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New insights into the diets of seven hymenopteran species using trnL metabarcoding in a Malaysian tropical forest reserve

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Abstract

Historically, wasps were considered merely flower visitors but are now recognized as playing a significant role in interactions with flowering plants. Recent studies indicate that certain wasp families exhibit pollen transport capacity and plant fidelity comparable to some well-known bee pollinators. This study examined the diet on 19 samples comprised of seven hymenopteran species (wasps; *Polistes* sp., *Paramblynotus* sp., *Polybioides* sp., and *Auplopus* sp., and bees; *Tetrigona apicalis*, *Apis cerana* and *Nomia strigata*) collected from a model site, the protected primary forest of Tengku Hassanal Wildlife Reserve (THWR), Pahang, Malaysia. All 19 hymenopteran samples were subjected to metabarcoding analysis of trnL utilising the Illumina MiSeq platform. Through bioinformatic analyses, the single phylum Streptophyta, comprising 44 known families and 100 known species, was detected, and 15 top species were discussed. Fabaceae (11.45%) emerges as the most predominant plant family recorded, followed by Gesneriaceae (11.03%), Podostemaceae (10.18%), Asteraceae (8.99%), and Poaceae (6.43%). *Rachunia cymbiformis* (Gesneriaceae), *Polypleurum chinense* (Podostemaceae), *Taraxacum platycarpum* (Asteraceae), *Chusquea* sp. (Poaceae), and *Lycoris* sp. 1 (Amaryllidaceae) are the top five species being consumed, with 10.90%, 10.18%, 8.14%, 5.84%, and 4.57%, respectively. Notably, *Dipterocarpus turbinatus* (Dipterocarpaceae), listed as Vulnerable by the IUCN, was recorded in four hymenopteran species. Molecular evidence also revealed that several forest trees and crop species from nearby villages were foraged by both wasps and bees. The data would be beneficial for relevant authorities in formulating a management and conservation strategy for the forest.

Keywords Next-Generation Sequencing · Primary forest · Bee · Wasp · Flower-insect interaction

Introduction

Hymenoptera, a diverse order that includes bees, wasps, and ants, play crucial roles in maintaining ecological balance through pollination and other ecosystem services. Bees are well known for their effectiveness as pollinators across agricultural and natural habitats, contributing significantly to plant reproduction, food security, and ecosystem stability (Calderone 2012; Khalifa et al. 2021; Katumo et al. 2022). For instance, several tropical forest trees such as *Dryobalanops* sp., *Dipterocarpus tempehes*, and *Dillenia excelsa* rely on the effectiveness of bee pollination (Momose et al. 1998; Nagamitsu et al. 1999). Conversely, wasps are often perceived as less efficient pollinators or mere floral visitors (Ballantyne et al. 2015) and have therefore been understudied despite their ecological importance (Pereira 2024). Adult wasps frequently visit flowers to forage for nectar and other plant-derived resources, and during these visits they

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can carry pollen on their bodies, indicating regular contact with flowering plants.

Understanding the role of wasps and other non-bee Hymenoptera in utilizing floral resources remains limited, in part due to the lack of molecular studies exploring their dietary associations with plants. Metabarcoding analysis has emerged as a useful tool for examining diet composition, enabling the identification of plant material consumed by insects and providing indirect evidence of their floral interactions (Fahimee et al. 2021). While the pollination role of bees can often be inferred from their direct consumption of pollen, wasps although they do not feed on pollen, may still contribute to pollination through the incidental transfer of pollen during flower visits (Goulson 1999). Recent study demonstrate that wasps can effectively transfer pollen, with families such as Sphecidae and Vespidae showing pollen-carrying capacities and plant fidelity comparable to certain bee taxa. They often visit distinct subsets of plant communities, occupying unique ecological niches that complement other pollinators and contribute to overall pollination stability (Borchardt et al. 2024). Addressing this gap can deepen our understanding of how different hymenopteran species use floral resources and associated with forest plants.

Traditional methods such as direct field observations and pollen analyses remain fundamental for identifying plant–insect interactions. Field observations provide behavioural insight but are often time-consuming and limited by observer bias (Teng et al. 2024). Similarly, pollen analysis offers valuable taxonomic information but typically requires expert knowledge and provides limited resolution, often restricted to family or genus levels (Lucek et al. 2019). When combined, these methods yield robust data, and metabarcoding can serve as a complementary approach to broaden taxonomic detection and improve ecological inference.

Metabarcoding has been successfully applied to assess plant diversity, track pollinator foraging patterns, and reveal complex ecological networks, complementing traditional techniques such as visual observation and camera trapping (Johnson et al. 2023). Studies using the trnL marker have demonstrated its utility in identifying plants associated with Hymenoptera species (Hawkins et al. 2015; Pompanon et al. 2012).

In Malaysia, where tropical forests harbor significant biodiversity, pollination research has focused primarily on bees, especially in agricultural contexts. However, the ecological roles of non-bee hymenopterans, particularly wasps, remain poorly understood. This gap is especially evident in the Tengku Hassanal Wildlife Reserve (THWR) in Pahang, a 60,000-hectare protected area representing diverse forest types. Although both bees and wasps are recognized pollinators of forest trees (Faraz et al. 2023), few studies have supported these observations with molecular evidence (Aziz et al. 2022). Understanding which plant taxa are associated with Hymenoptera in this forest is essential for designing conservation strategies that integrate pollinator diversity, plant reproduction, and wildlife food sources.

To address this gap, this study tested two hypotheses: (1) plant species identified from both nectar and pollen in the diet of bees are potential candidates for bee-mediated use of floral resources, and (2) plant species detected from the nectar-associated DNA of waps indicate plant taxa that are regularly visited and may also be pollinated through incidental pollen transfer during floral visitation. Accordingly, trnL metabarcoding was used primarily to characterise the floral resources associated with seven bee and wasp species from THWR, rather than to quantify pollination effectiveness. The plant DNA signatures recovered provide a baseline of their foraging patterns in a Malaysian primary forest, without inferring pollination effectiveness or plant reproductive outcomes. These data further clarify their dietary composition and potential contributions to pollination networks within tropical forest ecosystems.

