 2024), but are also criticised by some researchers for an assumed bias due to varying floral environment (Portman et al. 2020; Prendergast & Hogendoorn 2021). One advantage of flight interception traps (FITs) compared to pan traps is the absence of an attractive stimulus as a trapping mechanism. Instead, FITs intercept the insect's flight without changing its behaviour before and hence likely reflect true local activity density of bees. Thus, Howlett et al. (2009) observed positive correlations between trap counts from FITs and direct observations for several bee taxa visiting ground-stratum flowers. Accordingly, FITs have been used for assessing bee population dynamics in the past (Inari et al. 2012), but guidance on the FIT design to be used for pollinator research is very limited so far, and in particular not specific to bees (Knuff et al. 2019).

Important design features of FITs include the material of the interception surface, which is either gauze in the case of aerial Malaise traps (AMTs) or transparent (acrylic) glass in the case of window interception traps (WITs). Further, the position of the collecting jar (collector) containing the trapping liquid in relation to the interception surface determines the taxa that are sampled by FITs. Wilkening et al. (1981) introduced the simultaneous use of collection units above and below the interception surface in WITs, distinguishing between fast-flying and slow-flying insects dropping and rising upon flight interception, respectively. While early FIT designs had two interception surfaces (one vertical gauze sheet or window; Malaise 1937; Townes 1962; Juillet 1963), later trap designs consisted of four interception surfaces (two crossed gauze sheets or windows; Hines & Heikkenen 1977). Also, the size of the interception surface is pivotal for trap efficacy (Carrel 2002; Robert et al. 2021).

While an increased utility and use of FITs for sampling Hymenoptera has been predicted some time ago (Bogusch & Schlaghamersky 2010), we hypothesise that the potential of this method for sampling bees in flowering canopies has not been realised yet. For example, Ulyshen et al. (2020) still described the FIT method as unconventional. One reason for this may be the insufficient, scattered knowledge about this method specific to bees, especially because until now there is no comprehensive review about the FIT method for sampling bees.

In this study, we used two approaches to further our knowledge about FITs, specifically AMTs and WITs, for bee research. First, we conducted a short-term pilot study with limited spatial replication to gain insights into the suitability of FITs for bee sampling in flowering tree canopies, addressing the following questions:

1) Do samples from flight interception traps (FITs) mirror plausible flower-visiting bee communities as we would expect them in relation to sampling season?
2) Is there a benefit of using top collectors (above the interception surface) in addition to bottom collectors (below the interception surface)?

3) Do aerial Malaise traps (AMTs) and window interception traps (WITs) yield similar samples?

Second, we conducted a systematic literature review to evaluate if FITs (AMTs and WITs) have been used for bee sampling in flowering canopies before and to gauge the degree of variation among studies regarding trap design and usage. Combining the outcomes from the pilot study and the literature review, for the first time we derive recommendations on best practice for sampling bees in flowering canopies with FITs and identify persisting knowledge gaps for this method.

MATERIALS AND METHODS

PILOT STUDY

We conducted the study using trees of five species: *Salix caprea* L. (goat willow), *Malus domestica* Borkh. (apple), *Robinia pseudacacia* L. (black locust), co-flowering *Tilia platyphyllos* Scop. (large-leaved linden) and *T. cordata* Mill. (small-leaved linden); henceforth referred to by genus name. Trees were planted in isolation from other trees or in single rows, and were located mostly on the campus of the Julius Kühn Institute (JKI) in Braunschweig, Lower Saxony, Germany (latitude, longitude, EPSG:4326 - WGS 84: 52.275°, 10.567°; Fig. 1). For logistic reasons and to avoid personal hazard from collapsing traps, our sampling mainly took place within a small area, i.e., on the JKI campus. We selected three *Malus*, four *Robinia*, four *Tilia*, and seven *Salix* trees of the same flowering stage. Two of the selected apple trees were located outside the JKI campus. We aimed at sampling during the peak flowering stage. However, in *Malus* we only started sampling after peak flower. We sampled bees in the canopies of all selected trees of the same species simultaneously, using six (*Robinia*, *Malus*) to eight (*Salix*, *Tilia*) window interception traps (WITs). In *Tilia*, we additionally used four aerial Malaise traps (AMTs), pairing two WITs and one AMTs per tree (Fig. 2). We adjusted the number and spread of the traps to the availability of suitable flowering crowns and to the spatial distribution of the trees. That is, we avoided spatial aggregation of traps as best as possible. Traps were placed in the lower canopies (approximately 2-7 m above ground) as close as possible to tree flowers that

