

Pollen source diversity in *Apis cerana* beekeeping around Ir. H. Djuanda Grand Forest Park, West Java, Indonesia

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Abstract. Amalia CA, Amakpe F, Azzahra HR, Hasanah DN, Putri VK, Ati AS, Ramadan AD, Shanida SS, Kusmoro J, Hermawan W, Wulandari I, Husodo T. 2025. Pollen source diversity in *Apis cerana* beekeeping around Ir. H. Djuanda Grand Forest Park, West Java, Indonesia. *Biodiversitas* 26: 5405-5422. Honey bees play a crucial role in maintaining ecosystem functioning through pollination, yet their foraging ecology is strongly influenced by floral resource availability across habitats and seasons. This study investigated the pollen spectrum of *Apis cerana* in the Ir. H. Djuanda Grand Forest Park, West Java, Indonesia, during the rainy season. Pollen traps were installed in apiaries located at the Deer Breeding Site (interior forest) and Maribaya Site (forest edge) to collect samples for palynological analysis. A total of 32 pollen types from 20 families were identified, with higher richness in the Deer Breeding Site (25 types) than in Maribaya (21 types). Family-level analyses indicated the dominance of Asteraceae, followed by Fabaceae and Lauraceae. At the species level, *Tithonia diversifolia* emerged as the most dominant pollen type based on the Important Value Index (IVI), accompanied by *Mimosa pudica*, *Sphagneticola trilobata*, and *Persea americana*. Diversity indices showed moderate pollen diversity overall (H' : 1.76), with greater heterogeneity in the interior forest (H' : 1.87) compared to the edge habitat (H' : 1.31). These results demonstrate both the ecological importance and risks of invasive species such as *T. diversifolia* and *S. trilobata*, which provide abundant forage but may threaten native flora. Conversely, native species such as *Schima wallichii* and *Arenga pinnata* highlight sustainable alternatives. Integrating native forage plants into apiary landscapes is therefore recommended to support apiculture while conserving biodiversity in tropical forest ecosystems.

Keywords: *Apis cerana*, beekeeping, biodiversity conservation, invasive species, pollen diversity

Abbreviations: DB: Deer Breeding Area, GFP: Grand Forest Park, MB: Maribaya Road

INTRODUCTION

Honey bees hold a fundamental role in ecosystems as pollinators and as producers of hive products such as honey, wax, and propolis. Their ecological functions sustain biodiversity by facilitating plant reproduction, while their economic contributions support agricultural productivity and rural development (Yakupova and Svetalakov 2025). Honey production has increasingly become a vital livelihood strategy, especially in developing countries where it contributes to both household income and food security (Hunde 2025). In Indonesia, honey is considered an important Non-Timber Forest Product (NTFP), particularly in marginal and forest-adjacent communities. Beyond economic value, beekeeping enhances livelihood resilience and strengthens conservation-oriented practices. The growing domestic demand for honey has further stimulated the expansion of apiculture across the country, reflecting its rising socio-economic importance and development (Harianja et al. 2023; Dusengimana and Maake 2024).

Among the various bee species used in Asian apiculture, *Apis cerana* Fabricius, 1793, the eastern honey bee, is particularly prominent. In Indonesia, this species is widely favored due to its adaptability to diverse environments, relatively low maintenance requirements, and effectiveness in small-scale beekeeping systems (Buchori et al. 2022). However, beekeeping practices often lack essential management strategies, such as systematic monitoring of floral resources or clear guidelines for optimal harvesting times (Schouten et al. 2019). A major determinant of successful beekeeping lies in the availability and diversity of foraging resources. Understanding these resources not only supports colony health and productivity but also underscores the broader socio-ecological significance of apiculture in sustaining biodiversity and local livelihoods (Patel et al. 2020). We suppose that knowledge of seasonal foraging ecology is critical, since fluctuations in honey productivity may be closely linked to seasonal flowering phenology, as reported by Fassil et al. (2023).

Pollen analysis provides a robust tool to explore the foraging ecology of honey bees. As the primary source of proteins, amino acids, and lipids, pollen plays an essential role in larval nutrition and colony development. Its quality varies considerably across plant species, influencing bee physiology and productivity. Studies have shown differential effects of rape (*Brassica napus* L.), apricot (*Armeniaca sibirica* L.), and pear (*Pyrus bretschneideri* Rehd.) pollen on larval development and colony performance (Mattila and Otis 2006; Pang et al. 2022; Rompas et al. 2023). Seasonal availability may shape phenological variation in flowering that differs among months, which is important given that flowers are the sites where pollen is produced (Martins et al. 2021; Novita and Basri 2024). Seasonal influences have been demonstrated in *A. cerana* populations in India, where diversity in pollen resources was found to decline during periods of heavy rainfall, reduced sunlight, and overcast weather conditions (Pradeepa and Belavadi 2017). These findings highlight the importance of understanding seasonal pollen dynamics in tropical settings such as Indonesia, where climatic variability influences floral resource availability.

The Ir. H. Djuanda Grand Forest Park (GFP), spanning Bandung and West Bandung Districts in West Java, Indonesia, provides an ideal setting to investigate these dynamics. As a conservation forest embedded within a rapidly urbanizing landscape, GFP represents a mosaic of ecological conditions. Surveys by Husodo et al. (2024) documented 249 flowering plant species between December 2021 and May 2022, distributed across forest remnants, shrublands, open fields, and residential areas. This floristic richness illustrates the park's role as both a refuge for pollinators and a provider of foraging resources that can sustain local beekeeping activities.

Beekeeping with *A. cerana* is commonly practiced around GFP, particularly near the Deer Breeding Area, located inside the conservation forest, and along Maribaya Road at the park's edge. Earlier palynological research in the region has provided important baselines: Nuriyah et al. (2021) collected pollen data in August, Haydar (2022)

analyzed samples from the Deer Breeding Area in September–October, and Asyraf (2022) studied Maribaya during the same dry season months. Internationally, studies on *A. cerana* pollen analysis have also been conducted; for example, in Nagasaki and Saga Prefectures by Donkersley et al. (2021), in Southeast India by Lazar et al. (2024), and in the eastern Himalaya by Basak et al. (2025). While these regional studies advanced understanding of floral resource use, they largely represent the dry season, leaving a significant gap regarding pollen dynamics in the rainy season.

Therefore, the present study was conducted to examine the diversity of pollen sources utilized by *A. cerana* during the rainy season (May 2024) in two contrasting sublocations of GFP. The aims were to: 1. Identify dominant pollen taxa and assess species richness and diversity indices, 2. Evaluate the extent to which colonies rely on native versus non-native plant resources.

MATERIALS AND METHODS

Study area

This study was conducted at two sublocations within Ir. H. Djuanda Grand Forest Park (GFP), spanning Bandung and West Bandung Districts in West Java, Indonesia. A site near the Deer Breeding Area (-6.84348601,107.64827584) an enclave surrounded by GFP vegetation and frequently visited by tourists, and a site near Maribaya Road (-6.83106416,107.65416593), located at the park's outer edge and bordered by residential and recreational facilities (Figure 1).

Each apiary contained around 20 hives of *A. cerana*. In addition, one beekeeper maintained a few hives of *Trigona* sp., although their numbers were limited due to the species' territorial behavior. By contrast, *A. cerana* was more abundant. None of the beekeepers managed *Apis mellifera* Linnaeus 1758, as its cultivation generally requires migratory practices and plantation-based foraging systems.

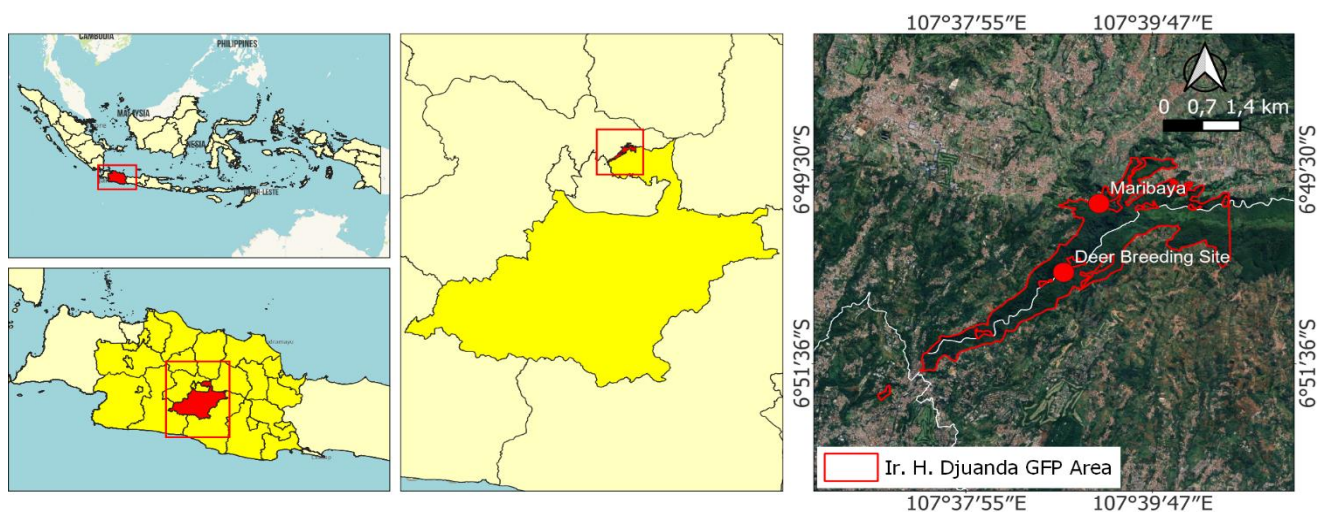


Figure 1. Map showing the locations of *Apis cerana* beekeeping sites within and surrounding Ir. H. Djuanda Grand Forest Park (GFP), Bandung, West Java, Indonesia. The map illustrates two main sublocations: the Deer Breeding Area located inside the park (interior) and Maribaya situated on the forest edge

Procedures

The pollen preparation procedure in this study followed several established references. According to Erdtman (1960) and Halbritter et al. (2018), pollen processing for microscopic observation generally involves acetolysis to remove organic materials from the grain surface and enhance exine visibility (Husodo et al. 2022). The process

comprised two main stages: namely chlorination and acetolysis (Halbritter et al. 2018). A key adjustment was the substitution of Glacial Acetic Acid (GAA) for acetic anhydride to improve laboratory safety and adapt to material availability. The complete procedure is summarized in Table 1.