Table 1 Sampling locations of Hymenoptera specimens within the Tengku Hassanal Wildlife Reserve (THWR), including site codes, geographic coordinates, and associated ecosystem types

Sample code	Location	Grid	Ecosystem
LK	Pahang: THWR, Lembah Klau	03°41.354'N, 102°1.196'E	Lowland dipterocarp forest
BR	Pahang: THWR, Bukit Rengit	03°35.580'N, 102°10.817'E	Lowland dipterocarp forest
PP	Pahang: THWR Pos Perlok	03°50.544'N, 102°12.234'E	Lowland dipterocarp forest
KL	Pahang: THWR, Kuala Lompat	03°42.957'N, 102°17.286'E	Lowland dipterocarp forest, Riverine

Materials and methods

2.1 Study site, sample collection, and species identification

The Tengku Hassanal Wildlife Reserve (THWR) in Pahang, Malaysia, which spans an area of 60,551,608 hectares. Three Townes style malaise traps with dimension L165 x W115 x H200 cm (tall end) and H110 cm (short end) were positioned at four designated places within the THWR for hymenopteran sample collection, namely Lembah Klau, Bukit Rengit, Kuala Lompat, and Pos Perlok (Table 1**).** The sites are not adjacent to each other. Other than the similarity in forest types which is lowland dipterocarp forest, they are distanced more than 10 km away from each other. The traps were left for 12 months, from February 2023 to January 2024. Alcohol solution (70%) was used to preserve the hymenopteran body intended for molecular laboratory analysis before performing molecular identification of the hymenopteran specimens (bees and wasps). Initially, their identification was based on the morphological characteristics based on species key provided by Goulet and Huber (1993) and Michener (2007) using a Stemi-D4 stereomicroscope (Carl Zeiss, Germany) and a Dino-Lite digital microscope to facilitate detailed species identification.

2.2 DNA extraction.

Subsequently, their identification was further confirmed through DNA barcode analysis. Prior to molecular analysis, the whole insect body was used for DNA extraction. Each sample was surface-sterilized by immersion in 70% ethanol, followed by three rinses in distilled water for 2–3 s each (Avanesyan 2014; Cooper et al. 2016). The samples were extracted using NucleoSpin DNA Insect Kit (Macherey-Nagel) and DNeasy Blood and Tissue Kit (Qiagen) following Idris et al. (2023). Polymerase chain reaction (PCR) was performed using the universal primers by Folmer et al. (1994) following the profile by Fahimee et al. (2021), Salbi et al. (2022) and Jaapar et al. (2025).

DNA sample quality control

Fluorometric quantification was performed on the extracted DNA samples, which involved a spectrophotometer and agarose gel, followed by the quality control (QC) procedure of the samples. Subsequently, amplicon PCR QC was conducted for the purified DNA after it passed the DNA sample QC. After passing the amplicon PCR QC, the DNA samples were subjected to amplicon library preparation using two-step PCR, adhering to Illumina's library preparation guidelines. This process has become one of the precautionary measures to avoid contamination in samples. First, the purified DNAs were tested on a 1% TAE agarose gel to assess their quality. A spectrophotometer (Implen NanoPhotometer® N60/N50) and a fluorometric quantification kit (iQuant™ Broad Range dsDNA Quantification Kit) were employed for the quantification of DNA concentration.

Amplicon PCR QC

After passing the DNA sample QC, the purified DNA was amplified using locus-specific sequence of trnL primers, with PCR forward primer, g-A49425 (5'-GGGCAATCCTG AGCCAA-3') and PCR reverse primer, h-B49466 (5'-CCA TTGAGTCTCTGCACCTATC-3'). REDiant 2X PCR Master Mix (1st base) was used to perform all PCR reactions.

First part of library construction (1st stage PCR)

Locus-specific sequence primers with overhang adapter sequences (forward overhang of -5' CGTCGGCAGCGTC AGATGTGTATAAGAGACAG-3' and reverse overhang of -5' GTCTCGTGGGCTCGGAGATGTGTATAAGAGACA G-3') were used to amplify the custom gene of the selected trnL regions. KOD-Multi & Epi-® (Toyobo) was used to perform all PCR reactions.

Second part of library construction (2nd stage PCR)

As per the manufacturer's protocols, the Illumina Nextera XT Index Kit v2 was employed to attach dual indices to the amplicon PCR. Accordingly, the libraries were assessed for their quality using an Agilent Bioanalyzer 2100 System with the Agilent DNA 1000 Kit, followed by fluorometric quantification using the Helixyte GreenTM Quantifying Reagent.

Next-Generation sequencing

The libraries were standardised and combined using the protocol suggested by Illumina. The MiSeq platform with 150 bp paired-end reads was used for sequencing the libraries. Subsequently, the raw data were subjected to bioinformatics analysis step which is also one of the possible measures to avoid sample contamination. All the read sequences were submitted to the Sequence Read Archive of the National Center for Biotechnology Information (NCBI), which can be accessed at http://www.ncbi.nlm.nih.gov/sra with the references number SRR29452685, SRR29505051, SRR29505052, SRR29505326-SRR29505330, SRR29507618-SRR29507628.

Bioinformatics analysis

The removal of sequence adaptors and low-quality reads from paired-end reads was carried out using BBDuk from the BBTools package. Afterwards, the forward and backward reads were merged using USEARCH v11.0.667. The sequences obtained from the MiSeq platform were excluded from further analysis if their average quality score was below 150 bp or above 600 bp (Edgar 2010). Subsequently, the NCBI database was used to align the reads with trnL sequences. Amplicon sequence variants (ASVs) were grouped together based on their similarity using UPARSE v11.0.66 (Edgar 2013) with a 97% similarity cut-off. A single representative sequence was randomly selected from each ASV. A phylogenetic tree was constructed against the NCBI database using PyNAST (Caporaso et al. 2010a), whereas the taxonomic assignment of ASVs was performed using QIIME 1.9.1 (Caporaso et al. 2010b). A rarefaction curve was generated using R V3.6.2 (R Core Team 2018) to assess the adequacy of sequence depth. A heatmap was produced using R software to visually illustrate the relative abundances of taxa (family) by different colour shades.