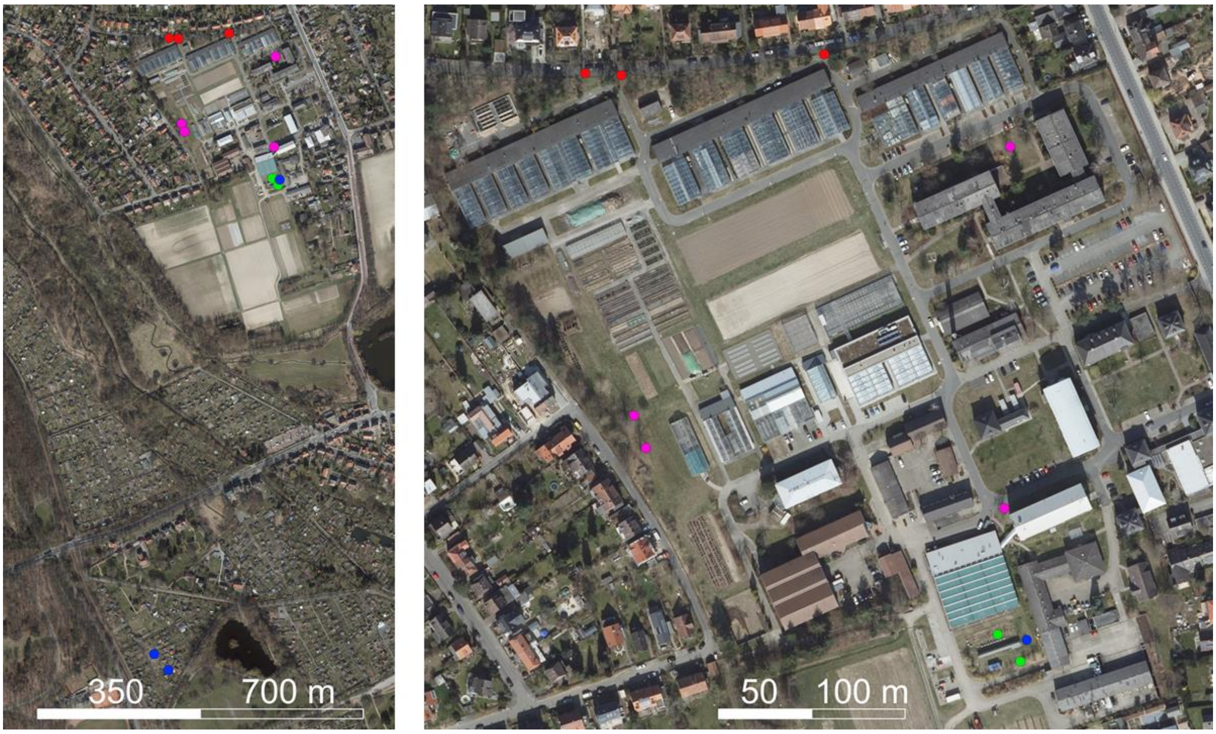

Figure 1. Location of trees with flight interception traps (FITs) used for sampling bees in canopies (A: total study area; B: FITs placed on the JKI campus; top facing north). ● *Salix*, ● *Malus*, ● *Robinia*, ● *Tilia*. One point represents a single tree, and in the case of *Salix* a planted row containing three or four sampled trees. Digital orthophoto (DOP): © GeoBasis-DE / BKG (2025). Terms of use: https://sg.geodatenzentrum.de/web_public/nutzungsbedingungen.pdf

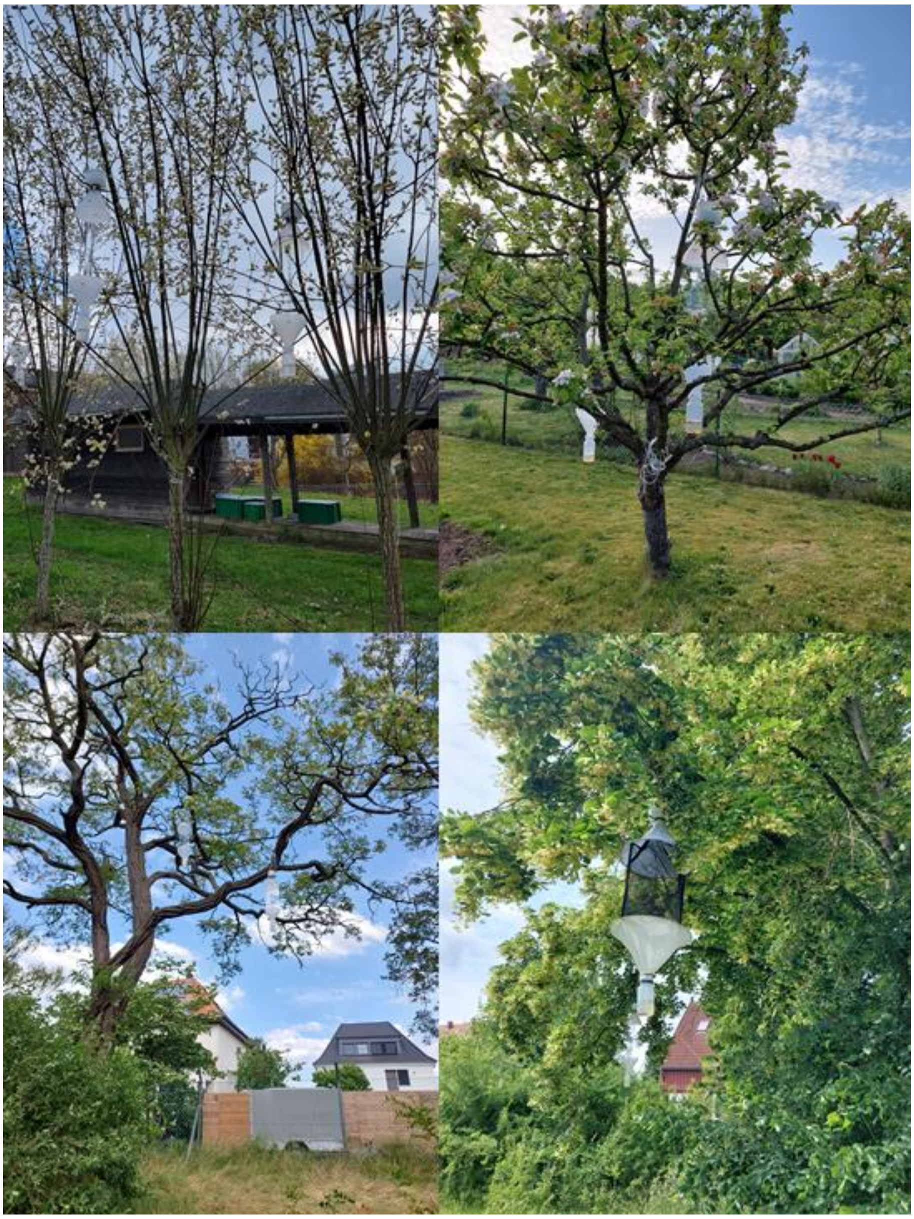

Figure 2. Exemplary photos of flight interception traps used for sampling bees in canopies of different tree species. From upper left to lower right: *Salix*, *Malus*, *Robinia* (all window interception traps), and *Tilia* (aerial Malaise traps and window interception traps). © Julius Kühn Institute (JKI), Institute for Bee Protection.

were observed to be visited by bees and/or were sun-exposed, by hanging them from canopy branches (Fig. 2). Within a tree species, we selected tree individuals and trap positions to hold flower density around the traps (1 m radius) as constant as possible. Depending on weather and flowering progress, sampling periods ranged from three (*Malus*) to six (*Robina*, *Tilia*) and up to 14 days (*Salix*, two sampling periods of seven days, with the first sampling week featuring cold and overcast weather unfavourable for bee flight). In case of damage to a trap during collection, which rendered the exact end date of the sampling period unknown, we excluded the respective sample from further analysis.

We purchased WITs and AMTs from a commercial supplier (ecoTech Umwelt-Messsysteme GmbH, Bonn; WIT: "Air eclector (plastic)"; AMT: "Air eclector (Gauze)"). Traps had two acrylic glass plates (WIT; each plate 65 x 25 cm; interception surface: 0.65 m^2) or two black gauze walls (AMT; each gauze wall 50 x 50 cm; interception surface: 1 m^2) as intercepting structures. These structures were arranged in a crosswise fashion providing four vertical interception surfaces. Funnels below and above the intercepting structures led insects into a bottom and a top collecting jar (bottom and top collector), respectively. We used water with a few drops of detergent (non-fragrant liquid soap) as trapping solution.