Table 1. Procedures for pollen analysis in Ir. H. Djuanda GFP, West Java, Indonesia, May 2024, based on several established references

Method	Process	Reference
Hive selection procedures	Hive selection was based on active returning foragers. Foraging activity of <i>Apis cerana</i> varies during the day, with a decline after 11:00 a.m and peak activity at 8:00 a.m. Counts were conducted at 10:00 a.m. to represent moderate activity. Foragers were recorded over a two-minute interval, and the three most active colonies were selected at each sublocation, resulting in six colonies in total.	Aryal et al. (2016), Nuriyah (2024) Kusmoro et al. (2024)
Pollen trapping	After selecting three hives at each sublocation, pollen traps were installed at the hive entrances (Figure 2). Pollen collection was carried out in three 72-h intervals during May 2024 (19-21 May). Traps were installed one day prior to each sampling event and removed after 72 h. Pollen was collected with a brush to minimize contamination, placed in collection tubes sealed with plastic wrap to prevent external pollen contamination, and stored at ~4 °C until further processing	Dimou et al. (2006) Lestari and Susandarini (2019), Ardi et al. (2020), Campos et al. (2021)
Slide preparation	The slide preparation process began with weighing the collected pollen grains. The total pollen mass per sample ranged from 2.46 g to 4.47 g, with an average of 2.57 g. Pollen collected within each 72-h period was pooled per hive into a single tube. A 5% subsample from each tube was then used for slide preparation and subsequent microscopic observation. In total, six pollen sample tubes were processed: three from the Deer Breeding Area and three from Maribaya.	Dimou et al. (2006)
Chlorination	Pollen suspensions were treated with GAA and hydrochloric acid, followed by heating and centrifugation steps adapted from Dimou et al. (2006) and Nuriyah et al. (2021) to remove cytoplasmic contents.	The procedure followed the standard acetolysis method of Erdtman (1960) with modifications from Nuriyah et al. (2021)
Acetolysis	In the acetolysis stage, a 9:1 mixture of GAA and sulfuric acid (H ₂ SO ₄) was applied, heated briefly, and centrifuged to eliminate residual organic matter. After successive rinses with distilled water to neutralize acids, the sediment was preserved in vials at 4 °C until further microscopic analysis.	Halbritter et al. (2018), Nuriyah et al. (2021) This wet preservation method is consistent with Halbritter et al. (2018), who emphasized that hydrated storage maintains pollen integrity and prevents fungal contamination
Pollen types identification	After acetolysis, approximately 1 mL of pollen suspension was mounted on microscope slides and covered with a cover glass. To minimize grain movement, a thin layer or a spread of glycerine can be applied around the restricted area of the cover glass to prevent pollen movement into the corner of the cover glass. Pollen grains were examined under an Olympus CX21 microscope at 100×, 400×, and 1000× magnifications. Identification was based on morphological features such as grain shape, unit, aperture type, and exine ornamentation. Images and descriptions were compared with online databases. Pollen types were identified to the species level when possible, and coded when identification was limited.	Louveaux et al. (1978) Kusmoro et al. (2024) Halbritter et al. (2018) PalDat (Palynological Database; https://www.paldat.org/), Australian Pollen and Spore Atlas (apsa.anu.edu.au). Additional references used for species-level identification included El Ghazali et al. (1997), Crutcher (2007), Wondracek-Lüdke et al. (2015), Salamah et al. (2018), Singh and Dixit (2018), Thakodee et al. (2018), Abdulrahman et al. (2019), Azeez et al. (2019), Nuriyah et al. (2021), Pacella and Di Pasquo (2022), Saensouk and Saensouk (2022), Normasiwi and Kurniawati (2023), Permatasari et al. (2024)



Figure 2. Photographs of *Apis cerana* hives equipped with a pollen trap at the bottom (A) and the collected pollen grains obtained during sampling (B)

Data analysis

Data were tabulated in Microsoft Excel for qualitative analysis of pollen units (monad, tetrad, polyad), shapes (spheroidal, oblate, prolate), ornamentation (clavate, echinate, psilate), and aperture types (biporate, colporate, inaperturate, etc.). Quantitative analysis was conducted by counting pollen grains with a Thoma hemocytometer under an Olympus CX21 microscope. The Relative Density (RD), Relative Frequency (RF), Important Value Index (IVI), and Shannon–Wiener diversity index (H') were calculated to characterize pollen type composition and diversity.

Several abbreviations were used in this study. Abbreviations of study sites used in tables and figures include DB: Deer Breeding Area and MB: Maribaya. Abbreviations for column titles are Occ: Occurrences, Mon: Months, and Ref: Flowering reference source. Abbreviations for pollen characteristics include: M: Monad, T: Tetrad, P: Polyad, Doc: Docahedric, Sph: Spheroidal, Pro: Prolate, Spro: Subprolate, Obl: Oblate, AYR: All Year Round, Pan: Pantoporate, Por: Porate, Mon: Monosulcate, Sul: Sulcate, Tcr: Tricolporate, Bip: Biporate, Zon: Zonoporate, Col: Colporate, Ina: Inaperturate, Monp: Monoporate, and Tcp: Tricolpate. Abbreviations in the tables also indicate reference sources—for example, Bu and So refer to Budumajji and Raju (2018), and Hu to Husodo et al. (2024)—with the complete list shown in Table 2. Native and non-native status of the identified pollen plants was determined using Plants of the World Online, Nparks Flora & Fauna Web, and GBIF (GBIF Secretariat 2025).

Relative Density (RD) and Relative Frequency (FR)

RD was calculated as the proportion of pollen grains of a species relative to the total pollen grains in each group or season, while RF was the proportion of hive samples in which a species occurred relative to the total number of hives (Amakpe et al. 2024). In this study, both formulas were adapted for pollen grains obtained from pollen traps rather than honey samples. The modified equations are presented below.

$$RD = \frac{1}{TP} \sum_{i=1}^n p_i$$

$$RF = \frac{1}{TF} \sum_{i=1}^n f_i$$

Where, RD: Relative Density, TP: Total Pollen grains, FR: Relative Frequency, TF: Total Frequency

The Important Value Index (IVI)

The IVI was calculated using a modified formula from Pantoja et al. (2010), originally developed for honey samples. It combines relative Frequency (RF), Relative Density (RD), and Relative Abundance (RA), where RA is the average number of grains of a species per sample divided by the sum of averages across all species.

$$IVI: DR + FR + AR$$

Where: RD: Relative Density, FR: Relative Frequency, RA: Relative Abundance

The Shannon Wiener (H') Diversity Index

The Shannon–Wiener Diversity Index (H') measures species richness and evenness, with higher values indicating greater diversity (Maknun 2017). Its application in palynological studies has been reported by Soeprbowati et al. (2020). The index was calculated following Odum (1996):

$$H': \sum \frac{N_i}{N} \sum \frac{N_i}{N} \ln \frac{N_i}{N}$$

Where, H' : Shannon–Wiener Diversity Index, n_i : Number of individuals of species I, N: Total number of individuals across all species

RESULTS AND DISCUSSION

Pollen richness across sublocations and hives

A total of 32 pollen types from 20 plant families were identified during the rainy season across both sublocations. Their distribution varied, with some types unique to one sublocation and others shared between the Deer Breeding Site and Maribaya. The Deer Breeding Site recorded 25 pollen types from 17 families (12 types in Hive 1, and 16 types each in Hives 2 and 3). Maribaya had 21 pollen types from 15 families (14 types in Hive 1, and 11 types in Hives 2 and 3). Family distribution based on IVI is shown in Figure 3, with detailed pollen attributes listed in Table 2.

Differences in pollen richness between the sublocations likely reflect microhabitat conditions and surrounding land use. The Deer Breeding Site, situated within interior forest, supports more tree species with continuous flowering, while Maribaya, near recreational and residential areas, experiences edge effects that lower native forest taxa but increase ruderal or ornamental species. Similar spatial foraging patterns of *A. cerana* have been reported elsewhere in Indonesia (Lestari and Susandarini 2019; Nuriyah et al. 2021).

Hive-specific variation within each sublocation also reflects localized foraging dynamics. Although hive-level richness did not differ greatly, the patterns suggest effects of hive placement and microclimatic conditions. Since *A. cerana* typically forages within a 1 km radius (Koetz 2013), small differences in hive position relative to vegetation patches can alter the pollen spectrum collected. Similar subtle variations have been reported in Central Java, where

nearby villages showed distinct pollen profiles despite close proximity (Jayuli et al. 2018; Syifa et al. 2023).

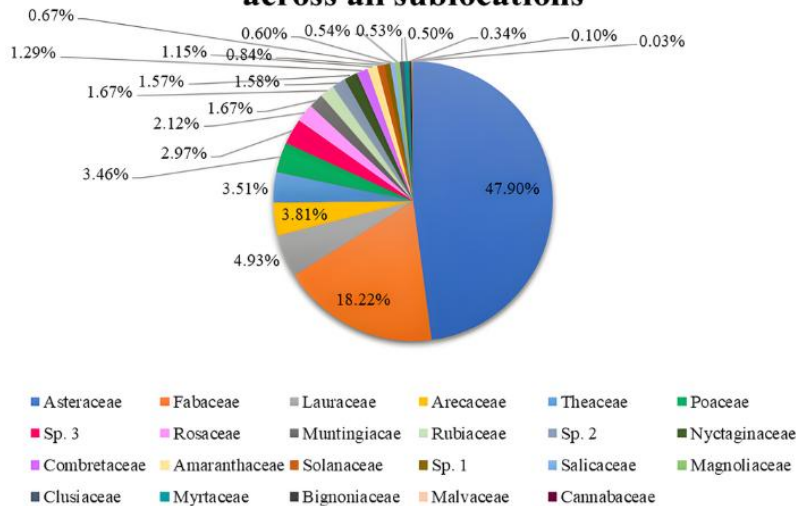
Overall, the greater richness in the Deer Breeding Site supports the view that interior forests maintain more diverse pollen resources, consistent with Ren et al. (2023), who noted higher pollinator abundance in forest interiors compared to edges. These results highlight the ecological importance of forested habitats for sustaining diverse pollen sources for *A. cerana*, while showing that edge and peri-urban areas still offer complementary resources. Combined with the IVI patterns (Figure 3) and taxonomic data (Table 2), these findings form a strong basis for later analyses of dominance, diversity indices, and species contributions.

Family-level dominance based on the Important Value Index

Analysis at the family level revealed clear patterns of dominance across the two sublocations. The overall composition showed that Asteraceae was the most

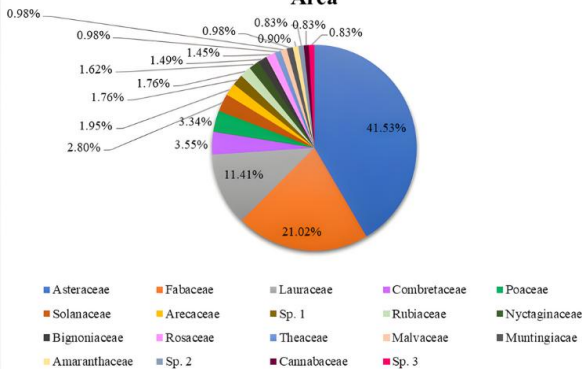
dominant family, contributing nearly half of the total pollen composition (47.90%), followed by Fabaceae (18.22%) and Lauraceae (4.93%). In the Deer Breeding Site, Asteraceae remained the leading family (41.53%), but Fabaceae (21.02%) and Lauraceae (11.41%) also made substantial contributions. In contrast, in Maribaya, Asteraceae accounted for an even higher proportion (50.40%), followed by Fabaceae (11.27%) and Theaceae (8.10%). These distributions are visualized in Figure 3, while taxonomic details at the species level are presented in Table 2. Fabaceae emerged as the second most dominant family. In the Deer Breeding Site, Fabaceae provided 21.02% of the total pollen composition, while in Maribaya, its share dropped to 11.27%. Lauraceae contributed 11.41% of pollen types in the Deer Breeding Site, largely driven by *Persea americana* Mill., whereas in Maribaya, Theaceae accounted for 8.10%, primarily represented by *Schima wallichii* (DC.) Korth..