The calculation and construction of alpha-diversity indices (Shannon-Wiener, Simpson, Evenness, and CHAO 1) and the rarefaction curve, as well as the beta-diversity analysis using the unweighted pair group method with arithmetic mean (UPGMA) tree, were performed. The shared plant species utilised by hymenopterans were classified into two groups: between bee species (Apidae) and between wasp species. These categories were visually represented using Venn diagrams.

Results

A total of 1,649,005 raw reads and 993,549 non-chimeric trnL plant sequences were obtained from 19 hymenopteran samples representing seven species (Table 2). The rarefaction curve representing sampling depth was sufficient, as all curves leveled off (Fig. 1). Among the species studied, BR4 *Tetrigona apicalis* exhibited the highest number of reads with 170,572, while BR5 *T. apicalis* had the lowest number of reads with 5,786 reads. BR13 *Polybioides* sp. was identified with the highest diversity of 2.501 and 23 ASVs based on the Shannon-Wiener index (H'), while KL1 *Auplopus* sp. had the lowest diversity of 0.002 and 2 ASVs. Out of the total 161 ASVs, 72.84% (118 ASVs) were identified at the genus and species level through a match in the NCBI database. All known ASVs are from the phylum Streptophyta. The known ASVs represent 67 plant species and another 34 ASVs classified at the genus level, originating from 43 plant families.

The family Fabaceae was found to be the most abundant family among hymenopterans, representing 11.45% of

Table 2 Number of observed ASVs and alpha-diversity indices for plant DNAs in all samples

Sample	Non-chimeric sequence	Observed ASVs	Shannon -Wiener	Simpson	Evenness	Chao1
BR9 *Polistes* sp. (Vespidae)	25,916	15	2.021	0.797	4.927	15
BR11 *Polistes* sp. (Vespidae)	54,994	16	2.208	0.864	7.344	16
BR15 *Polistes* sp. (Vespidae)	8,885	17	2.049	0.809	5.231	17
BR13 *Polybioides* sp. (Vespidae)	90,241	23	2.501	0.887	8.819	23
BR21 *Polybioides* sp. (Vespidae)	81,404	10	1.790	0.814	5.388	10
BR22 *Polybioides* sp. (Vespidae)	40,574	19	1.306	0.481	1.928	19
KL11 *Polybioides* sp. (Vespidae)	115,646	20	1.695	0.665	2.981	20.75
LK14 *Polybioides* sp.(Vespidae)	22,804	9	1.517	0.723	3.605	9
BR3 *Tetrigona apicalis* (Apidae)	29,123	6	1.380	0.728	3.681	6
BR4 *Tetrigona apicalis* (Apidae)	170,572	21	0.845	0.311	1.452	21
BR5 *Tetrigona apicalis* (Apidae)	5,786	8	0.083	0.024	1.024	8
KL1 *Auplopus* sp. (Pompilidae)	132,507	2	0.002	0.0003	1.000	2
KL2 *Auplopus* sp. (Pompilidae)	21,933	3	0.814	0.473	1.897	3
KL13 *Apis cerana* (Apidae)	39,708	28	1.062	0.559	2.267	28.5
KL15 *Apis cerana* (Apidae)	27,267	4	0.880	0.551	2.226	4
KL16 *Apis cerana* (Apidae)	16,695	2	0.672	0.479	1.919	2
LK7 *Paramblynotus* sp. (Liopteridae)	20,134	11	1.774	0.737	3.806	11
PP17 *Paramblynotus* sp. (Liopteridae)	57,863	13	1.682	0.661	2.948	13
BR7 *Nomia strigata* (Halictidae)	31,497	31	2.466	0.810	5.275	31

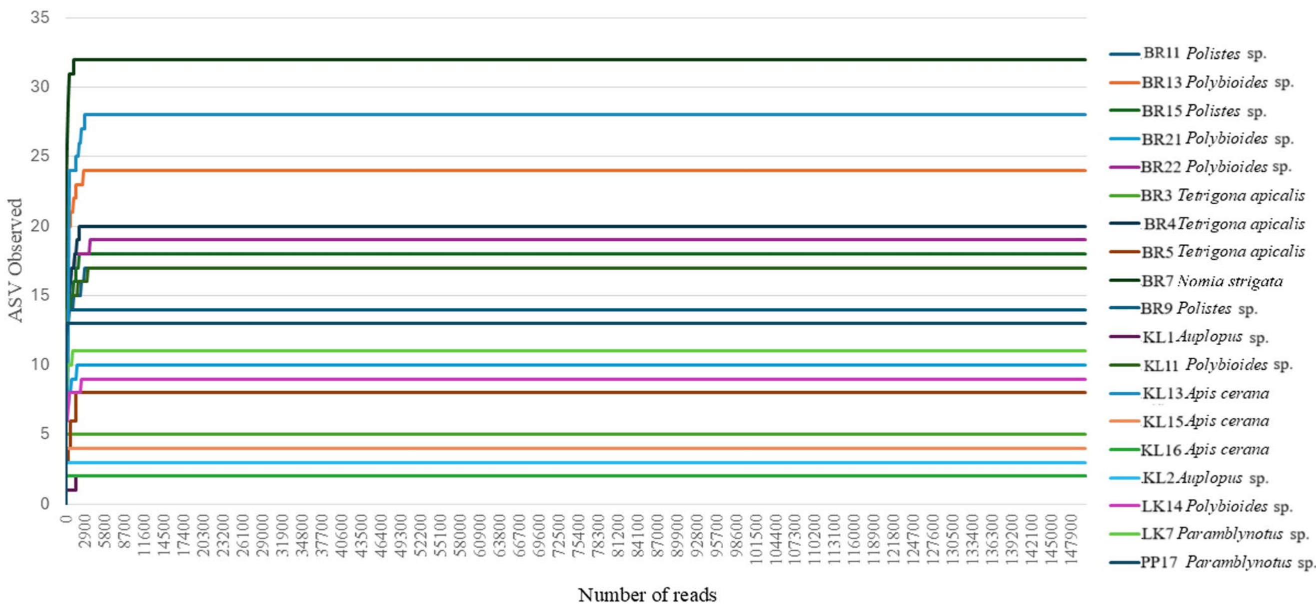

Fig. 1 Rarefaction curve of the trnL gene sequence determined for ASVs at 97% similarity