All collected bees were dried, pinned and identified to species level under a microscope by S. Josten and A. Krahner (Julius Kühn Institute, Institute for Bee Protection), using the keys listed in Krahner et al. (2021). Due to difficulties in separating species morphologically, we aggregated *Andrena dorsata* Kirby and *A. propinqua* Schenck as *Andrena dorsata* agg.; *Bombus cryptarum* Fabricius, *B. terrestris* L., *B. lucorum* L., *B. magnus* Vogt as *Bombus terrestris* agg.; and *Halictus eurygnathus* Blüthgen, *H. langobardicus* Blüthgen and *H. simplex* Blüthgen as *Halictus simplex* agg. We treated these species aggregates as species in the analysis. We excluded wild bee specimens that we could not identify to species level from the analyses. All collected specimens are deposited in the bee collection of the Julius Kühn Institute, Institute for Bee Protection, in Braunschweig, Germany (unique identifiers provided in the accompanying dataset, Krahner & Dietzsch 2025).

For comparing sampled bee communities among tree taxa, we only used *Salix* samples from the second week of sampling with favourable weather for bee flight. For the analysis of sampled community composition, we used NMDS (k = 3) based on Bray-Curtis distance and transformation (ln + 1) of individual numbers, thereby downweighing the difference in individual numbers due to varying sampling effort across tree taxa. We assessed spatial autocorrelation of the samples by testing for correlation between the community dissimilarity matrix and the spatial distance matrix, using RELATE function (Spearman rank coefficient). We calculated the spatial distance matrix in QGIS Version 3.28 (QGIS.org 2022), based on trap coordinates (EPSG:4647 – ETRS89/ UTM zone 32N(zE-N)). We used a permutation-based multivariate analysis of variance (PERMANOVA; Anderson 2001) for analysing differences between communities sampled in different tree taxa, using tree taxon as fixed factor. We used site nested in tree taxon as random factor to account for spatial autocorrelation in samples. For NMDS, RELATE and PERMANOVA, we used PRIMER 7 Version 7.0.24 (Clarke & Gorley 2015), including the PERMANOVA+ add-on Version 1 (Anderson et al. 2008), and 999999 permutations, respectively (permutation of residuals under a reduced model). Moreover, we investigated the proportion of honeybee individuals within a sample by modelling the probability of a sampled individual to represent a honeybee using a Generalised Linear Mixed Model (GLMM) approach in the R environment (v4.2.2; R Core Team 2022). To this end, we used tree taxon as the only fixed factor, a logit-link function, and a binomial error distribution. We used sample nested in site and the number of sampled individuals per trap as random intercept factors to account for spatially aggregated samples and differences in sampling effort, respectively. We fitted GLMMs using the package 'glmmTMB' (v1.1.5; Brooks et al. 2017). We compared the full model to the null model using Akaike Information Criterion (AICc) and holding the random effect structure constant. For model selection, we used the package 'MuMIn' (v1.47.5; Bartoń 2022). The final model was validated through visual inspection of residual plots and testing for over-/underdispersion and spatial autocorrelation (Moran's I) of the residuals using the package 'DHARMa' (v0.4.6; Hartig 2022) and abovementioned trap coordinate information. Finally, we performed post hoc tests using the package 'emmeans' (v1.8.3; Lenth 2022), and correcting *P* values via the Tukey method. We determined significant statistical differences at alpha = 0.05. We created figures within the R environment using packages 'ggplot2' (v3.4.2; Wickham 2016), 'dplyr' (Wickham et al. 2023) and 'ggpubr' (v0.5.0; Kassambra 2022). Because we sampled apple trees only after peak flower, and because two sampling sites for apple trees were far outside the main sampling area, potentially resulting in sampling of a different local bee community, we repeated all analyses excluding apple trees as sensitivity analyses. Results of these analyses, as well as the results of model validation and post-hoc tests are provided in the appendices.

LITERATURE REVIEW

We systematically searched the peer-reviewed literature in the Web of Science Core Collection, following the guideline of the PRISMA 2020 statement (Page et al. 2021). We used the following search string: "TS = ((hymenoptera OR hymenopter* OR bee OR bees OR bumblebee OR bumblebees OR *bee OR *bees OR apidae OR apoidea OR honeybee OR honeybees OR honey

OR mellifera)) AND TS = (interception trap OR interception trap* OR window trap* OR window trap)". We deliberately excluded the term "Malaise trap", as it would have retrieved a plethora of studies using ground-based Malaise traps, rendering the following analysis unfeasible. In addition, we identified the studies citing and cited by Knuff et al. (2019), which we regard as the key publication on Hymenoptera collection in top and bottom collectors of WITs. We retrieved publications on 11 December 2024 and screened them for relevance. Screening records (title and abstract), we included only papers published in peer-reviewed journals, and we excluded studies that did not contain information about bees or FITs (window traps and aerial Malaise traps). We retrieved full reports (full texts) for all but five records, which we excluded in the first screening step. During full-text screening, again we considered a publication relevant in case it contained information on bees sampled with FITs. Our selection process is documented in Fig. S5 and Table S9. From the relevant studies, we extracted information about FIT design (trap type, number of interception directions, interception surface, and position of the collector units) and usage (sampling habitat, sampled strata and height, duration of the sampling period, and target taxa) in addition to basic bibliographic information.

RESULTS

PILOT STUDY

All data sampled in this study can be accessed via the OpenAgrar repository (Krahner & Dietzsch 2025). We sampled 395 bee individuals, comprising 34 species and including 247 individuals of *Apis mellifera* L.. We excluded one *Robinia* WIT, which collapsed during sampling and contained two honeybee individuals, from the analysis. We were unable to identify one specimen (c.f. *Andrena haemorhoa* Fabricius) reliably due to missing body parts, and we excluded this specimen from analyses of species richness. Thus, for analyses, we used samples from 7 *Salix* trees (8 traps: 6 trees with 1 trap, 1 tree with 2 traps), 3 *Malus* trees (6 traps: 2 traps per tree), 3 *Robinia* trees (5 traps: 2 trees with 2 traps, 1 tree with 1 trap), and 4 *Tilia* trees (12 traps: 3 traps per tree, i.e., 2 WITs and one AMT per tree). Sampled communities were spatially autocorrelated (rho = 0.33, $P < 0.004$).