Aggregation of pollen type families by IVI across all sublocations



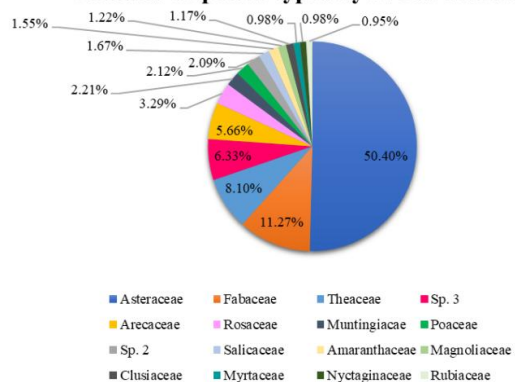
A

Families of pollen types by IVI in Deer Breeding Area



B

Families of pollen types by IVI in Maribaya



C

Figure 3. Comparison of pollen type families categorized by Importance Value Index (IVI) in Ir. H. Djuanda GFP, West Java, Indonesia. The upper panel shows aggregated IVI values across all sublocations (A), while the lower panels present data for the Deer Breeding Area (B) and Maribaya (C)

Table 2. List of pollen types with references in Deer Breeding Area and Maribaya, Ir. H. Djuanda GFP, West Java, Indonesia, May 2024

Possible taxon of the pollen types	Local name	Occurrence			Pollen characteristics			Flowering			Plant category			Ref	IVI		H'	
		DB	MB	Unit	Shape	Ornamentation	Aperture	Mon	Ref	Habit	Origin	Ecological role	DB		MB	DB	MB	
Amaranthaceae																		
<i>Alternanthera sessilis</i> (L.) R.Br. ex DC.	Kremah	✓	✓	M	Dod	Scabrate, Granulated	Pan	AYR	Ja	Herb	Native	Invasive	Pow, Npar	2.71	4.64	0.01	0.02	
Arecaceae																		
<i>Areca catechu</i> Burm.f., 1768	Pinang		✓	M	Pro	Psilate	Mon	Nov-May	Wa	Tree	Native	Potential for cultivation	Orwa, Oem		2.93		0.002	
<i>Arenga pinnata</i> (Wurmb) Merr.	Aren/kawung	✓	✓	M	Sph	Echinate	Sul	AYR	Ja	Tree	Native	Potential for cultivation	Npar, Rah	5.84	14.07	0.03	0.08	
Asteraceae																		
<i>Ageratum conyzoides</i> L.	Bandotan/babadotan	✓	✓	M	Sph	Perforate, echinate	Tcr	AYR	Wul	Herb	Non-native, intro	Potentially invasive/ruderal	Pow, Sepd	13.79	5.79	0.14	0.005	
<i>Bidens pilosa</i> L.	Ajeran	✓		M	Sph	Perforate, echinate	Tcr	AYR	Bu and So	Herb	Non-native, intro	Potentially invasive/ruderal	Pow, Sepd	11.22		0.09		
<i>Sphagneticola trilobata</i> (L.) Pruski	Wedelia	✓	✓	M	Sph	Perforate, echinate	Tcr	AYR	Aul	Herb	Non-native	Invasive	Npar	23.60	39.56	0.23	0.24	
<i>Tithonia diversifolia</i> (Hemsl.) A.Gray	Kipait	✓	✓	M	Sph	Echinate	Tcr	AYR	Ja	Herbaceous shrub	Non-native, intro	Invasive	Pow, Gbif	75.98	105.84	0.37	0.37	
Bignoniaceae																		
<i>Spathodea campanulata</i> Beauverd	Ki acret/kayu ambon	✓		M	Spro	Smooth	Tcr	AYR	DAF-Q	Tree	Non-native	Invasive	Gbif, La and M	4.48		0.03		
Cannabaceae																		
<i>Trema orientale</i> (L.) Blume	Kuray, anggerung	✓		M	Obl	Scabrate, psilate	Bip	Dec-Feb	Hy1	Tree	Native	Invasive (in Hawaii)	Pow, Marj	2.49		0.005		
Clusiaceae																		
<i>Calophyllum inophyllum</i> L.	Nyamplung		✓	M	Sph	Reticulate	Tcr	Mar-Agt	Win	Tree	Native	Norep	Pow		3.52		0.01	
Combretaceae																		
<i>Terminalia catappa</i> L.	Ketapang kencana	✓		M	Pro	Psilate	Por	Dec-May	Hu	Tree	Native	Cultivated (ornamental/shade)	Pow, Marj	10.65		0.09		
Fabaceae																		
<i>Arachis pintoi</i> Krapov. & W.C.Greg.	Kacang hias	✓		T	Pro	Reticulate	Tcp	AYR	He and Ku	Herb	Non-native	Norep	Gbif	2.71		0.01		
<i>Caesalpinia pulcherrima</i> (L.)	Bunga merak	✓		M	Sph	Verrucate, gemmate,	Tcr	AYR	Npar	Tree	Non-native,	Cultivated	Pow, Sant	4.92		0.04		

Sw. <i>Calliandra calothyrsus</i> Meisn.	<i>Kaliandra merah</i>	✓		P	Obl	scabrate Reticulate	Zon	AYR	Wi	Shrub	intro Non native, intro	Potentially invasive	Gbif, Sepd	2.85	0.001		
<i>Mimosa pigra</i> L.	<i>Putri malu raksasa</i>	✓		T	Obl	Psilate	Col	AYR	Ja	Herb	Non native, intro	Invasive	Gbif	8.25	0.04		
<i>Mimosa pudica</i> L.	<i>Putri malu</i>	✓	✓	T	Obl	Psilate	Ina	AYR	Ja	Herb	Non native, intro	Invasive	Gbif	47.17	30.96	0.34	0.19
Lauraceae																	
<i>Persea americana</i> Mill.	<i>Alpukat</i>	✓		M	Obl to Sph	Granulate, Microechinate	Ina	Feb- May, and Agt- Oct	Mu	Tree	Non- native	Cultivated	Gbif, Se and Su	34.23	0.23		
Magnoliaceae																	
<i>Magnolia champaca</i> (L.) Baill. ex Pierre	<i>Cempaka kuning</i>	✓		M	Obl	Scabrate	Sul	Jun- Sept	Je	Tree	Native	Cultivated	Npar, Hy2	3.67	0.01		
Malvaceae																	
<i>Sida</i> sp.	*	✓		M	Sph	Echinate	Pant	*	*	Herb	*	*	*	2.93	0.23		
Muntingiaceae																	
<i>Muntingia calabura</i> L.	<i>Kersen</i>	✓	✓	M	Sph	Reticulate	Tcr	AYR	Ja	Tree	Non- native, intro	Norep	Pow	2.93	6.64	0.01	0.02
Myrtaceae																	
<i>Syzygium</i> sp.	*	✓		M	Obl	Psilate	Tcr	*	*	Tree	*	*	*	2.93	0.002		
Nyctaginaceae																	
<i>Pisonia aculeata</i> L.	<i>Taji ayam</i>	✓	✓	M	Pro	Microreticulate	Tcr	Mar- May	La	Scandent shrub (Caraballo-Ortiz et al. 2021)	Native	Norep	Pow	4.85	2.93	0.01	
Poaceae																	
<i>Zea mays</i> L.	<i>Jagung</i>	✓	✓	M	Pro to Sph	Psilate	Monp	AYR	Ja*	Herb	Non- native, intro	Cultivated	Pow, Npar	5.27	2.85	0.02	
Rosaceae																	
<i>Prunus</i> sp.	*	✓	✓	M	Pro to Sph	Reticulate	Tcp	*	*	#	*	*	*	10.03	6.36	0.07	0.01
Rubiaceae																	
<i>Haldina cordifolia</i> (Roxb.) Ridsdale	<i>Haldu</i>	✓	✓	M	Obl	Reticulate	Tcp	#	#	Tree (Muthupandiyan et al. 2019)	Non- native	Norep	Pow	4.34	9.86	0.03	0.05
Salicaceae																	
<i>Flacourtia rukam</i>	<i>Rukam</i>	✓		M	Pro to	Reticulate	Tcp	#	#	Tree	Native	Norep	Npar	5.01	0.02		

Zoll. & Moritzi		Sph																
Solanaceae																		
<i>Physalis angulata</i> L.	<i>Ciplukan</i>	✓		M	Sph	Microverrucate, microechinate	Col	AYR	Ja	Herb	Non-native, intro	Potentially invasive	Pow, Ri	2.71		0.01		
<i>Solanum lycopersicum</i> L.	<i>Tomat</i>	✓		M	Sph	Psilate	Col	Dec-May	Hu	Herb	Non-native, intro	Cultivated	Pow, Npar	5.70		0.03		
Theaceae																		
<i>Schima wallichii</i> (DC.) Korth.	<i>Puspa</i>	✓	✓	M	Obl	Reticulate	Col	Dec-May	Hu	Tree	Native	Norep	Npar	2.93	24.31	0.01	0.16	
Famili Unidentified																		
Species A		✓		M	Sph	Echinate	Tcr	*	*	*	*	*	*	5.27		0.02		
Species B		✓	✓	M	Sph	Microreticulate, lophate, echinate	Tcr	*	*	*	*	*	*	2.49	6.27	0.005		
Species C	*	✓	✓	M	Pro	Smooth	Tcr	*	*	*	*	*	*	2.49	19	0.005	0.12	

Note: ✓: Pollen type detected in the month, *: Undetermined due to limited identification, #: No report found, DB = Deer Breeding Area, MB = Maribaya Road, Norep: No reports of invasive or cultivated status, Mon: Months; Ref: Flowering reference source, M: Monad, T: Tetrad, P: Polyad, Dod: Dodecahedral, Sph: spheroidal, Pro: Prolate, Spro: Subprolate, Obl: Oblate, AYR: All Year Round, Pan: Pantoporate, Por: Porate, Mon: Monosulcate, Sul: Sulcate, Tcr: Tricolporate, Bip: Biporate, Zon: Zonoporate, Col: Colporate, Ina: Inaperture, Monp: Monoporate, Tcp: Tricolpate, Ref: References, Aul: Aulya et al. (2021), Bu and So: Budumajji and Raju (2018), DAF-Q: Department of Agriculture and Fisheries, The State of Queensland (2024), Gbif: GBIF Secretariat 2025, He and Ku: Herdiansyah and Kusnanto (2020), Hu: Husodo et al. (2024), covering December to May; Hy1: Hyde et al. (2025b), Hy1: Hyde et al. (2025a), Ja: Jasmi (2017), Ja*= Jasmi (2017), blooming depends on the growing season; Je: Jesia et al. (2024), Kra: Kratz et al. (2025), La: Lady Bird Johnson Wildflower Center (2020), La and M: Labrada and Medina (2011), Marj: Marjenah (2021), Mu: Mulwa et al. (2019), Oem: Oematan et al. (2020), Orwa: Orwa et al. (2009), Npar: Nparks 2025, Pow: POWO 2025, Rah: Rahayu et al. 2025, Ri: Ritawati et al. (2023), Sant: Sangeetha et al. (2024), Se and Su: Septiadi and Sudjatmiko (2023), Wa: Waghmare et al. (2022), Wi: Widyastuti et al. (2023), Win: Windyarini et al. (2020), Wul: Wulandari et al. (2025)

The dominance of Asteraceae highlights its ecological importance for *A. cerana*, driven by floral traits like the capitulum that increase visibility and pollen access (Fu et al. 2023). This pattern is consistent with earlier studies: Salamah et al. (2018) identified Asteraceae as a major pollen source in Depok, and Cınbirtoğlu and Sıralı (2023) documented 156 Asteraceae taxa as key contributors in Turkish beekeeping regions.

Beyond Asteraceae, Fabaceae contributes structurally diverse pollen—ranging from monads to polyads, with reticulate, psilate, or verrucate ornamentation—which increases its attractiveness to *A. cerana* (Antonio-Domingues et al. 2018; Aswini et al. 2024). However, its lower IVI in Maribaya indicates reduced abundance or accessibility in edge-dominated areas. Lauraceae’s role aligns with studies showing frequent visits of *A. cerana* to avocado and related taxa in tropical regions (Mala and Rami 2020). Likewise, *S. wallichii* is an important native tree providing stable pollen and nectar resources (Basrowi et al. 2022; Kusmoro et al. 2024).