Table 3 Top 15 plant families and its highest relative abundance species representative detected in hymenoptera samples based on trnL metabarcoding

Plant family	Family relative abundance (%)	Representative species	Species relative abundance (%)
Fabaceae	11.45	*Dialium tessmannii*	2.32
Gesneriaceae	11.03	*Rachunia cymbiformis*	10.90
Podostemaceae	10.18	*Polypleurum chinense*	10.18
Asteraceae	8.99	*Taraxacum platycarpum*	8.14
Poaceae	6.43	*Chusquea* sp.	5.84
Amaryllidaceae	4.67	*Lycoris* sp. 1	4.57
Apocynaceae	3.98	*Voacanga* sp.	3.16
Annonaceae	3.90	*Monoon* sp.	3.76
Myrtaceae	3.72	*Myrcia* sp.	3.10
Arecaceae	3.36	*Elaeis guineensis*	2.67
Malvaceae	3.20	*Hibiscus rosa-sinensis*	3.13
Convolvulaceae	3.17	*Camonea* sp.	3.17
Moraceae	2.76	*Ficus* sp.	1.61
Anacardiaceae	2.43	*Mangifera indica*	2.43
Acanthaceae	2.27	*Asystasia gangetica*	2.27

the total families. Other families, including Gesneriaceae (11.03%), Podostemaceae (10.18%), Asteraceae (8.99%), and Poaceae (6.43%), were also found to be present. These families account for the top five families consumed by the sampled hymenopterans (Table 3). In the samples, the five most abundant plant food species identified are *Rachunia cymbiformis* (Gesneriaceae) with 10.90%, followed by *Polypleurum chinense* (Podostemaceae) with 10.18%, *Taraxacum platycarpum* (Asteraceae) with 8.14%, *Chusquea* sp. (Poaceae) with 5.84%, and Lycoris sp. 1 (Amaryllidaceae) with 4.57% (Table 3).

The heatmap constructed shows the abundance of all plant families for the samples foraged by hymenopterans from the THWR (Fig. 2). Each plant family's abundance is represented by the intensity of its colour in the heatmap. In this case, red and blue denote higher and lower abundance, respectively. The family Asteraceae was found to be the most dominant family, particularly in one sample identified as KL11 *Polybioides* sp. Most cells are blue, indicating a low abundance of many families across samples. Certain plant families, such as Asteraceae, Poaceae, and Fabaceae, showed significant abundance in some samples.

There were overlapping plant species for the Apidae members, which are *T. apicalis* and *Apis cerana* (Fig. 3). Both shared seven ASVs of plant species, which are *P. chinense* (Podostemaceae), *R. cymbiformis* (Gesneriaceae), *Combretum coccineum* (Combretaceae), *Dialium tessmannii* (Fabaceae), *Chusquea* sp. (Poaceae), and one unknown species. However, there was no overlapping of plant species between all five species of wasp species: *Auplopus* sp., *Polybioides* sp., *Nomia strigata*, *Polistes* sp., and *Paramblynotus* sp., and each of these unique species did not overlap with 2, 40, 15, 24, and 17, respectively (Fig. 4).

The constructed UPGMA tree based on the relative abundance of phyla (%) across all samples showed that the *Rachunia cymbiformis* and *Polypleurum chinense* plant species were dominant with more than 40% abundance, and clustered together for samples LK7 *Paramblynotus* sp., BR9 *Polistes* sp., KL2 *Auplopus* sp., BR5 *T. apicalis*, KL 16 *A. cerana*, and LK14 *Polybioides* sp. (Fig. 5). Other than BR5