In *Tilia* canopies, WITs sampled 231 individuals (eight traps), while AMTs yielded ten individuals (four traps). AMTs sampled fewer individuals and species per interception area than WITs (Fig. 3), while we observed no apparent differences in the proportion of sampled honeybees between trap types (Fig. 4B). Top collectors did not sample a single bee individual in the course of this study, neither in WITs nor in AMTs. We also observed

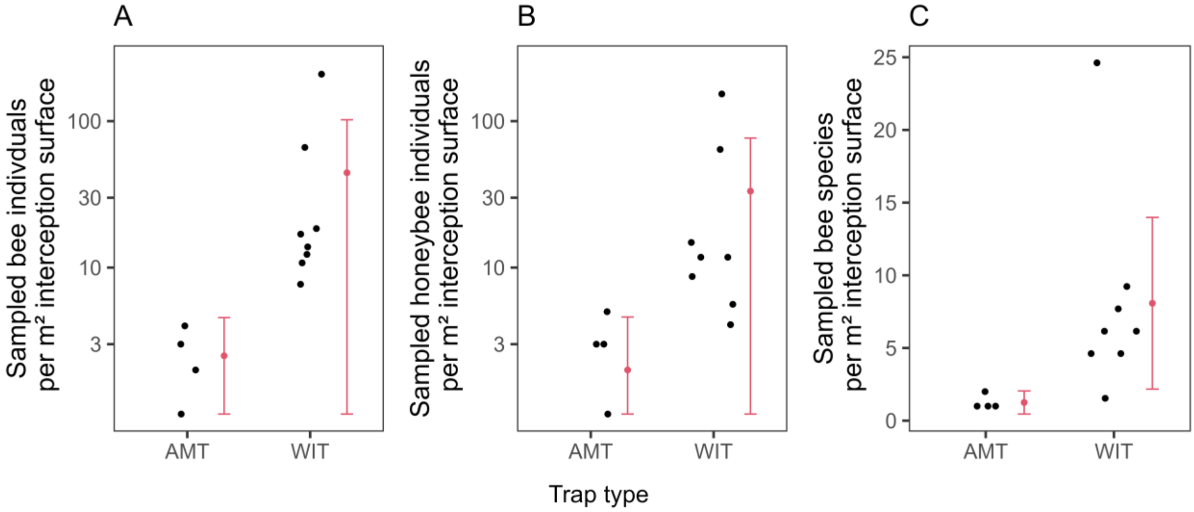

Figure 3. Number of bee individuals (A), honeybee individuals (B) and bee species (C) per area of interception surface, sampled with aerial Malaise traps (AMT) and window interception traps (WIT) in flowering canopies of *Tilia* trees. Points were jittered slightly on the x-axis in (B) and (C) for better visibility. Red points and error bars represent sample mean and 95% confidence intervals, respectively.

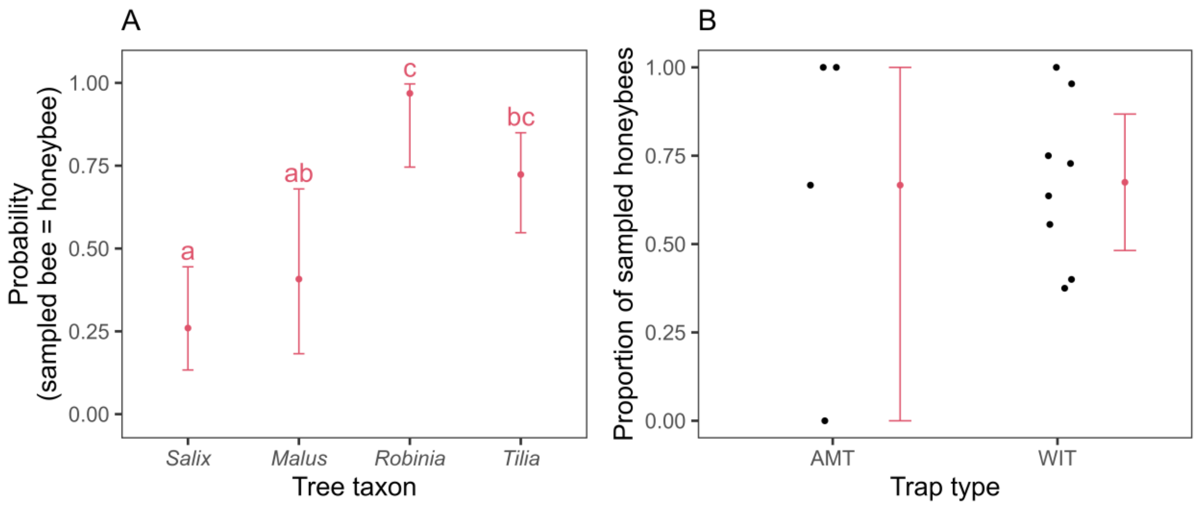

Figure 4. A) Modelled probability of a sampled bee individual representing a honeybee individual in samples from window interception traps in flowering canopies of different tree taxa. Different letters represent significant differences between tree taxa (Binomial GLMM (logit-link) & Tukey test, df = 382, $P \leq 0.023$), while error bars represent 95% confidence intervals. B) Proportion of sampled honey bees per trap, sampled in *Tilia* trees, as a function of trap type (AMT: aerial Malaise trap, WIT: window interception trap). Black points are jittered slightly along the x-axis and represent observations. Red points and error bars represent sample means and 95% confidence intervals, respectively.

low amounts of bycatch in top collectors compared to bottom collectors, with the exception of several individuals of Chrysopidae and Coccinellidae found in top collectors in some sampling rounds (pers. obs.). We observed a significant correlation between tree taxon and the composition of bee communities sampled with WITs (PERMANOVA, Pseudo-F = 4.640, df = 3, $P < 0.003$; Fig. 5), also when excluding samples from apple trees from the analysis (Pseudo-F = 6.995, df = 2, $P < 0.002$; Fig. S1). The proportion of sampled honeybee individuals in WIT samples varied between tree taxa (Fig. 4A). Compared to *Salix* trees, WITs sampled a significantly greater proportion of honeybees in *Robinia* trees (binomial GLMM (logit-link), odds ratio = 11.714, SE = 14.714, $P = 0.003$) and in *Tilia* trees (odds ratio = 7.448, SE = 4.279, $P = 0.003$). WITs in *Robinia* trees also sampled a greater proportion of honeybees compared to WITs in *Malus* trees (odds ratio = 44.499, SE = 59.124, $P = 0.023$). We found similar differences between *Tilia* and *Salix* samples, as well as *Robinia* and *Salix* samples, when excluding *Malus* samples from the analysis (Fig. S2).