The differences between the Deer Breeding Site and Maribaya in terms of family-level dominance suggest the influence of habitat characteristics on foraging dynamics. The interior forest setting of the Deer Breeding Site supports a more balanced representation among families. In comparison, the edge and peri-urban environment of Maribaya promotes a stronger dominance of Asteraceae, particularly invasive taxa such as *Tithonia diversifolia* (Hemsl.) A.Gray. Seasonal influences may further reinforce this dominance, as *T. diversifolia* blooms year-round and provides abundant pollen resources during the rainy season (Jasmi 2017; Santos-Gally 2023).

Together, these results show that although Asteraceae is the primary pollen source for *A. cerana*, Fabaceae and other families enhance resource diversity and help buffer seasonal shifts in floral availability. The dominance patterns in Figure 4 and species details in Table 2 provide a

foundation for assessing their ecological roles and relevance to sustainable beekeeping.

Species-level dominance and diversity indices

At the species level, the analysis of the Important Value Index (IVI) revealed strong dominance by a small number of taxa. Across both sublocations, *T. diversifolia* (Asteraceae) emerged as the most abundant pollen type, with a total IVI score of 94.22. Its contribution was even higher in Maribaya (IVI: 105.84) compared to the Deer Breeding Site (IVI: 75.98) as shown in Figure 4. Key contributors included *Mimosa pudica* L. (Fabaceae), with IVI values of 47.51 overall, 47.17 in the Deer Breeding Site, and 30.96 in Maribaya, and *Sphagneticola trilobata* (L.) Pruski (Asteraceae), which reached 39.56 in Maribaya and 23.60 in the Deer Breeding Site. *Persea americana* (Lauraceae) also showed a high IVI in the Deer Breeding Site (34.23). Overall pollen diversity was moderate ($H' = 1.76$), with higher diversity in the Deer Breeding Site ($H' = 1.87$) than in Maribaya ($H' = 1.31$). These results are presented in Table 2 and the dominant taxa distribution in Figure 4.

The dominance of *T. diversifolia* highlights the reliance of *A. cerana* on this invasive but highly productive species. Jasmi (2017) noted its capacity to bloom year-round, while Santos-Gally (2023) emphasized its richness in both nectar and pollen. Studies on its congener, *T. rotundifolia*, provide additional insight into pollen production potential, with estimates of up to 39.08 mg per capitulum and over 10 g per plant (Wróblewska et al. 2016). Such abundant pollen yield explains the high IVI of *T. diversifolia* in our samples. Its structural traits—monad unit, spheroidal shape, tricolporate apertures, and echinate ornamentation (Heigl 2021)—further support its efficiency as a pollen source. However, its invasive status (Dai et al. 2021; Hasibuan et al. 2021) raises concerns regarding long-term ecological balance, as its expansion may displace native species while simultaneously sustaining bee populations.

Pollen types distribution based on IVI score

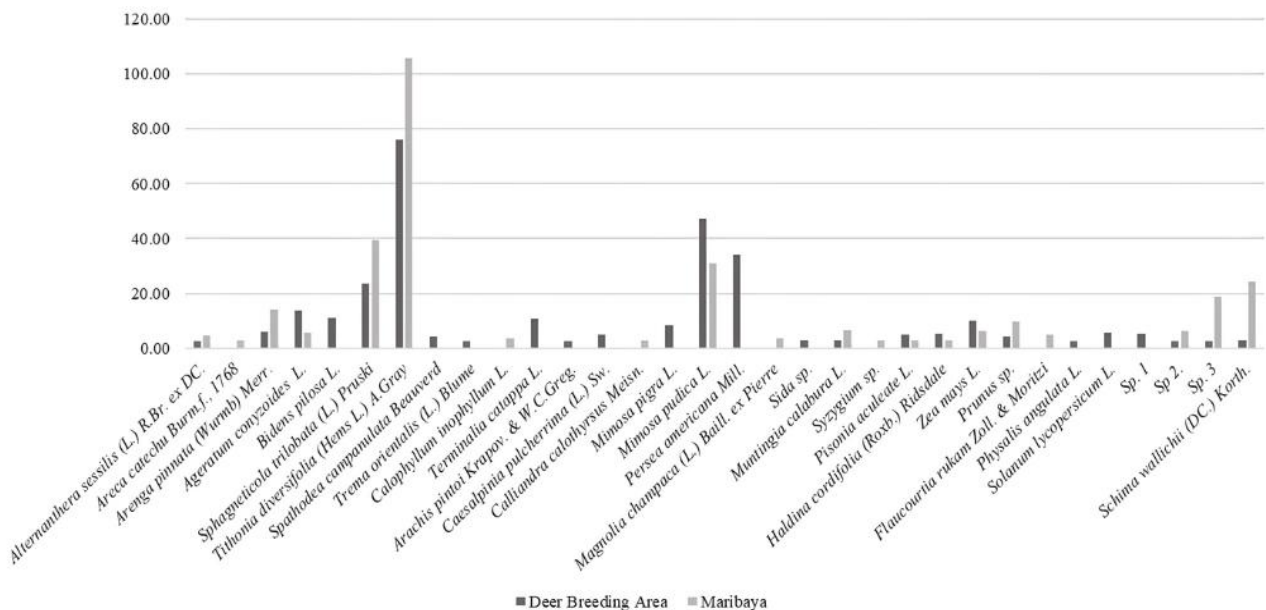


Figure 4. Distribution of pollen types based on Importance Value Index (IVI) in the Deer Breeding Area and Maribaya, Ir. H. Djuanda GFP, West Java, Indonesia, during May 2024

The role of *M. pudica* and *S. trilobata* as secondary dominants is also significant. Both species are ground-cover plants commonly found along pathways and roadsides in the study area. Their accessibility and continuous flowering make them consistent resources for *A. cerana*. Vishnu et al. (2024) similarly observed high foraging activity of *A. cerana* on *S. trilobata* in Kerala, India, confirming its attractiveness beyond the Indonesian context. The presence of *P. americana* in pollen samples, despite its limited local abundance, suggests that nearby plantations outside the forest park contribute to the bees' foraging spectrum. Koetz (2013) reported a foraging range of up to 1 km for *A. cerana*, which likely explains the detection of cultivated taxa like avocado in pollen loads.

Diversity analysis using the H' provided further insights into species composition. The Deer Breeding Site showed higher diversity compared to Maribaya. This pattern suggests that the forest interior supports a broader range of pollen sources. At the same time, Maribaya, being closer to anthropogenic influences, is characterized by fewer but more dominant species such as *T. diversifolia*. The higher H' in the forest site aligns with Ren et al. (2023), who documented greater pollinator abundance and diversity in forest interiors relative to edges.

Taken together, the results demonstrate that a small set of dominant species, particularly *T. diversifolia*, disproportionately shape the pollen spectrum of *A. cerana* during the rainy season. While these species ensure continuous foraging resources, their prevalence reduces evenness and may increase ecological dependence on non-native plants. The combination of IVI scores (Table 2) and diversity indices (Figure 4) highlights both the abundance of resources available and the potential vulnerabilities associated with reliance on a narrow set of dominant taxa.

Pollen morphological traits, flowering period, and plant habits

The pollen types identified in this study displayed a considerable range of morphological diversity, which reflects the wide array of floral resources utilized by *A. cerana*. Based on pollen unit type, monads were overwhelmingly dominant, representing 88.24% of the total taxa recorded. Tetrads and polyads occurred less frequently, restricted primarily to Fabaceae taxa such as *M. pudica* and *Calliandra calothyrsus* Meisn.. In terms of shape, spheroidal pollen grains were most frequently observed, accounting for 43.33% of the total. Other forms, including prolate, subprolate, and oblate, also occurred but at lower proportions. Ornamentation patterns varied among families, with reticulate structures (25%) being the most common, followed by echinate, perforate, and granulate forms. Aperture type was another diagnostic trait, with tricolporate pollen dominating the dataset (40.63%). Other aperture configurations, including colpi, porate, sulcate, and inaperturate forms, were recorded in smaller numbers. Nearly half of the pollen types (43.75%) were also characterized by year-round (AYR) flowering. In terms of growth habit, trees represented the largest proportion of taxa (43.75%), followed by herbs (34.38%)

and shrubs (9.38%), with a small fraction unclassified due to limited identification.

The predominance of pollen diagnostic traits observed in this study is also reported in several previous studies. The predominance of monads unit, for instance, is consistent with general trends in angiosperm palynology, where solitary pollen grains are more common than aggregated units (Antonio-Domingues et al. 2018). The presence of multiple unit types, however, broadens the resource spectrum and demonstrates the capacity of *A. cerana* to exploit structurally diverse pollen. In terms of pollen ornamentation, echinate ornamentation, particularly prevalent in Asteraceae such as *T. diversifolia* and *S. trilobata*, is notable because its thorn-like projections may enhance adherence to pollinators (Salamah et al. 2018). Similarly, Fabaceae exhibited more complex reticulate and verrucate ornamentations, which align with previous palynological characterizations of this family (Aswini et al. 2024). Tricolporate pollen, a characteristic of many eudicots, provides structural flexibility that facilitates germination under different environmental conditions (El Ghazali et al. 1997). Table 2 illustrates the range of reproductive strategies represented in the study sites.

Flowering phenology also played an important role in shaping the pollen spectrum. Species such as *T. diversifolia*, *M. pudica*, and *Arenga pinnata* (Wurmb) Merr. provide continuous resources, ensuring that *A. cerana* has stable foraging options throughout the year. Seasonally restricted taxa, for example, *P. americana* (flowering February-May and August-October) and *S. wallichii* (December-May), complemented these resources, thereby contributing to temporal continuity (Jasmi 2017; Mulwa et al. 2019). Hosamani et al. (2019) emphasized the importance of peak flowering months (May-June) for maximizing foraging activity, which coincides with our sampling period.

Plant growth habit also influenced pollen availability. Interestingly, although trees dominated in terms of taxonomic richness, herbs and shrubs contributed higher relative pollen densities, suggesting more intensive foraging activity on ground-level vegetation. This pattern corresponds with Nagamitsu and Inoue (1999), who noted that *A. cerana* often forages on both tall trees and herbaceous cover, reflecting its generalist foraging behavior.

Overall, the morphological, phenological, and growth-form diversity of pollen types underscores the ecological flexibility of *A. cerana*. The reliance on monad, spheroidal, and tricolporate pollen types indicates a preference for common and structurally accessible resources, while the mixture of perennial and seasonal bloomers ensures year-round pollen availability. The dominance of tree taxa in richness, contrasted with herbaceous dominance in relative density, further suggests a dynamic balance between forest canopy resources and understory or ruderal plants. These findings, supported by Table 2, highlight the importance of maintaining structurally and phenologically diverse vegetation to sustain robust foraging networks for *A. cerana*.

Seasonal comparison with previous studies (rainy vs dry season)

The results of this study, conducted during the rainy season, revealed marked differences in pollen richness and composition compared to previous surveys carried out in the dry season. We recorded 32 pollen types across both sublocations, exceeding the 28 types documented collectively by Asyraf (2022) and Haydar (2022) in September. In the Deer Breeding Site, 25 pollen types were identified, far surpassing the 15 types previously reported by Haydar (2022). Meanwhile, Maribaya yielded 21 pollen types, which is almost consistent with the 20 types noted by Asyraf (2022), but with a distinct taxonomic composition. Such discrepancies reinforce the influence of seasonal factors on pollen diversity, as noted by Hosamani et al. (2019), who associated May and June with peak foraging activity in *A. cerana*. These contrasts emphasize the role of seasonal variation in shaping floral resources available to *A. cerana*. The detailed taxonomic list in Table 2 and the micrographs in Figure 5 illustrate the broader resource base during the rainy season.