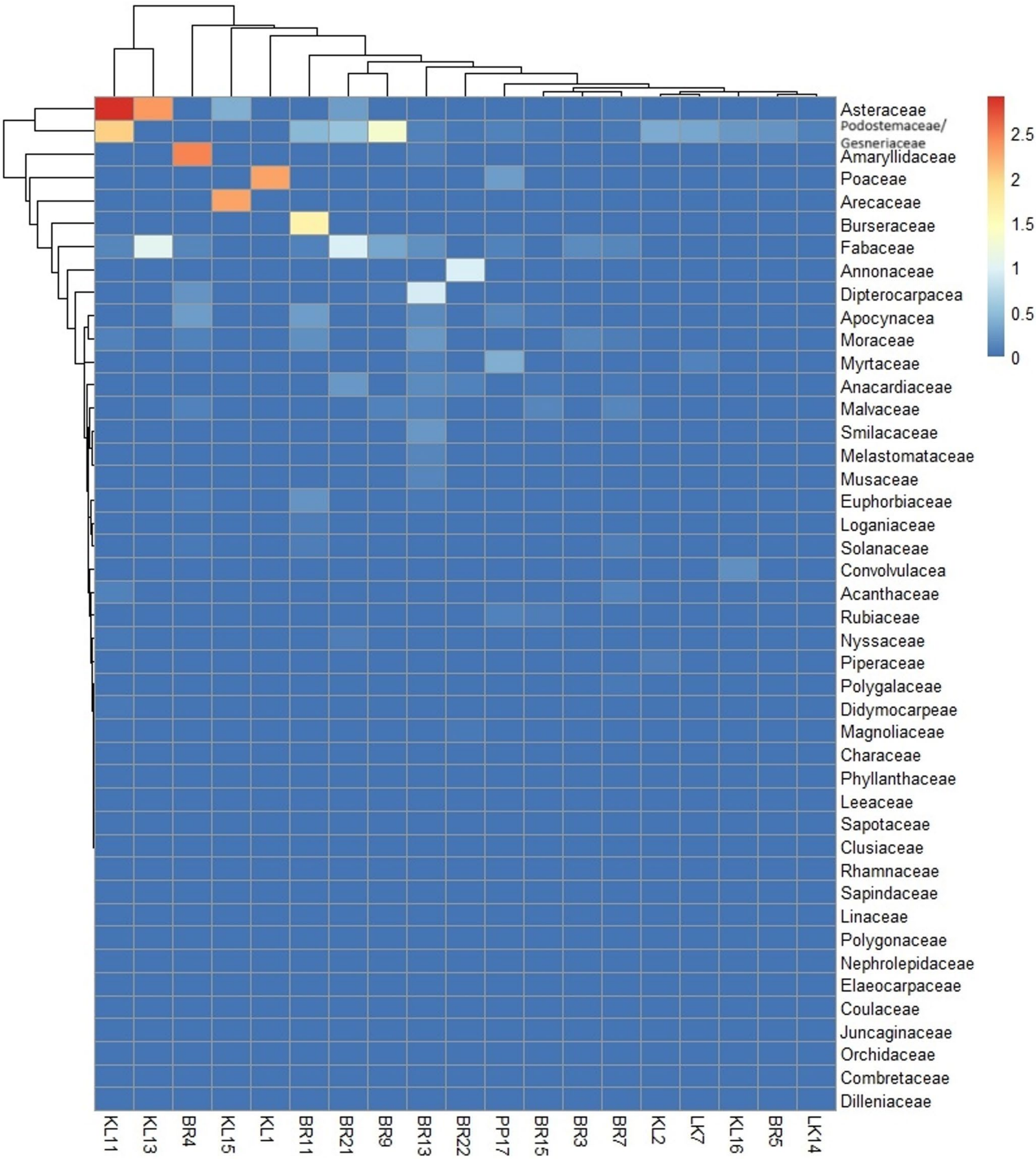

Fig. 2 Heatmap with a dendrogram at the family level displayed using a gradient heatmap

and KL16 samples, all other Apidae species showed a more balanced distribution of multiple phyla, indicating higher diversity. The 'Others' or unknown plant species can be observed across all the samples.

In this study, many plant families and species were recorded from the metabarcoding analysis results. It is not only limited to the top 15 families and species listed in Tables 2 and 3. Several other families that were detected with low abundance also appeared to be significantly

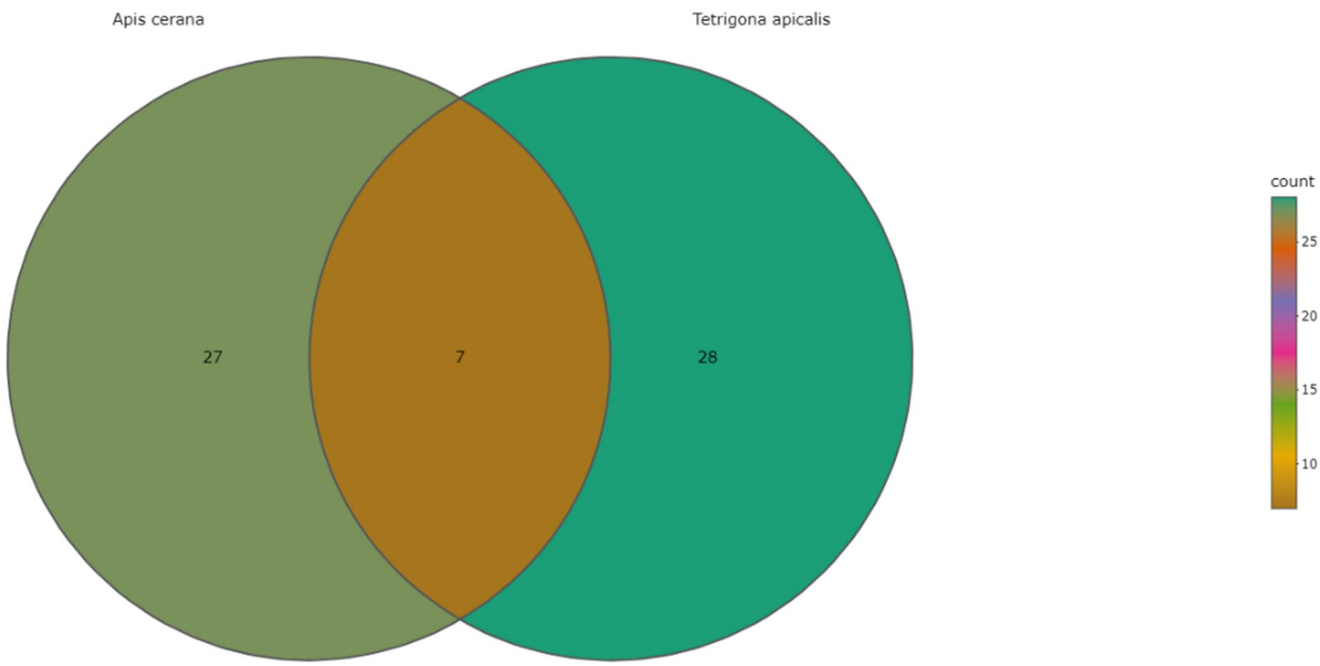

Fig. 3 Venn diagrams of the number of shared plant species among bee species (Apidae), *A. cerana* and *T. apicalis* from all localities