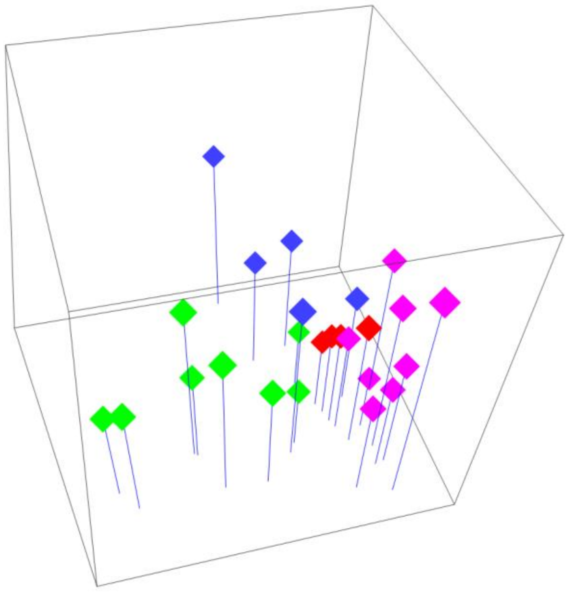

Figure 5. NMDS ordination for bee communities sampled in flowering canopies of different tree taxa (◆ *Salix*, ◆ *Malus*, ◆ *Robinia*, ◆ *Tilia*) using window interception traps. Bray-Curtis dissimilarity and log(x+1) transformation, 3D stress = 0.09.

LITERATURE REVIEW

Our systematic literature search yielded 138 studies: 33 citations of Knuff et al. (2019), 33 references cited by Knuff et al. (2019), and 72 additional studies identified using our search term. Out of these studies, we excluded five studies during record screening (title and abstract) and 113 studies during report screening (full text; Fig. S5). Studies were excluded because they provided no specific information about bees (78 studies; Table S9), because they reused data that were used by an earlier study already considered

(1), they were not a peer-reviewed publication (2) or they did not provide specific information about AMTs or WITs (32). We identified a subset of 19 relevant studies (Table 1), which contained information about bee samples obtained with AMTs or WITs. Studies originated across all continents except Africa and Antarctica. With the exception of two studies (Samkov & Tshernyshev 1983; Basset 1988), all studies were conducted after 2000. We observed methodological variation among studies in terms of both trap design and usage.

The majority of studies used WITs instead of AMTs (16 out of 19 studies; Table 1). Traps intercepting flight in four directions were more common (13 studies) than traps with two interception directions (six studies). Interception surface per trap was generally below 1 m² (median: 0.45 m², range: 0.08-6.72 m²; excluding Wells & Decker (2006), who provide only a range). Separating the AMT part from the WIT part of the composite FIT in Basset (1988), interception trap surface was larger in AMTs compared to WITs (AMT, median: 3.71 m², range: 0.7-6.72 m²; WIT, median: 0.48 m², range: 0.08-2.63 m²). A minority of studies used top collectors (three out of 19 studies).

While about half of the studies placed FITs at crown height (up to 27.5 m above ground; Table 1; Nagamitsu et al. 2007; Vance et al. 2007; Nagamitsu et al. 2010), including crowns that flowered during the sampling period (Basset 1988; Inari et al. 2005; Müller et al. 2008; Bogusch & Schlaghamersky 2010; Ulyshen et al. 2010; Wildermuth et al. 2023), the other studies mostly sampled in the understorey or used ground-based FITs (Samkov & Tshernyshev 1983; Ushimaru et al. 2008; Howlett et al. 2009; Rubene et al. 2015; Steinert et al. 2021; Shi et al. 2022). All studies that placed traps in crowns sampled in forest habitats. Moreover, we identified seven relevant studies that sampled simultaneously at different strata. In general, the sampling periods were in the order of months (median: 3 months, range: 1-12 months) and thus markedly exceeded the flowering period of trees, when FITs were placed in the canopy stratum.

Most studies used FITs for sampling a broad spectrum of flying insect taxa, but six out of 19 studies used FITs specifically to sample bees (Table 1). These six bee studies differed in some aspects from the complete set of relevant studies: smaller interception surface (median: 0.31 m² vs. 0.45 m²), more frequent use of four flight directions (5 out of 6 studies vs. 13 out of 19 studies), and less frequent use of top collectors (no study vs. 3 out of 19 studies). We did not observe marked differences between bee-targeting studies and the complete set of relevant studies with regard to median sampling duration (3.5 vs. 3 months, respectively). All relevant and bee-targeting studies used WITs for sampling.

DISCUSSION

We successfully sampled distinct bee communities in flowering trees with WITs. Sampled bee community compositions were distinct for each tree taxon, often reflecting specialised or favored foraging associations with the corresponding tree taxa previously reported in the literature. This indicates that WITs yield representative samples of the bee community foraging in flowering canopies. Thus, WITs may represent a valuable tool for bee inventories and assessments of conservation measures by including bees that forage at elevated floral resources often neglected by bee researchers given the difficulty of accessing canopy flowers and bee communities in canopies. To our knowledge, our pilot study is the first to show that top collectors above the interception surface of the traps proved unsuitable for sampling bees. This finding negated our expectations, which were based on results from ground-based Malaise traps. The systematic literature review yielded mostly studies from forest habitats and not focussing on bees and indicated a general consensus with regard to several methodological details: (a) use of WITs rather than AMTs, (b) use of four rather than two interception directions, and (c) use of bottom collectors rather than top and bottom collectors. Most studies have been conducted after the year 2000, which corroborates the observation by Bogusch & Schlaghamersky (2010) for central Europe that researchers have only recently started using FITs for sampling Hymenoptera.

FIT SAMPLES ARE LIKELY TO REPRESENT FLOWER-VISITING BEES IN TREE CANOPIES

Our pilot study provides support for FIT samples representing local resource use in

Table 1. Overview of the 19 relevant studies identified during the systematic literature search. We regarded studies relevant in case they contained information about sampled bees and used window interception traps (WIT) or aerial Malaise traps (AMT). For the complete list of studies and the reasons for excluding a specific study, refer to Table S9.