Seasonal differences were especially evident in the dominance hierarchy of species. During the rainy season, *T. diversifolia* emerged as the principal pollen source, contributing 39.72% of relative density in the Deer Breeding Site and 51.14% in Maribaya. By contrast, dry season studies showed a sharp decline in the dominance of this taxon. Haydar (2022) reported that in September, *T. diversifolia* contributed only 13.00%, with *Ageratum conyzoides* L. becoming dominant at 46.10%. Similarly, Asyraf (2022) observed that *A. conyzoides* represented 77.31% of pollen loads in Maribaya during the late dry season, while *T. diversifolia* was reduced to only 4.13%. These findings highlight a temporal shift in resource availability, with *T. diversifolia* dominating under rainy conditions and *A. conyzoides* under dry conditions.

The seasonal patterns observed here align with broader ecological studies linking rainfall to pollinator foraging. Kamaraj and Rasappan (2024) documented a negative correlation between rainfall and foraging activity in *A. cerana*, attributing reduced activity to hive departure constraints and higher mortality under heavy rains. Conversely, Hosamani et al. (2019) emphasized that May and June coincide with peak foraging activity due to synchronized floral blooms, which matches our sampling period. This duality suggests that while heavy rains may suppress bee flight activity, the abundance of blooming plants during the rainy season provides sufficient incentive for sustained pollen collection.

The study also underscore the role of invasive taxa in shaping seasonal dynamics. The dominance of *T. diversifolia* during the rainy season is facilitated by its capacity for year-round flowering (Jasmi 2017; Santos-Gally 2023) and high pollen productivity (Wróblewska et al. 2016). In contrast, *A. conyzoides* thrives during the dry season, when its ruderal nature and stress tolerance give it a competitive advantage (Wang et al. 2024). This seasonal alternation of invasive species dominance underscores the complexity of managing floral landscapes for beekeeping and conservation.

The implications for local apiculture are significant. Beekeepers operating in the Deer Breeding Site and Maribaya must contend with seasonal fluctuations in pollen composition that influence honey quality and colony health. For instance, honey derived from *T. diversifolia*—commercially valued as "madu insulin"—is abundant during the rainy season, while *A. conyzoides* likely dominates honey production during the dry season. These seasonal signatures, as found in our studies and previous studies by Asyraf (2022) and Haydar (2022), emphasize the need for temporal monitoring of pollen sources to support sustainable apiculture strategies.

In summary, the comparison between rainy and dry seasons demonstrates that *A. cerana* foraging ecology is strongly seasonal, shaped by the phenology of dominant plant species and the prevalence of invasive taxa. While the rainy season expands resource richness and diversity, it also reinforces dependence on non-native species such as *T. diversifolia*. The integration of Table 2 and Figure 4 provides empirical evidence of this seasonal turnover and underscores the importance of longitudinal studies to capture temporal variation in pollen availability.

Regional and international context of pollen diversity in *Apis cerana*

The 32 pollen types identified in this study during the rainy season indicate a moderate richness compared with other *A. cerana* studies. In Indonesia, reported values range widely: Nuriyah et al. (2021) found 70 pollen types near the study area, whereas other studies recorded lower richness, such as 23 species (Yolanda et al. 2020), 21–69 types across sites (Lestari and Susandarini 2019), 7 types (Syifa et al. 2023), 16–17 types (Jayuli et al. 2018), and 11 types (Rasyiid et al. 2025). Together, these comparisons highlight the high heterogeneity of *A. cerana* foraging spectra in Indonesia, driven by local vegetation and land-use context.

The present study also aligns with international observations that *A. cerana* exploits a wide but variable range of floral resources. In Kyushu, southern Japan, Donkersley et al. (2021) reported 50 biotypes of pollen in honey samples, while Basak et al. (2025) identified 78 morphotypes in the eastern Himalayan region. In India, diversity estimates span from 15 pollen types in Guntur, southern India (Mamatha et al. 2018), to 87 taxa documented over a three-year survey in southeastern regions (Lazar et al. 2024). Studies from West Bengal recorded intermediate levels, with 58 pollen types in pollen loads (Mondal et al. 2023) and 47 in crop–nectar samples (Das et al. 2024). In China, Guo et al. (2023) applied molecular methods such as DNA barcoding and high-throughput sequencing, identifying 64 pollen types, which demonstrates how advanced techniques can uncover more comprehensive spectra compared to morphology alone.

Table 3. Representative pollen micrographs from the Deer Breeding Area and Maribaya, Ir. H. Djuanda GFP, West Java, Indonesia, May 2024.

Number	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.
Pollen type	<i>Alternanthera sessilis</i> (L.) R.Br. ex DC.	<i>Areca catechu</i> Burm.f., 1768	<i>Arenga pinnata</i> (Wurmb) Merr.	<i>Ageratum conyzoides</i> L.	<i>Bidens pilosa</i> L.	<i>Sphagneticola trilobata</i> (L.) Pruski	<i>Tithonia diversifolia</i> (Hems L.) A.Gray	<i>Spathodea campanulata</i> Beauverd	<i>Trema orientalis</i> (L.) Blume	<i>Calophyllum inophyllum</i> L.	<i>Terminalia catappa</i> L.
Personal Micrograph											
Number	12.	13.	14.	15.	16.	17.	18.	19.	20.	21.	22.
Pollen type	<i>Arachis pintoii</i> Krapov. & W.C.Greg.	<i>Caesalpinia pulcherrima</i> (L.) Sw.	<i>Calliandra calothyrsus</i> Meisn.	<i>Mimosa pigra</i> L.	<i>Mimosa pudica</i> L.	<i>Persea americana</i> Mill.	<i>Magnolia champaca</i> (L.) Baill. ex Pierre	<i>Sida</i> sp.	<i>Muntingia calabura</i> L.	<i>Syzygium</i> sp.	<i>Pisonia aculeata</i> L.
Personal Micrograph											
Number	23.	24.	25.	26.	27.	28.	29.	30.	31.	32.	
Pollen type	<i>Haldina cordifolia</i> (Roxb.) Ridsdale	<i>Zea mays</i> L.	<i>Prunus</i> sp.	<i>Flacourtia rukam</i> Zoll. & Moritzi	<i>Physalis angulata</i> L.	<i>Solanum lycopersicum</i> L.	Sp. A	Sp. B	Sp. C	<i>Schima wallichii</i> (DC.) Korth.	
Personal Micrograph											

Note: Notes on uncertainly identified pollen types: *Arachis* sp. (pollen type number 14) was based on *Arachis pintoii* Krapov. & W.C.Greg., as referenced in Wondracek-Lüdke et al. (2015), *Sida* sp. (pollen type number 22) was based on *Sida rhombifolia* L, as referenced in Singh and Dixit (2018), *Syzygium* sp. (pollen type number 24) was based on *Syzygium aqueum* (Burm.fil.) Alston as referenced in Permatasari et al. (2024), *Prunus* sp. (pollen type number 27) was based on *Prunus dulcis* Mill. ex Rchb., as referenced in Abdulrahman et al. (2019)

Compared with international studies, the 32 pollen types found here indicate moderate richness—lower than multi-season or molecular studies but higher than short-term surveys in more limited habitats. The overall diversity ($H' = 1.76$) fits the moderate category of Ahsan et al. (2021), supporting the generalist foraging behavior of *A. cerana* (Liu et al. 2020). The higher diversity in the Deer Breeding Site ($H' = 1.87$) compared to Maribaya ($H' = 1.31$) aligns with global trends showing that interior forests maintain greater pollen diversity than edge or peri-urban environments (Ren et al. 2023).

In conclusion, the diversity patterns observed in this study position the Ir. H. Djuanda forest landscape within the broader spectrum of *A. cerana* foraging ecology in Asia. While richness is moderate compared to regions like India or the Himalayas, the dominance of invasive taxa parallels observations across Southeast Asia. The integration of our palynological dataset with regional and global evidence, as depicted in Figure 5, underscores both the ecological flexibility of *A. cerana* and the need for conservation strategies that balance reliance on invasive species with the enrichment of native floral resources.

Key dominant species and ecological implications

The analysis of dominant species based on IVI and relative density underscores the critical role of a few taxa in shaping the pollen spectrum of *A. cerana* during the rainy season. Among them, *T. diversifolia* (Asteraceae) was the most dominant species, with IVI values of 75.98 in the Deer Breeding Site and 105.84 in Maribaya, contributing to a total IVI of 94.22. Its relative density was equally high, reaching 42.30% overall.

These results of IVI in Deer Breeding Site and Maribaya highlight the overwhelming importance of *T. diversifolia* as a pollen source (Table 2; Figure 4). Its pollen is characterized by spheroidal shape, monad unit, echinate ornamentation, and tricolporate apertures (Heigl 2021), features that enhance its efficiency as a foraging resource. Moreover, its year-round flowering (Jasmi 2017) and high pollen and nectar productivity (Wróblewska et al. 2016; Santos-Gally 2023) explain its consistent dominance. However, as an invasive species originating from the Americas (Hasibuan et al. 2021), *T. diversifolia* raises ecological concerns. Its rapid spread across Asia and Africa (Dai et al. 2021) and potential behavioral effects on bees via nectar phenolics (Jiang et al. 2021) highlight the dual role of this plant as both a valuable forage source and a potential ecological threat.

The second most dominant taxon was *M. pudica* (Fabaceae), locally known as putri malu. It contributed IVI values of 47.17 in the Deer Breeding Site and 30.96 in Maribaya, indicating its consistent role across both sublocations. Despite its lower overall abundance compared to *T. diversifolia*, *M. pudica* provided substantial pollen resources, supported by its widespread occurrence as a ground-cover plant in disturbed areas near the apiaries. Its morphological characteristics, particularly oblate shape and inaperturate apertures (Table 2), make it distinct among Fabaceae pollen sources. As a species with year-round flowering, *M. pudica* stabilizes pollen availability, and its

foraging importance has also been recognized in other tropical landscapes (Gopal 2023).

Sphagneticola trilobata (Asteraceae), another invasive species, emerged as the third most dominant pollen source, particularly in Maribaya, where its IVI reached 39.56 compared to 23.60 in the Deer Breeding Site. Its accessibility as a creeping herb along roadsides and forest edges makes it an easily available forage for *A. cerana*. Vishnu et al. (2024) similarly noted *A. cerana*'s preference for this species in Kerala, India, reinforcing its role as an attractive invasive pollen source across different regions. While its dominance in our samples reflects its ecological prevalence, it also underscores potential risks of pollination-driven expansion of invasive ground covers in forest margins.

Persea americana (Lauraceae) also contributed notably in the Deer Breeding Site (IVI 34.23). Although not abundant nearby, its pollen suggests *A. cerana* foraged on cultivated avocado trees outside the forest park, consistent with its ~1 km foraging range (Koetz 2013). Similar observations in India (Mala and Rami 2020) confirm avocado as an important cultivated resource, highlighting the connectivity between agricultural landscapes and forest habitats.

These four dominant taxa—a mix of invasive, potentially invasive, and cultivated plants—that sustain *A. cerana* populations in the study area have significant practical implications. *Tithonia diversifolia* and *S. trilobata*, while providing abundant but ecologically problematic resources, pose a challenge that needs to be addressed. On the other hand, *M. pudica* and *P. americana* demonstrate how disturbed habitats and agroecosystems can be integrated into the species' foraging networks. The patterns we've uncovered, as detailed in Table 1 and Figure 4, underscore the remarkable ecological adaptability of *A. cerana* and the practical management challenges we face in balancing reliance on non-native dominants with the conservation of native species.