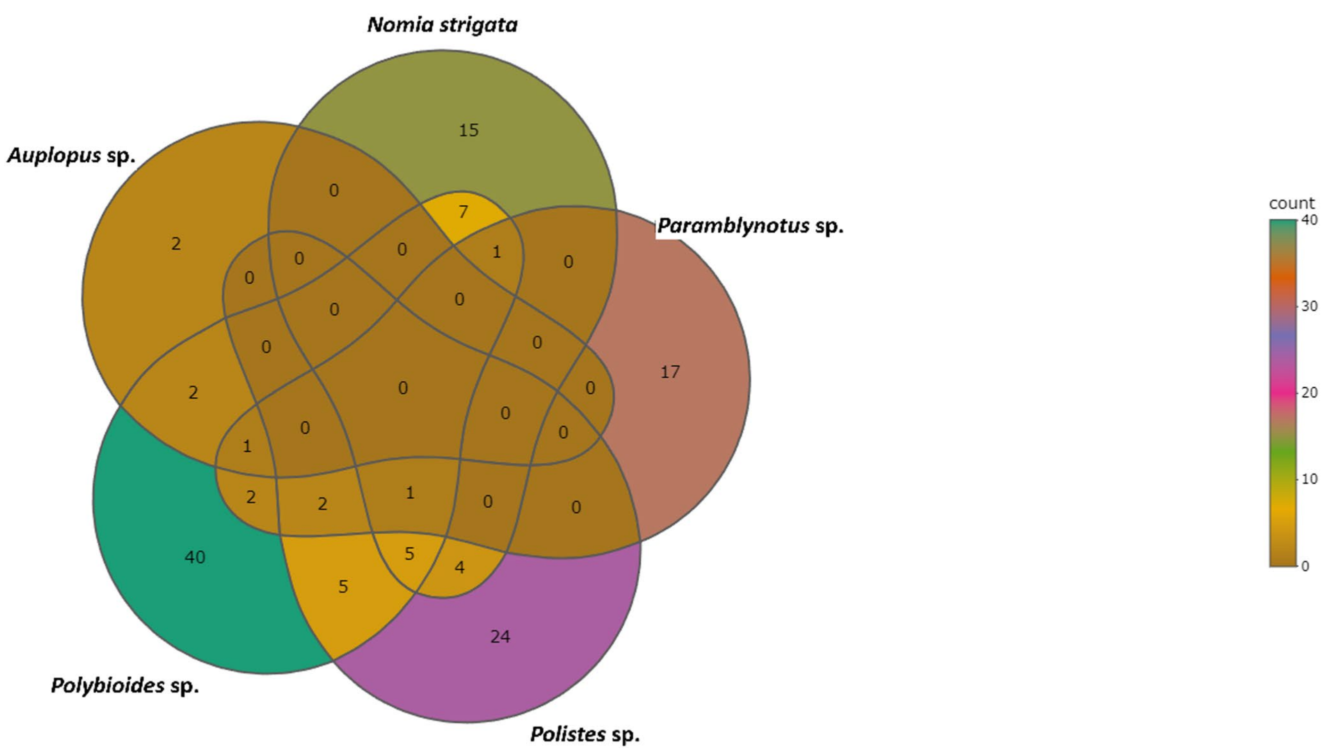

Fig. 4 Venn diagrams of the number of shared plant species among wasp species from all localities

important. It refers to several plant families and also species that are highly diverse, including forest species like *Dipterocarpus turbinatus (Dipterocarpaceae) and Macaranga tanarius* (Euphorbiaceae). Several crop plant species were also recorded from this study, for example, *Elaeis guineensis* (Arecaceae), *Musa acuminata* (Musaceae), and *Zea mays* (Poaceae). *E. guineensis* also was found in several species, such as *A. cerana* (KL13, KL15) and *Paramblynotus* sp. (PP17, LK7).