Reference	Country	Trap type[1]	Interception directions	Interception surface [m^2]	Collectors[2]	Habitat	Sampling layer	Sampling height [m]	Sampling period [mm/yyyy]	Target taxa
Basset (1988)	Australia	composite AMT/WIT	2 (AMT)/ 4 (WIT)	0.70 (AMT) + 0.55 (WIT)	bottom & top	forest	canopy	about 25	02/1986-02/1987	canopy arthropods
Bogusch & Schlaghamersky (2010)	Czech Republic	WIT	4	0.24, 0.48 & 0.6	bottom	forest	canopy & understorey	12 & 25	05-10/2002 & 05-10/2003	Coleoptera
Borges et al. (2022)	Portugal	AMT	4	NA	top	forest	unknown	unknown	2019-2020	exotic arthropods
Howlett et al. (2009)	New Zealand	WIT	4	0.36	bottom	arable crop	herbaceous flower stratum	unknown	01 & 12/2004; 01/2005	flower-visiting arthropods
Inari et al. (2005)	Japan	WIT	4	NA	bottom	forest belt	ground & canopy	1; 7-15	05-09/2003	bumblebees
Müller et al. (2008)[3]	Germany	WIT[4]	4	0.96	bottom	forest edge	ground & canopy	1.5; 12-25	05-09/2006	Coleoptera, Hemiptera, Hymenoptera Aculeata
Muñoz et al. (2021)	Chile	WIT	4	0.24	bottom	orchard	unknown	unknown	10/2017, 01/2018, 04/2018, 10/2018	Apiformes, Coleoptera: Coccinellidae
Nagamitsu et al. (2007)	Japan	WIT	4	NA	bottom	forest belt	canopy & understorey	0.9-1.7; 6.8-13.3	06-09/2004	bumblebees
Nagamitsu et al. (2010)	Japan	WIT	4	NA	bottom	forest & forest belt	canopy	7.0-13.3	06-09/2004; 06-09/2005; 06-09/2006	bumblebees
Rubene et al. (2015)	Sweden	WIT	2	0.08	bottom	clear-cut	understorey	1.5	06-08/2011	Hymenoptera Aculeata
Samkov & Tshernyshev (1983)	Russia	WIT	4	2.63	bottom	unknown	ground	ground level	05-09/1981	various insect orders

Table 1 continued.

Reference	Country	Trap type[1]	Interception directions	Interception surface [m^2]	Collectors[2]	Habitat	Sampling layer	Sampling height [m]	Sampling period [mm/yyyy]	Target taxa
Shi et al. (2022)	China	WIT	2	0.42	bottom	arable crop	herbaceous flower stratum	1.6	02-04/2018; 02-04/2019	flower-visiting insects
Shi et al. (2023)	China	WIT	2	0.55	bottom	arable crop	unknown	unknown	02-04/2022	pollinator insects
Steinert et al. (2021)	Norway	WIT	4	0.31	bottom	clear-cut	shrub[5]	unknown	04-09/2013, 04-09/2015	bumblebees
Ulyshen et al. (2010)	USA	WIT	4	0.24	bottom	forest	ground & canopy	0.5; 15-24	04-10/2005	bees (not originally)
Ushimaru et al. (2008)	Japan	WIT	2	0.32	bottom	forest; clear-cut; paddy field; pasture	ground, shrub & understorey	0.5; 1.5; 3; 8-20	04-10/2003	bumblebees
Vance et al. (2007)	Canada	AMT	4	6.72	bottom & top	forest	canopy & understorey	0.3-0.45; 18-27.5	06-08/2001	Hymeoptera; Mymaridae
Wells & Decker (2006)	Commonwealth of Dominica	WIT[6]	2	2-3	bottom	forest	unknown	unknown	05-06/2003	Non-Formicidae Hymenoptera
Wildermuth et al. (2023)	Germany	WIT	4	0.48	bottom	forest	canopy	10-24	06-07/2022	canopy arthropods

[1] AMT: aerial Malaise trap; WIT: window interception trap

[2] bottom/top: collector positioned below/above the interception surface

[3] sampling methodology also extracted from a cited reference, i.e. Müller et al. (2007)

[4] color stimulus added to the windows (yellow adhesive tape)

[5] assessed from photograph

[6] using mesh-wire windows in WIT, in addition to ground-level Malaise traps

flowering trees. In flowering *Robinia* crowns, which are known as a good forage for honeybees, we almost exclusively sampled *Apis mellifera*. In *Salix* trees, oligolectic bee species specialised on *Salix* pollen, i.e., *Andrena clarkella* (Kirby), *A. praecox* (Scopoli), *A. vaga* Panzer, and *Colletes cunicularius* (L.), contributed more than one third of the sampled individuals. Although we did not analyse pollen samples from collected bees, oligolectic behaviour in these bee species indicates that the collected individuals utilised sampled trees for foraging. Our observation of one specimen of *Sphecodes ferruginatus* von Hagens in a flowering *Tilia* crown is in accordance with the findings of Bogusch and Schlaghamersky (2010) that these cuckoo bees of ground-nesting hosts may exploit elevated food resources. Given the strong association of the sampled bee community to tree floral resources, we think it unlikely that our samples may contain mostly bees travelling through the canopy, which has been suggested by Ulyshen et al. (2020) regarding sampling in non-flowering canopies. To some extent, this may be the case for our samples from apple trees, which we collected after peak flower. The timing of our sampling rounds corresponded to sampling different wild-bee communities as a result of temporal species turnover. In order to exclude this effect and effects of vertical stratification of the bee communities, future studies should simultaneously sample in non-flowering environments at the same stratum and location as the floral resources. This may be best achieved in species-rich mixed forest stands or arboreta. Alternatively, flower visitation could be measured directly via focal observations and compared to FIT samples, which may be unfeasible in tall trees.

Although our systematic search focussed on hymenopterans and thus filtered out many studies about other taxa, we identified only a small subset of studies reporting results on bees sampled with FITs, and only few studies that specifically targeted bees (Table 1). This indicates that FITs are a method not well established among bee researchers. While FITs have occasionally been used for detecting bee taxa, such as introduced bumblebees, within wider landscapes (Inari et al. 2005; Borges et al. 2022), previous studies indicate that they are potentially useful in characterising bee communities at a much smaller spatial scale. For Apidae, Colletidae and Halictidae in near-ground floral resources, Howlett et al. (2009) observed strong correlations in counts from FITs and direct observations. Some of the seven studies identified through our systematic literature search which sampled simultaneously at different strata, found differences in samples between these strata (Inari et al. 2005; Nagamitsu et al. 2007; Ushimaru et al. 2008; Ulyshen et al. 2010), as did Müller et al. (2007). Inari et al. (2005) sampled more native and exotic bumblebee individuals in the canopy compared to the ground stratum, and Nagamitsu et al. (2007) observed a positive correlation between trap height and sampled bumblebee abundance for some species, depending on local abundance of other bumblebee species. Müller et al. (2007) sampled more bee species in the ground compared to the canopy stratum. Finally, Vance et al. (2007) did not find an association between sampled bee taxa and the sampling stratum (canopy and understorey), but this is likely a consequence of only few collected bee individuals (less than six individuals of Apidae and Halictidae, respectively).