Native vs non-native species: Management and conservation perspectives

The results of this study reveal that *A. cerana* relies heavily on non-native and invasive plants. A total of 50.00% non-native plants were found, 31.25% were native plants, and the remaining are limitedly unidentified with percentage of 18.75%. Regarding ecological roles such as invasiveness or cultivation traits, invasive or potentially invasive plants dominated the dataset (32.26%), followed by cultivated or potentially cultivated species (25.81%). However, limited information was available for several pollen types (41.93%), including native plants such as *A. pinnata*, *S. wallichii*, and *Trema orientale* (L.) Blume, which are rarely reported as either cultivated or invasive.

Our finding of non-native dominance across all sublocations contrasts with the report by Koyama et al. (2018), which stated that *A. cerana* primarily forages on native plants, followed by cultivated (crop and garden) trees, and lastly on weeds of both native and non-native origin. This difference may be attributed to the fact that their observations were conducted in an arboretum area in Tsukuba, Ibaraki Prefecture, Japan, whereas ours were

made around a conservation forest and recreational sites. Similarly, Koyama et al. (2018) reported a higher number of pollen types recorded in June compared to those observed after August.

In our study sites, non-native plants dominated the Deer Breeding Area, whereas Maribaya showed a balanced composition with eight native and eight non-native pollen types. The origins of four types in the Deer Breeding Area and five in Maribaya could not be determined. Notably, despite being an interior forest habitat, the Deer Breeding Area showed a high reliance on non-native plants. However, because this reflects only one sampling period, it cannot confirm whether *A. cerana* contributes to the reproduction of non-native species. Even so, the results indicate that *A. cerana* has broad foraging preferences across both native and non-native plants.

Tithonia diversifolia and *S. trilobata*, the non-native and dominant pollen types, dominating the rainy season in our study. These species accounted for the highest IVI scores across both sublocations (Table 1; Figure 5), highlighting their dominance as pollen resources. Their ability to bloom year-round (Jasmi 2017; Santos-Gally 2023) and produce large quantities of pollen and nectar (Wróblewska et al. 2016) ensures continuous foraging opportunities for bees. However, this dependence raises ecological concerns, as invasive plants may alter local plant–pollinator networks and outcompete native flora (Dai et al. 2021; Hasibuan et al. 2021). By facilitating pollination of invasive taxa, *A. cerana* may inadvertently contribute to their spread, intensifying pressures on native ecosystems.

Despite the prominence of invasive species, several native plants also contributed significantly to the pollen spectrum. Notably, *S. wallichii* (Theaceae) recorded IVI values of 24.31 in Maribaya and 10.54 overall, indicating its importance as a native pollen source. This species has been recognized in previous studies as a key component of stingless bee and honey bee diets (Basrowi et al. 2022; Kusmoro et al. 2024). Its ecological value lies not only in providing stable pollen resources but also in supporting broader forest community structures. Similarly, *A. pinnata* (Arecaceae) was identified as a recurring pollen type across seasons and studies, with potential value for beekeeping due to the high enzymatic activity of its nectar and pollen (Erwan and Agussalim 2022). These findings suggest that native taxa can complement non-native dominants, offering more sustainable forage options for long-term apiculture.

Our study also the coexistence of invasive and native species in the foraging spectrum underscores the need for a nuanced management approach. *Tithonia diversifolia* has an established role in supporting honey production and is already recognized in local markets, as shared by the beekeepers. However, it appears to possess strong reproductive capacity, as indicated by its recurring presence in September observations—13.00% in the Deer Breeding Area (Haydar 2022) and 4.13% in Maribaya (Asyraf 2022). Instead, enrichment planting of native forage trees like *S. wallichii* and *A. pinnata* around apiaries and within forest edges could provide a balanced resource base. Such strategies would reduce overreliance on

invasive taxa while enhancing biodiversity conservation. The integration of native plants into managed landscapes would also align with the dual goals of sustaining apiculture and restoring ecological integrity.

The importance of balancing native and non-native resources has been emphasized in broader studies of *A. cerana*. Ren et al. (2023) noted that pollinator assemblages at forest edges often shift toward generalist bees and invasive plants, leading to competition and potential loss of specialist taxa. Our findings reinforce this dynamic, as Maribaya—with its edge-dominated environment—showed lower Shannon–Wiener diversity (H' : 1.31) compared to the Deer Breeding Site (H' : 1.87). The ecological constancy of *A. cerana* foraging on a few species, reported in other regions (Shrotri et al. 2024), further highlights the risks of dependency when dominant taxa are invasive.

The palynological data summarized in Table 1 and Figure 5 demonstrate the dual role of non-native species as both critical forage resources and ecological challenges. Sustainable management should not focus solely on removing invasives but rather on enhancing native species that can provide equivalent or complementary resources. By strategically integrating native forage plants into apiary landscapes, stakeholders in the Ir. H. Djuanda forest park can support both the economic needs of beekeepers and the ecological goals of biodiversity conservation.

Overall, this study shows that *A. cerana* foraging in Ir. H. Djuanda Grand Forest Park is driven by high pollen richness, clear dominance patterns, and strong seasonal variation. Asteraceae—especially *T. diversifolia*—supplied most rainy-season pollen, while Fabaceae and other families added structural and functional diversity. Dependence on invasive taxa (*T. diversifolia*, *S. trilobata*) reflects the species' adaptability but also highlights ecological risks, whereas native plants such as *S. wallichii* and *A. pinnata* remain important sustainable forage sources. Comparisons with dry-season and regional studies confirm that foraging patterns are highly seasonal and shaped by habitat context, with edge areas supporting fewer dominant taxa. These findings emphasize the need for management strategies that balance the short-term benefits of invasive forage plants with the long-term goal of conserving and restoring native biodiversity to support sustainable apiculture and forest resilience.

In conclusion, this study revealed that *A. cerana* in the Ir. H. Djuanda Grand Forest Park forages on a moderately diverse spectrum of 32 pollen types from 20 plant families during the rainy season. Pollen richness was higher in the Deer Breeding Site than in Maribaya, reflecting differences between interior forest and edge habitats. Family-level analyses showed the consistent dominance of Asteraceae, while species-level results highlighted *T. diversifolia* as the primary pollen source, followed by *M. pudica*, *S. trilobata*, and *P. americana*. Diversity indices confirmed higher heterogeneity in the interior forest compared to the edge sites. The heavy reliance on invasive plants such as *T. diversifolia* and *S. trilobata* underscores both their ecological importance and potential risks, while native species like *S. wallichii* and *A. pinnata* represent sustainable alternatives. These findings emphasize the need

for management strategies that integrate native forage species to support both apiculture and biodiversity conservation. Furthermore, conducting pollen analyses across different time periods could improve the accuracy of understanding *A. cerana*'s foraging preferences. Thus, we recommend applying this similar approach in different months for future studies.

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REFERENCES

- Abdulrahman SS, Selamoglu Z, Shahbaz SE. 2019. Pollen morphology of *Prunus* subg. *Amygdalus* (Rosaceae) growing in Iraq. *Fresenius Environ Bull* 28 (11): 8254-8265. DOI: 10.36808/ief/2022/v148i2/160011.
- Ahsan AWA, Sukmawaty E, Pratama BA. 2021. Analysis of tree vegetation in the Kalimantan Ecoregion Ecology Park Area, Bogor Botanical Gardens. *Filogeni Jurnal Mahasiswa Biologi* 1 (3): 107-114. DOI: 10.24252/filogeni.v1i3.26236. [Indonesian]
- Amakpe F, Kenali HI, Sinsin B. 2024. A melissopalynologic dynamics appraisal revealed the strategic foraging adaptation of the honeybees (*Apis mellifera* Linnaeus 1758) to the anthropogenic impacts in the Republic of Benin. *Heliyon* 10 (13): e33753. DOI: 10.1016/j.heliyon.2024.e33753.
- Antonio-Domingues H, Corrêa AMS, Queiroz RT, Bitar NAB. 2018. Pollen morphology of some Fabaceae species from Patos de Minas, Minas Gerais State, Brazil. *Hoehnea* 45 (1): 103-114. DOI: 10.1590/2236-8906-54/2017.
- Ardi RDW, Aswan, Maryunani KA, Yulianto E, Putra PS, Nugroho SH, Istiana. 2020. Last deglaciation—Holocene Australian-Indonesian monsoon rainfall changes off southwest Sumba, Indonesia. *Atmosphere* 11 (9): 932. DOI: 10.3390/atmos11090932.
- Aryal L, Thapa R, Tiwari S, Chaudhary NK. 2016. Foraging behavior of native honeybee (*Apis cerana* F.) and European honeybee (*Apis mellifera* L.) on flowers of common buckwheat (*Fagopyrum esculentum* M.) in Chitwan, Nepal. *Intl J Appl Sci Biotechnol* 4 (2): 236-239. DOI: 10.3126/ijasbt.v4i2.15131.
- Aswini A, Kumarasamy D, Lazar J, Deebika K, Arun VP, Nahendran C. 2024. Exploring pollen morphology diversity within the Fabaceae family: A study from Annamalai Nagar, Chidambaram. *Intl J Biosci* 25 (1): 93-105. DOI: 10.12692/ijb/25.1.93-105.
- Asyraf MN. 2022. Analysis of Pollen as a Feed Source of Honeybees, *Apis cerana* Fabr, 1793, in the Maribaya Area, Ir. H. Djuanda Forest Park, West Bandung District. [Thesis]. Universitas Padjadjaran, Bandung. [Indonesian]
- Aulya W, Mardina V, Sari MS. 2021. Phytochemical analysis and antioxidant activity of n-hexane and ethyl acetate in flower. *Intl J Sci Technol Res* 10 (3): 208-211.
- Azeez SO, Faluyi JO, Oziegbe M. 2019. Cytological, foliar epidermal, and pollen grain studies in relation to ploidy levels in four species of *Physalis* L. (Solanaceae) from Nigeria. *Intl J Biol Chem Sci* 13 (4): 1960-1972. DOI: 10.4314/ijbcs.v13i4.4.
- Basak S, Biswas O, Chhetri B, Rai S, Paruya DK, Patra DC, Bera S. 2025. Nectar and pollen source of natural honey produced by *Apis cerana* skorikovi Engel (= Himalaya): Palynological analysis from tropical to sub-tropical forests of eastern Himalaya. *Rev Palaeobot Palynol* 332: 105210. DOI: 10.1016/j.revpalbo.2024.105210.
- Basrowi M, Qayim I, Raffiudin R. 2022. Modeling of potential bee forage habitat for *Apis dorsata* in Membalong, Belitung. *Jurnal Ilmu Pertanian Indonesia* 27 (4): 562-573. DOI: 10.18343/jipi.27.4.562. [Indonesian]
- Buchori D, Rizali A, Priawandiputra W, Raffiudin R, Sartiami D, Pujiastuti Y, Jauharlina, Pradana MG, Meilin A, Leatemia JA, Sudiarta IP, Rustam R, Nelly N, Lestari P, Syahputra E, Hasriyanti, Watung JF, Daud IDA, Hariani N, Jihadi A, Johannis M. 2022. Beekeeping and managed bee diversity in Indonesia: Perspective and preference of beekeepers. *Diversity* 14 (1): 52. DOI: 10.3390/d14010052.
- Budumajji U, Raju AJS. 2018. Pollination ecology of *Bidens pilosa* L. (Asteraceae). *Taiwania* 63 (2): 89-100. DOI: 10.6165/ta.2018.63.89.
- Campos MG, Anjos O, Chica M et al. 2021. Standard methods for pollen research. *J Apic Res* 60 (4): 1-109. DOI: 10.1080/00218839.2021.1948240.
- Caraballo-Ortiz MA, Campbell KCSE, Cross SJ. 2021. A new *Pisonia* (Nyctaginaceae) from Jamaica, with an updated list of species in the genus and a key to the West Indian taxa. *Webbia* 76 (1): 53-63. DOI: 10.36253/jopt-10083.
- Cınırtoğlu Ş, Sıralı R. 2023. The importance of plants belonging to the Asteraceae family as a pollen source in beekeeping. *Bee Stud-Apicult Re Institute* 15 (1): 21-24. DOI: 10.51458/BSTD.2023.32.
- Crutcher R. 2007. Avocado Pollen through the Microscope. *MicroLabNW*. <https://microlabgallery.com>.
- Dai G, Wang S, Geng Y, Dawazhaxi, Ou X, Zhang Z. 2021. Potential risks of *Tithonia diversifolia* in Yunnan Province under climate change. *Ecol Res* 36 (1): 129-144. DOI: 10.1111/1440-1703.12182.
- Das N, Mondal R, Layek U, Karmakar P. 2024. Nectar sources of Asian honeybees (*Apis cerana* Fabricius) in West Bengal, India: Determined by pollen analysis of honey and bee crop nectar. *Palynology* 49 (2): 1-12. DOI: 10.1080/01916122.2024.2398052.
- Department of Agriculture and Fisheries, The State of Queensland. 2024. African tulip tree *Spathodea campanulata*. <https://www.publications.qld.gov.au>.
- Dimou M, Thrasylvoulou A, Tsirakoglou V. 2006. Efficient use of pollen traps to determine the pollen flora used by honey bees. *J Apic Res* 45 (1): 42-46. DOI: 10.1080/00218839.2006.11101312.
- Donkersley P, Covell L, Ota T. 2021. Japanese honeybees (*Apis cerana japonica* Radoszkowski, 1877) may be resilient to land use change. *Insects* 12 (8): 685. DOI: 10.3390/insects12080685.
- Dusengimana JD, Maake A. 2024. Contribution of beekeeping in socio-economic development of communities in Nyamagabe District: A case of beekeeping cooperatives around Nyungwe National Park from 2020 to 2023. *J Biol Environ Sci* 25 (3): 2222-3045.
- El Ghazali GEB, Satti AM, Tsuji S. 1997. Intra-specific pollen polymorphism in *Mimosa pigra* (Mimosaceae). *Grana* 36 (5): 279-283. DOI: 10.1080/00173139709362617.
- Erdtman G. 1960. The Acetolysis method—A revised description. *Svensk Botanisk Tidskrift* 54: 561-564.
- Erwan E, Agussalim. 2022. Honey quality from the bee *Apis cerana*, honey potency produced by coconut and sugar palm saps. *Biodiversitas* 23 (11): 5854-5861. DOI: 10.13057/biodiv/d231139.
- Fassil A, Habtamu T, Tahir M, Aga TT. 2022. Diversity, floral phenology, and socio-economic importance of melliferous plants in Eastern Ethiopia. *Nusantara Biosci* 14 (2): 172-181. DOI: 10.13057/nusbiosci/n140207.
- Fu L, Palazzesi L, Pellicer J, Balant M, Christenhusz MJM, Pegoraro L, Pérez-Lorenzo I, Leitch IJ, Hidalgo O. 2023. Let's pluck the daisy:

- Dissection as a tool to explore the diversity of Asteraceae capitula. Bot J Linn Soc 201 (4): 391-399. DOI: 10.1093/botlinnean/boac0055.
- Global Biodiversity Information Facility (GBIF) Secretariat. 2025. GBIF Backbone Taxonomy. Global Biodiversity Information Facility. <https://www.gbif.org>.
- Gopal TC. 2023. Identification of Bee Forage Plants by Pollen Analysis of *Apis cerana* Honey Collected from Tropical Areas of Tumkur District, Karnataka, India. Appl Ecol Environ Sci 11 (1): 15-21. DOI: 10.12691/aees-11-1-3.
- Guo X, Wang S, Feng J. 2023. Diversity of plants foraged by *Apis cerana* Fabricius around Qinling Mountains (Central China) based on honey pollen samples. Sociobiology 70 (3): e8876. DOI: 10.13102/sociobiology.v70i3.8876.
- Halbritter H, Ulrich S, Grímsson F, Weber M, Zetter R, Hesse M, Buchner R, Svojtka M, Frosch-Radivo A. 2018. Illustrated Pollen Terminology. Springer International Publishing, Cham. DOI: 10.1007/978-3-319-71365-6.
- Harianja AH, Adalina Y, Pasaribu G et al. 2023. Potential of beekeeping to support the livelihood, economy, society, and environment of Indonesia. Forests 14 (2): 321. DOI: 10.3390/f14020321.
- Hasibuan I, Sarina, Damayanti A. 2021. Utilization of titionia weed (*Tithonia diversifolia*) as organic fertilizer on sweet corn. Jurnal Agroqua Media Informasi Agronomi dan Budidaya Perairan 19 (1): 55-63. DOI: 10.32663/ja.v%vi%i.1829. [Indonesian]
- Haydar MRA. 2022. Plant Pollen Diversity Obtained from the Pollen Basket of Honey Bees (*Apis cerana*) Cultivated in the Deer Breeding Area of the Ir. H. Djuanda Forest Park (Tahura), Bandung. [Thesis]. Universitas Padjadjaran, Bandung. [Indonesian]
- Heigl H. 2021. *Tithonia diversifolia*. PalDat - Palynological Database. <https://www.paldat.org>.
- Herdiandyah E, Kusnanto T. 2020. Benefits of *Arachis pintoi*. <https://cybex.id>. [Indonesian]
- Hosamani V, Reddy MS, Venkateshalu BC, Lingamurthi KR, Ashoka N, Ravikumar B. 2019. Studies on foraging activity, pollen quantification, and natural enemies of Indian honey bee, *Apis cerana*, on mixed vegetation. J Entomol Zool Stud 7 (6): 162-167.
- Hunde TA. 2025. The potential and transformation of beekeeping for natural resource conservation and poverty reduction in the case of Ethiopia: A review. Intl J Environ Prot Policy 13 (1): 1-13. DOI: 10.11648/j.jjepp.20251301.11.
- Husodo T, Sumiyati D, Winantris, Laili N, Wulandari I. 2022. Identification of pollens and spores at the Cilarangan and Kupu Kupu in neolithic period, Mekarsari Village, Lebak Regency, Banten, Indonesia. Pros Sem Nas Masy Biodiv Indon 8: 24-30. DOI: 10.13057/psnmbi/m080104. [Indonesian]
- Husodo T, Wulandari I, Syaputri Y, Kasmara H, Hermawan W, Kusmoro J, Shanida SS, Khairina F, Haydar MRA, Asyraf MN, Febrian RR. 2024. Blooming calendar and polliniferous plants in Djuanda Great Forest Park, West Java, Indonesia: Implication for beekeeping management. Biodiversitas 25 (7): 3216-3229. DOI: 10.13057/biodiv/d250743.
- Hyde MA, Wursten BT, Ballings P, Coates Palgrave M. 2025a. Flora of Zimbabwe: Species Information: *Magnolia champaca*. <https://www.zimbabweflora.co.zw>.
- Hyde MA, Wursten BT, Ballings P, Coates Palgrave M. 2025b. Flora of Zimbabwe: Species Information: *Trema orientale* (L.) Blume. <https://www.zimbabweflora.co.zw>.
- Jasmi J. 2017. Diversity and blooming season of food source plants of *Apis cerana* (Hymenoptera: Apidae) in a polyculture plantation in West Sumatra, Indonesia. Biodiversitas 18 (1): 34-40. DOI: 10.13057/biodiv/d180106.
- Jayuli M, Junus M, Nursita IW. 2018. Effect of land altitude on pollen diameter *Apis cerana* in Malang Regency. Jurnal Ternak Tropika 19 (1): 9-21. DOI: 10.21776/ub.jtapro.2018.019.01.2. [Indonesian]
- Jesia NS, Alam M, Karmokar A, Ashrafuzzaman M. 2024. Taxonomic study on the six species of genus *Magnolia*. J Bangladesh Agric Univ 22 (2): 158-165. DOI: 10.3329/jbau.v22i2.74548.
- Jiang X, Gao J, Sharif MZ, Zhang X, Liu F. 2021. Synergistic and dichotomous effects of nectar phenolics on honey bee colonies. Pakistan J Zool 54 (1): 1-7. DOI: 10.17582/journal.pjz/20200506050516.
- Kamaraj N, Rasappan K. 2024. Temporal and spatial foraging activity of Indian honey bee (*Apis cerana indica* F.) at different migratory sites. Sociobiology 71 (1): e9733. DOI: 10.13102/sociobiology.v71i1.9733.
- Koetz A. 2013. The Asian Honey Bee (*Apis cerana*) and Its Strains - with Special Focus on *Apis cerana* Java Genotype. The Department of Agriculture, Fisheries and Forestry, State of Queensland.
- Koyama A, Egawa C, Taki H, Yasuda M, Kanzaki N, Ide T, Okabe K. 2018. Non-native plants are a seasonal pollen source for native honeybees in suburban ecosystems. Urban Ecosyst 21 (6): 1113-1122. DOI: 10.1007/s11252-018-0793-3.
- Kratz M, Manning R, Milne L, Dods K, Baer B, Blache D. 2025. Environmental cues rather than quality of supplemented pollen drive the foraging behaviour of honey bees during avocado pollination. Sci Rep 15 (1): 29650. DOI: 10.1038/s41598-025-13981-6.
- Kusmoro J, Febrian RR, Shanida S, Husodo T, Zainal A. 2024. Identification of pollen as an indicator of plant diversity of honey bees (*Apis cerana* F.) food sources in urban forest conservation area in Bandung Regency, West Java. Jurnal Agrikultura 35 (1): 103-111. DOI: 10.24198/agrikultura.v35i1.42694. [Indonesian]
- Labrada R, Medina AD. 2009. The invasiveness of the African tulip tree, *Spathodea campanulata* Beauv. Biodiversity 10 (2-3): 79-82. DOI: 10.1080/14888386.2009.9712848.
- Lady Bird Johnson Wildflower Center. 2020. *Pisonia aculeata*. <https://www.wildflower.org>.
- Lazar J, Prasad S, Barboni D, Das L, Kumaresan V, Anupama K. 2024. Diversity matters: The diet of *Apis cerana* in southeast India includes one consistently occurring and several seasonally available floral sources. Palynology 48 (1): 1. DOI: 10.1080/01916122.2023.2255990.
- Lestari TH, Susandarini R. 2019. Pollen analysis of *Apis cerana* honey from Java, Indonesia. J Pharmacogn Phytochem 8 (4): 3224-3230.
- Liu F, Zhang G, Qin J, Jiang W, Luo Q, Xu X, Xi F, Yuan F, Yi Z, He H, Ye W, Dai P. 2020. Lowering forest habitat does not reduce forage availability to the eastern honey bees in summer and fall. Apidologie 51 (4): 609-619. DOI: 10.1007/s13592-020-00746-5.
- Louveaux J, Maurizio A, Vorwohl G. 1978. Methods of Melissopalynology. Bee World 59 (4): 139-157. DOI: 10.1080/0005772X.1978.11097714.
- Maknun D. 2017. Ecology: Population, Community, Ecosystem, Realizing a Green, Natural, Islamic and Scientific Campus. Nurjati Press, Cirebon. [Indonesian]
- Mala BRJ, Rami PV. 2020. Diversity and abundance of insect pollinators on avocado (*Persea americana* Mill.) and rambutan (*Nephelium lappaceum* L.) and their contribution to fruit set. Pest Manage Hortic Ecosyst 26 (1): 76. DOI: 10.5958/0974-4541.2020.00012.0.
- Mamatha K, Devender R, Kailash JG, Niranja S, Ramakrishna H. 2018. Comparative pollen analysis of *Apis cerana* Fabricius and *A. mellifera* L. honey samples from Guntur, Southern India. Mellifera 18 (1): 1-14.
- Marjenah M. 2021. The role of canopy structure of *Terminalia catappa* Linn. on light penetration and decreasing ambient temperature as climate change mitigation. Wood Res J 12 (1): 35-40. DOI: 10.51850/wrj.2021.12.1.35-40.
- Martins AE, Camargo MGG, Morellato LPC. 2021. Flowering phenology and the influence of seasonality in flower conspicuousness for bees. Front Plant Sci 11: 594538. DOI: 10.3389/fpls.2020.594538.
- Mattila HR, Otis GW. 2006. The effects of pollen availability during larval development on the behaviour and physiology of spring-reared honey bee workers. Apidologie 37 (5): 533-546. DOI: 10.1051/apido:2006037.
- Mondal R, Das N, Layek U, De SK, Karmakar P. 2023. Pollen sources of Asian honeybee (*Apis cerana* Fabricius) in Paschim Medinipur District of West Bengal, India. Grana 62 (5-6): 369-381. DOI: 10.1080/00173134.2023.2205556.
- Mulwa JM, Gathu RK, Matolo N, Guantai MM, Kasina JM. 2019. Avocado (*Persea americana*) floral calendar and diurnal visitation rates of its pollinators in Murang'a, Kenya. J Agri Res Adv 1 (2): 23-27.
- Muthupandiyam S, Gireesan K, Warriar KCS. 2019. *Haldina cordifolia* (Roxb.) Ridsdale – A promising tree for domestication. Intl J Agric Environ Biotechnol 12 (3): 225-228. DOI: 10.30954/0974-1712.08.2019.6.
- Nagamitsu T, Inoue T. 1999. Differences in pollen sources of *Apis cerana* and *Apis mellifera* at a primary beech forest in central Japan. J Apic Res 38 (1-2): 71-78. DOI: 10.1080/00218839.1999.11100997.
- Normasiwi S, Kurniawati F. 2023. Characteristics of pollen morphology and viability of four species of *Magnolia*. Buletin Kebun Raya 26 (1): 45-51. DOI: 10.55981/bkr.2023.743.