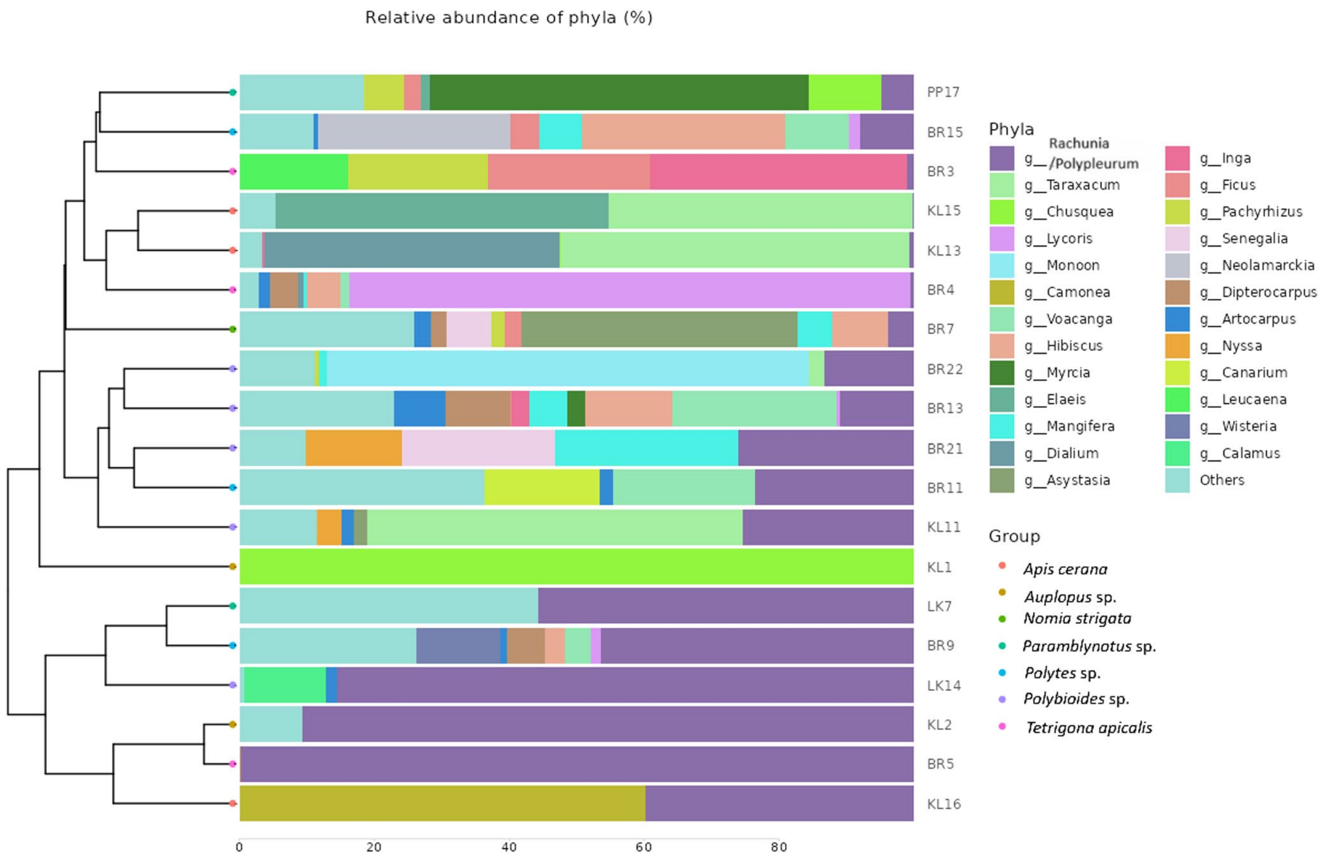

Fig. 5 UPGMA tree on the relative abundance of phyla (%) across all samples

Discussion

By employing the metabarcoding technique to analyse the plant species consumed by the hymenopteran pollinators, this study successfully reveals the broad diversity of plants visited by hymenopterans in the THWR for pollination. As no prior pollination studies were recorded from the THWR, except a brief study conducted by Idris et al. (2023) on barcoding analysis, this study serves as a forerunner for future studies involving more wasp species that act as potential pollinators (less effective) for forest plants towards conservation. Initially, it was believed that bee species were the primary pollinators (effective) of plant species due to their high efficiency and widespread presence (Calderone 2012; Khalifa et al. 2021). Nevertheless, this study has revealed that wasp species can also contribute and potential in pollination (less effective) of forest plants, and accidentally carries pollen of the visited flower for nectar (Goulson 1999). While flower visitation alone may not always confirm pollination, increasing evidence suggests that such interactions can still lead to effective pollen transfer, particularly among wasps that frequently visit flowers for nectar. Therefore, disregarding their role in pollination studies may underestimate their actual ecological contribution.

The diversity index, the Shannon-Wiener index, exhibits high values (2.0–3.0) for certain samples, suggesting a highly diverse community with numerous different species and a relatively even distribution of individuals (Spellerberg 2008). In this study, the rarefaction curve showed that the number of ASVs increased with the number of sequences sampled. The curve indicating sampling depth was adequate as all curves reached a plateau, indicating that additional sequencing would result in minimal new ASVs (Cayuela et al. 2015). Therefore, the sampling effort was deemed sufficient for estimating the species composition of hymemopteran-pollinated plant species. The family Fabaceae is the highest family collected by the hymenopteran species in this research, accounting for 11.45% of the total relative abundance. Fabaceae comprises over 795 genera and nearly 20,000 species distributed across different regions worldwide (Lewis et al. 2005). Fabaceae holds significant economic importance as a primary source of food and forage and has a wide range of diversity and garnered considerable attention in ecological studies (Acharya et al. 2004). Additionally, Scaccabarozzi et al. (2020) highlighted specialised interactions between Fabaceae and bee genera. The plant families Gesneriaceae and Podostemaceae exhibited the second and third highest relative abundance, respectively.

The family Gesneriaceae relied on pollination by the non-euglossine hymenopteran species, as indicated by a study conducted in Brazil (SanMartin-Gajardo et al. 2004), while Rutishauser (1997) determined the adaptation potential of polyandry in Podostemaceae for insect pollination. In addition, Asteraceae and Poaceae ranked fourth and fifth in terms of relative abundance, respectively. These plant families were found to be pollinated by the hymenopteran species by Muñoz and Cavieres (2019) and Gibson et al. (2024).

Rachunia cymbiformis and *P. chinense* are two dominant and abundant species consumed by all hymenopteran species in this study. *Polypleurum chinense* was found in all samples, except in all *Auplopus* sp. (KL1, KL2) and some *A. cerana* (KL15, KL16), *T. apicalis* (BR3, BR4), and *Polistes* sp. (BR15) samples. *R. cymbiformis* occurs in most species, such as *Polybioides* sp. (BR22), *T. apicalis* (BR5), *A. cerana* (KL16), and *Auplopus* sp. (KL2). According to Legardón and García-Plazaola (2023), Gesnerioideae is dominated by *R. cymbiformis* and is native to Thailand, and it is likely to be found in Peninsular Malaysia and pollinated by insects, while *P. chinense* was first described as a new species from China and is one of the plants pollinated by insects with specific pollination mechanisms (Chen et al. 2022). *Taraxacum platycarpum* is a perennial plant that is pollinated by insects and grows primarily in the temperate biome, and according to Kandori et al. (2009), *Taraxacum* spp. shows competition in pollination. *Chusquea* is the genus of woody bamboo with the highest level of diversity, consisting of 169 officially documented species. *Chusquea* species can sometimes play a crucial role in driving tree regeneration cycles by outperforming shade-intolerant seedlings of other plant species (Fisher et al. 2009, 2014). The recent findings from this study suggest that the insect species documented earlier probably refers to the hymenopteran species (bees and wasps).

Notable plant families such as Moraceae and Dipterocarpaceae were recorded. The Moraceae species identified include *Ficus* sp., *Maclura tricuspidata*, and *Artocarpus nitidus*. Members of the Moraceae family were detected in various hymenopteran samples, including *Paramblynotus* sp. (PP17), *Polistes* sp. (BR9, BR11, BR15), *N. strigata* (BR7), *T. apicalis* (BR3), and *Polybioides* sp. (BR13, LK14, KL11), indicating that both bees and potentially wasps play important roles in pollination. Bees are widely recognised as effective pollinators due to their morphology and pollen-collecting behaviour. However, recent studies show that wasps, despite their different foraging strategies, also facilitate pollen transfer and contribute to plant reproductive success (Borchardt et al. 2024; Pereira 2024). This suggests that pollination effectiveness is not limited to bees but extends to other hymenopterans such as wasps. Only seven overlapping species in *T. apicalis* and *A. cerana* bees (Apidae) indicated a small number of shared species pollinated, which are *P. chinense* (Podostemaceae), *R. cymbiformis* (Gesneriaceae), *C. coccineum* (Combretaceae), *D. tessmannii* (Fabaceae), *Inga* sp. (Fabaceae), *Chusquea* sp. (Poaceae), and one unknown species (Fig. 3). This is because the bee species, known for their general and diverse pollination activities, promotes rapid divergent evolution of bee pollination in plants growing in various soil conditions (Dorey and Schiestl 2024). The high number of non-shared taxa in wasps show their distinct specialisation in pollinating plant species, for example, a specific host plant for a fig wasp species (Oldenbeuving et al. 2023). Furthermore, the wasps also demonstrate their effectiveness as pollinating agents, even though their body is sparsely covered with hairs with limited ability to carry as much pollen and obtain the pollen while sucking nectar of flowers.