While these studies indicate that FIT samples may contain representative information about the active bee community in higher strata, the role of floral resources in shaping these observed patterns remains unclear. Often, sampling periods extend well beyond tree flowering periods (Table 1), and information on floral resources in the surroundings of FITs is lacking. Nevertheless, some authors hypothesise that differences in bee samples between strata are driven by floral resource use. Ushimaru et al. (2008) consider the use of different floral resources as an explanation for differences in sampled individuals of *Bombus ardens* Smith and *B. diversus* Smith between the shrub and the sub-canopy stratum in Japanese forests. Ulyshen et al. (2010), who sampled more individuals and species in the canopy stratum than at ground level in a hardwood forest in the eastern US, observed high bee activity in the canopy stratum, even in the absence of tree flowers. In addition to floral resource use, Ulyshen et al. (2010) discuss elevated nesting sites and non-floral sugar sources as potential explanations for their findings. Ulyshen et al. (2020) also discuss non-floral resources as an explanation for the presence of bees throughout the year in canopies of spring-flowering hardwood forest. Likewise, Bogusch & Schlaghamersky (2010) speculate on the use of honeydew resources in canopies by *Sphecodes* bees in a central European floodplain forest.

In conclusion, there is some evidence from the pilot study and in the literature for FIT samples to represent the species assemblage of a specific stratum, including flowering canopies. Future studies should investigate how well sampled abundance correlates with true activity density in flowering canopies. Because activity density associated with elevated floral resources is difficult to assess, e.g. by means of direct observation, we suggest studies looking for correlations between floral abundance and sampled bee abundance. Such studies should ideally sample simultaneously a gradient of floral abundance within the same stratum in order to avoid effects of spatial and temporal changes in community composition and activity density.

Top collectors do not offer a benefit to bee sampling with FITs

Contrary to our expectation, we sampled not a single bee individual in the top collectors of our FITs. Knuff et al. 2019, using WITs with both top and bottom collectors, sampled more Hymenoptera individuals in top collectors than in bottom collectors in forests with traps placed 1.5 m above ground. Our data clearly show no benefit in using FITs with top collectors in addition to bottom collectors when the focus is on bees. This is in accordance with our literature search results: most FIT studies that reported results on sampled bees used collectors placed below the interception surface only (including all six studies targeting bees; Table 1). Our field observations corroborate the findings of Basset (1988), who sampled fewer Apoidea individuals in the upper collecting unit than in the lower collecting unit of his composite FIT in crowns of a subtropical rainforest. Our results are also congruent with Vance et al. (2007), who observed an association between Halictidae and bottom collectors (based on few collected individuals). Likewise, Koch et al. (2024) observed winged ants in the bottom collector rather than the top collector of AMTs. This did not comply with their expectation of a positive phototropism of winged ants encountering the interceptive trap surface, which we also expected for bees. At least in our study area, top collectors also yielded low numbers of bycatch samples, which may indicate limited purpose of using top collectors at all.

We do not know of any behavioural data on the interception of bee individuals by FITs. For bumblebees, it is sometimes assumed that individuals colliding with WITs drop down upon flight interception (Nagamitsu et al. 2007; Nagamitsu et al. 2010; Ushimaru et al. 2008, referring to Inari 2002). Koch et al. (2024) interpreted their results of winged ants collected in the bottom rather than the top collectors as indicative of a specific behaviour of winged ants. These may, upon encountering the trap, land and walk towards the ground (Koch et al. 2024). Likewise, Noordijk et al. (2008) observed that small insects are able to land on the window or sometimes fly off upon flight interception by window traps. Thus, the variation among bee species, including size and behavioural variation, may result in a bias of caught bee species, a phenomenon well known for pan traps (Portman et al. 2020; Krahner et al. 2021). Classic ground-based Malaise traps are an effective method for sampling bees (e.g., Krahner et al. 2021), and in our study area, we regularly observed positive phototropism when sampling bees with a hand net swayed against the ground (A. Krahner, pers. obs.). Therefore, we hypothesise that bee individuals intercepted by FITs drop down before they are able to re-orientate and fly in the direction of light, thus ending up in the bottom collector. Video documentation may help in testing this hypothesis in the future. This should include an evaluation of roofs above the interception surface for keeping positively phototropic bees on the interception surface, which is one function of the roof (in addition to excluding rain from bottom collectors; Masner & Goulet 1981), but not always considered (e.g., Steinert et al. 2021). In the meantime, our results show that top collectors are unnecessary for sampling bees with FITs.

Further points to consider when sampling bees with FITs

Sometimes, researchers add an attractive stimulus to the FIT (Müller et al. 2007; Müller et al. 2008). Duelli et al. (1999) have also suggested combining different trapping mechanisms, i.e. flight interception and visual attraction, by adding crossed window plates on top of coloured funnels. Such traps have been recommended later on (Inari 2002), and have been proven effective for sampling bees (Thompson et al. 2021). The benefit of such combined traps over classic pan traps remain to be demonstrated experimentally. Moreover, introducing an attraction mechanism (with unknown range) to an interception trap is likely to reduce the correlation between the sample and local activity density. In our opinion, this correlation is one of the pivotal advantages of FITs over other sampling methods, and so we caution against such alterations to FITs based on present knowledge. Avoidance of visual attraction has also been suggested by Knuff et al. (2019), who painted funnels and collectors with green colour while referring to the results of a pan trap study (Ortiz-Sanchez & Aguirre-Segura 1993). Ulyshen et al. (2010) also speculated on a potential impact of using white bucket collectors on sampling efficacy. Likewise, we cannot rule out the possibility of the opalescent white colour of the plastic funnels in our window traps as well as the white cloth funnels of our aerial Malaise traps being visually attractive to the sampled bees. Due to the low sampled abundance in our AMTs and due to our WIT samples representing the association between many sampled bee species and pollen hosts well (see above), we think that attraction was not the major trapping mechanism in our study. Nevertheless, similar to the outer surface of pan traps (Krahner et al. 2024), future studies should investigate if camouflaging potentially attractive parts of FITs has an impact on bee samples. Such camouflaging may also prevent vandalism (Wilkening et al. 1981). For more accurate estimates of true flight activity, we advocate to use trapping liquids that are neither repellent nor attractive (Basset 1988).

Our findings are limited regarding sampling efficacy of AMTs compared to WITs, as this comparison is based on an imbalanced number of traps of each type and on a low absolute number of traps in only one tree taxon. Nevertheless, we would prefer WITs over AMTs based on the low number of bees sampled with AMTs in our pilot study. This seems to be in accordance with previous studies, the majority of which used WITs like all studies targeting bees (Table 1). Still, AMTs may have some advantages over WITs, which include easier transportation and lighter weight. The latter allows for placing the largest per-trap interception surface identified in our literature search (Table 1) at the canopy stratum (Vance et al. 2007) with interception surface being an important feature for FITs (Carrel 2002; Robert et al. 2021). The treatment of AMTs with insecticides in order to increase the number of sampled hymenopterans through rapid poisoning (Masner & Goulet 1981) needs further experimental investigation before it can be recommended for bee sampling.

Regarding directionality of the interception surface, the majority of relevant studies sampled in four directions (crossed surfaces) rather than two directions, especially when targeting bees (Table 1). We do not find a rationale for this practice, neither in the set of relevant studies nor in early method papers (Hines & Heikkenen 1977; Wilkening et al. 1981). However, we do not expect a strong directionality of flight for bees foraging within flowering canopies, unlike they orient their flight along linear landscape elements (Cranmer et al. 2012). Therefore, we would prefer FITs sampling in four directions to those sampling in two directions in order to increase sampling efficacy.

STUDY LIMITATIONS

The design of our pilot study is limited to a relatively low spatial replication: we sampled within a small area only, sampling points were often spatially aggregated, and sampled communities were spatially autocorrelated. Moreover, sampling effort varied among tree taxa, in terms of the number of trees sampled the number of traps used, and the number of sampling days. Therefore, the present results should be regarded as indicative. Future studies using replicated sites across a larger study area and a balanced study design are necessary to corroborate the present findings.

While we sampled bees in trees that were growing isolated or in small groups, all studies that we identified through our systematic search and that placed FITs in crowns involved forest trees (Table 1). Although we are not aware of any documented differences in flower visitation behaviour in bees between isolated and forest trees, potential differences should be kept in mind when relating our pilot study results to the findings of other studies. Moreover, the results of our pilot study mirror bee community composition of an urban setting and may not be comparable to results of studies conducted in forest habitats. Cities are known to filter bee communities, depending on trait (Ayers & Rehan 2021). Nonetheless, compared to bee communities from flower strips on agricultural sites around Braunschweig (69 species based on 1147 sampled individuals; Krahner et al. 2025), the city of Braunschweig is known to host a relatively high species richness of bees (102 species based on 1589 sampled individuals; Weber et al. 2023), which corresponds to about 17% of the German bee species inventory (Scheuchl et al. 2023). In contrast, only a few bee species in Germany are strongly associated with forests, especially closed-canopy forests (e.g., Dorow et al. 2019).

We find some indications of a regional bias in the few studies using FITs and providing results on bees (Table 1). Almost half of the relevant FIT studies originated in Asia and Australasia (Table 1), which are underrepresented in pan trap studies (Krahner et al. 2024). In particular, Japanese studies are well represented in Table 1. These studies either refer to an early guidance for this region (Inari 2002; cited in Inari et al. 2005 and Ushimaru et al. 2008) or have been conducted under participation of the author of this key publication (Nagamitsu et al. 2007; Nagamitsu et al. 2010). Thus, overrepresentation of Asia may be the consequence of a small cluster of researchers traditionally using FITs. Given the small number of relevant studies compared to a multitude of pan-trap studies (Krahner et al. 2024), apparent regional bias in Table 1 should not be over-interpreted.

CONCLUSION

While FITs have been used for decades for insect sampling (Malaise 1937; Townes 1962; Juillet 1963), including sampling in the understorey stratum (Hines & Heikkenen 1977) and in canopies (Basset 1988; Springate & Basset 1996), their use for sampling bees is still limited. Our pilot study and systematic literature review provide insight into the applicability of FITs for sampling bees in flowering canopies. Based on the existing knowledge, FITs, especially WITs, are a still underestimated tool for sampling ecologically meaningful data regarding plant-pollinator associations in trees and for assessing utilization of tree floral resources by bees. When using FITs for sampling bees in flowering canopies, we advocate for using WITs with bottom collectors only, without attractive stimuli (colour and scent), which sample in four directions. Future methodological studies should focus on the correlation between local flower availability and sampled activity-density, on the impact of camouflaging FITs, and on the behavioural response of bees to FITs (including potential differences between AMTs and WITs). Experimentally testing the advantages and limits of FITs in both tree canopies and the ground level will further the value of FITs in bee research.

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AUTHOR CONTRIBUTION

Concept and design AK, ACD & JP, data collection AK & ACD, data analysis AK, writing AK, edits and approval for publication AK, ACD & JP.

DISCLOSURE STATEMENT

The authors declare no potential conflict of interest.

DATA AVAILABILITY STATEMENT

The data are available from the OpenAgrar repositorium (Krahner & Dietzsch 2025).

APPENDICES

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

Figure S1. Ordination for bee communities sampled in flowering canopies of different tree taxa

Figure S2. Modelled probability of a sampled bee individual representing a honeybee individual in samples

Table S1. Correlation between the community dissimilarity matrix and the spatial distance matrix (complete dataset)

Table S2. Correlation between the community dissimilarity matrix and the spatial distance matrix (reduced dataset)

Table S3. PERMANOVA results (complete dataset)

Table S4. PERMANOVA results (reduced dataset)

Figure S3. DHARMa residual plots (complete dataset)

Table S5. DHARMa test results (complete dataset)

Table S6. Post-hoc test results (complete dataset)

Figure S4. DHARMa residual plots (reduced dataset)

Table S7. DHARMa test results (reduced dataset)

Table S8. Post-hoc test results (reduced dataset)

Figure S5. PRISMA 2020 flow diagram

Table S9. Complete list of studies resulting from the systematic literature search

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