Interestingly, four plant species recorded from this study are under monitoring in the Malaysian Red Plant List (Yong et al. 2021a, b). They are *Dodonaea viscosa* (Sapindaceae), *Nephrolepis biserrata* (Nephrolepidaceae), *Litchi chinensis* (Sapindaceae), and *Willughbeia edulis* (Apocynaceae). This study reveals that utilising metabarcoding yields a detailed taxonomic understanding of hymenopteran plant visitation. Adult wasps primarily visit flowers to forage for nectar, which supports their metabolic needs or colony maintenance in social species. During these visits, they may incidentally transfer pollen and have been recorded as floral visitors across numerous angiosperm families (Lukas et al. 2020).

This study did not aim to identify specific plant hosts used for nectar or pollen collection. Instead, the metabarcoding results reflect the plant taxa associated with the sampled hymenopterans, showing possible interactions that may lead to pollination. These associations provide an overview of the floral diversity potentially visited by both bees and wasps, though further field observation would be needed to confirm their foraging roles.

Although wasps are generally regarded as less-effective pollinators, recent evidence shows that some social species possess pollen transport and deposition abilities comparable to bees, particularly in late-blooming native flora (Borchardt et al. 2024). This study did not aim to measure pollination efficiency or effectiveness. Instead, the detection of plant DNA in hymenopteran samples confirms active interactions through flower visitation and pollen contact. These results suggest that both bees and wasps potentially play roles to some degree in pollination, contributing to the maintenance and ecological balance within the forest ecosystem. Brock et al. (2021) reported 602 species of aculeate wasps from nine families that includes Pompilidae and Vespidae, are associated with 798 plant species across 110 families. Though not specialised pollinators, these wasps visit flowers primarily for nectar and may incidentally transfer pollen. Their widespread association with diverse plant taxa underscores their ecological relevance, especially in systems with limited specialised pollinators (Pereira 2024). The significance of metabarcoding has been emphasised as a valuable technology for addressing unanswered questions in ecology and the potential pollination of forest tree species.

Based on the metabarcoding analysis, a wide range of species and plant families were identified, although some were found in low abundance. *Dipterocarpus turbinatus* (Dipterocarpaceae) and *M. tanarius* (Euphorbiaceae), which belong to the main plant forest families, are mostly pollinated by the bee species as they are good pollinators for high canopy plants and shrubs (Inari et al. 2012). *Dipterocarpus turbinatus* was recently assessed and listed as 'vulnerable' on the IUCN Red List of Threatened Species (Ly et al. 2017), indicating that the taxon is likely to become extinct in the near future, based on existing knowledge of its population trends and recent, ongoing, or potential future threats. This study identified the presence of *D. turbinatus* in *T. apicalis* (Apidae), *Polybioides* sp. (Vespidae), *Polistes* sp. (Vespidae), and *N. strigata* (Halictidae) samples, suggesting that other wasp families are also responsible for the interaction and pollination of the tree species. Besides, *M. tanarius* was reported to be pollinated by thrips and hemipteran species (Ishida et al. 2009); however, in this study, the data indicated that *M. tanarius* was pollinated by hymenopteran species as well. These findings collectively support that both bees and wasps contribute in plant–pollinator networks, albeit through different mechanisms. Recognizing this participation/contribution is essential for a more complete understanding of tropical pollination ecology.

Several crop species were also recorded in this study, such as banana *M. acuminata* (Musaceae), corn *Z. mays* (Poaceae), and Malaysian cash crop, *E. guineensis* (Arecaceae). A new insight for these crop pollination data for wasp species, namely wasp *Polybioides* sp. (Vespidae), was found to visit both crops, although it was mainly recorded by bees and other insects (Khalifa et al. 2021). *Zea mays* was recorded in another wasp species, *Paramblynotus* sp. (Liopteridae), indicating the presence of wild species and the possibility of the hymenopteran species flying far and reaching the human settlement ecosystem (Ulyshen et al. 2023). Basically, the *Z. mays* is wind-pollinated plants and increasingly acknowledged as pollen sources for bees (Saunders 2018; Splitt et al. 2021; Urban-Mead et al.2021). However, in this condition the pollen is preferred or offers nutritional benefits to the insect's colony and remains largely unexplored (Roulston et al. 2000; Wood et al. 2021). The pollen of *Z. mays* also be detected in the honey bee species *Apis cerana* due to their foraged activity for supplying nutrients to their colony (Danner et al. 2014). Thus, the pollination most probably has not occurred between *Z. mays* and insects, however in this study the pollen of *Z. mays* has been confirmed carried by the *A. cerana* and other wasp species. Pollinators often visit wind-pollinated plants to collect pollen or gather materials for nesting, but these interactions are largely overlooked (Saunders 2018). Additionally, *E. guineensis*, which is commercially pollinated by the introduced weevil species *Elaeidobius kamerunicus* from Cameroon, was previously recorded to be pollinated by thrip, *Thrips hawaiiensis* and moth, *Pyroderce*s sp. (Mohd-Azlan et al. 2023). In this study, *E. guineensis* was also utilized by both bee and wasp species in.

Conclusion

A detailed overview of selected hymenopteran species and their associated floral resources in a Malaysian primary forest was achieved through trnL metabarcoding. The results show that bees and wasps utilise a broad range of plant families and species, which constitute important components of their diets. The detection of plant DNA from both forest trees and nearby crop plants indicates that hymenopteran foraging links primary forest habitats with surrounding human-modified landscapes through shared floral resources. These findings identify specific plant families and species that support the floral resource requirements of bees and wasps in THWR, providing forest plant candidates for future ecological and behavioural studies. Further work integrating field observations, pollen microscopy, and experimental approaches will be necessary to elucidate how these plant–Hymenoptera associations influence plant reproductive outcomes and insect population dynamics.

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Data availability The data that support the findings of this study are available on request from the corresponding author. Data sharing is not applicable to this article as no new data were created or analyzed in this study.

Declarations

Competing interests The authors declare no competing interests.

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