- Nparks. 2025. Flora & Fauna Web. National Parks Board, Singapore. <https://www.nparks.gov.sg/florafaunaweb>.
- Nuriyah S, Husodo T, Hermawan W, Yusuf AA, Kasmara H, Kusmoro J, Wulandari I, Shanida SS. 2021. Short communication: Floral diversity of honey bee-collected pollen (*Apis cerana*) colonies in the Ir. H. Djuanda Forest Park, West Java, Indonesia. *Nusantara Biosci* 13: 185-193. DOI: 10.13057/nusbiosci/n130208.
- Nuriyah S. 2024. The Effectiveness of pollination by *Apis cerana* Fabr. honey bees in the Ir. H. Djuanda Forest Park, West Java. *Ranah Res: J Multidiscip Res Dev* 6 (6): 3048–3056. DOI: 10.38035/rj.v6i6.1595. [Indonesian]
- Odum EP. 1996. *Fundamentals of Ecology*. Tjahjono Samingan, Translator. 3rd Edition. Universitas Gadjah Mada Press, Yogyakarta. [Indonesian]
- Oematan OK, Soetedjo INP, Pellokila MR. 2020. Areca nut sustainable development strategy based on land suitability evaluation in North Mollo Regency, South Central Timor Regency. *Environmental Studies Development* 4 (1): 11-22. DOI: 10.20886/jpkf.2020.4.1.11-22. [Indonesian]
- Orwa C, Mutua A, Kindt R, Jamnadass R, Anthony S. 2009. *Areca catechu*. Agroforestry Database: A Tree Reference and Selection Guide. Version 4.0. <http://www.worldagroforestry.org/sites/treedbs/treedatabases.asp>
- Pacella LF, Di Pasquo M. 2022. Pollen and spores morphology from the Holocene of the Iberá Wetlands in northeastern Argentina. *Bol Soc Argent Bot* 57 (4): 727-750. DOI: 10.31055/1851.2372.v57.n4.35662.
- Pang C, Dong K, Guo Y, Ding G, Lu Y, Guo Z, Wu J, Huang J. 2022. Effects of three types of pollen on the growth and development of honey bee larvae (Hymenoptera: Apidae). *Front Ecol Evol* 10: 1-11. DOI: 10.3389/fevo.2022.870081.
- Pantoja G, Gómez M, Contreras C, Grimau L, Ramírez Quirama JF, Montenegro G. 2010. Determination of suitable zones for apitourism using multi-criteria evaluation in geographic information systems: A case study in the O'Higgins Region, Chile. *Cienc Inv Agr* 44 (3): 332. DOI: 10.7764/rcia.v44i2.1712.
- Patel V, Biggs EM, Pauli N, Boruff B. 2020. Using a social-ecological system approach to enhance understanding of structural interconnectivities within the beekeeping industry for sustainable decision making. *Ecol Soc* 25 (2): 24. DOI: 10.5751/ES-11639-250224.
- Permatasari I, Rangkyu SA, Fitriani D, Priyanti R. 2024. Morphology of pollen (pollen) of the Myrtaceae Family: *Psidium guajava*, *Syzygium aqueum*, and *Syzygium malaccense*. *BioEksakta: Jurnal Ilmiah Biologi Unsoed* 6 (3): 215-224. DOI: 10.20884/1.bioe.2024.6.3.11006. [Indonesian]
- POWO. 2025. Plants of the World Online. Royal Botanic Gardens, Kew. <https://powo.science.kew.org>.
- Pradeepa SD, Belavadi VV. 2017. Diversity of pollen collected by the Indian honey bee (*Apis cerana* F.). *Mysore J Agric Sci* 51 (2): 265-279.
- Rahayu AAD, Leksono B, Asmaliyah, Krisnawati, Rianawati H, Umroni A, Haryjanto L, Widyatmoko AYPBC, Putri AI, Sudomo A, Hani A, Octavia D, Andini S, Khotimah H, Mudhofir MRT, Anggadhanila L, Winarni I, Astarini IA, Artati Y, Baral H. 2025. The potential of *Arenga pinnata* (Wurmb) Merr. for enhancing soil health, food, energy, and water security in Indonesia: A comprehensive review. *Trees For People* 20: 100808. DOI: 10.1016/j.tfp.2025.100808.
- Rasyiid M, Iqbal M, Paserang AP, Budiono YK, Nugraha MAS, Wiguna T. 2025. Melissopalynological analysis of honey from Dolago Village, Central Sulawesi. *BIOLINK* 11 (2): 127-133. DOI: 10.31289/biolink.v11i2.13402.
- Ren P, Didham RK, Murphy MV, Zeng D, Si X, Ding P. 2023. Forest edges increase pollinator network robustness to extinction with declining area. *Nat Ecol Evol* 7 (3): 393-404. DOI: 10.1038/s41559-022-01973-y.
- Ritawati A, Zuhud EAM, Hidayati S. 2023. Analysis of the utilization of groundcherry (*Physalis angulata* L.) by the community around the Cibodas Resort, Gunung Gede Pangrango National Park. *J Nat Resour Environ Manag* 13 (4): 613-623. DOI: 10.29244/jpsl.13.4.613-623.
- Rompas JJI, Kiroh HJ, Kawatu MMH, Rotinsulu MD. 2023. Getting to Know Honey Bees (*Apis* species). Yayasan Bina Lentera Ihsan, Manado. [Indonesian]
- Saensouk S, Saensouk P. 2022. Pollen morphology of some species in the family Amaranthaceae from Thailand. *Biodiversitas* 23 (1): 601-611. DOI: 10.13057/biodiv/d230165.
- Salamah A, Luthfikasari R, Dwiranti A. 2018. Pollen morphology of eight tribes of Asteraceae from Universitas Indonesia Campus, Depok, Indonesia. *Biodiversitas* 20 (1): 152-159. DOI: 10.13057/biodiv/d200118.
- Sangeetha S, Saravanakumar A, Parthiban P, Kavinkumar C, Loganathan M, Heera G, Harshitha ST, Mohan SR, Pooja S, Mohan SR, Heera G. 2024. An overview of the marvelous plant: *Caesalpinia pulcherrima*. *Intl J Res Pharmacol Pharmacother* 13 (4): 714-728. DOI: 10.61096/ijrpp.v13.iss4.2024.714-728.
- Santos-Gally R. 2023. Sexual reproduction in *Tithonia diversifolia* and the implications for its use in intensive silvopastoral systems. In: Murgueitio E, Chará J, Cuartas C (eds). *Silvopastoral Systems of Meso America and Northern South America*. Springer, Cham. DOI: 10.1007/978-3-031-43063-3_15.
- Schouten C, Lloyd D, Lloyd H. 2019. Beekeeping with the Asian honey bee (*Apis cerana* javana Fabr) in the Indonesian islands of Java, Bali, Nusa Penida, and Sumbawa. *Bee World* 96 (2): 45-49. DOI: 10.1080/0005772X.2018.1564497.
- Septiadi D, Sudjatmiko DP. 2023. Prospect analysis of avocado cultivation in Pringgasela District, East Lombok Regency. *Jurnal Agrisistem: Seri Sosek dan Penyuluhan* 19 (1): 34-39. DOI: 10.52625/j-agr-sosekpenyuluhan.v19i1.264. [Indonesian]
- Shrotri S, Kaur S, Nawge V, Sandhya S, Dandavate R, Gowda V. 2024. Revisiting Aristotle's observation on bees: High floral constancy is common among bees, but it is shaped by the locally abundant flowering species. *bioRxiv* 2024: 1-648. DOI: 10.1101/2024.10.28.614270.
- Singh S, Dixit AK. 2018. Palynodiversity of some species of *Sida* from Bilaspur Region, Chhattisgarh. *Bull Pure Appl Sci Bot* 37 B (2): 112-116. 10.5958/2320-3196.2018.00015.0.
- Soeprbowati TR, Suedy SWA, Lubis AA, Miller J. 2020. Pollen and diatom evidence of seawater intrusion, east flood canal (Banjir Kanal Timur), Semarang, Indonesia. *Environ Earth Sci* 79: 462. DOI: 10.1007/s12665-020-09186-x.
- Syifa K, Haneda NF, Rachmawati E. 2023. Diversity of *Apis cerana* honey bee foraging plants in community forests based on pollen characteristics. *Jurnal Penelitian Hutan Tanaman* 20 (1): 51-62. DOI: 10.59465/jpht.v20i1.311. [Indonesian]
- Thakodee T, Deowanish S, Duangmal K. 2018. Melissopalynological analysis of stingless bee (*Tetragonula pagdeni*) honey in Eastern Thailand. *J Asia Pac Entomol* 21 (2): 620-630. 10.1016/j.aspen.2018.04.003.
- Vishnu AV, Bijoy C, Soumya R. 2024. Study on bee diversity in selected invasive plants of Manakody Kole Wetland, Thrissur District, Kerala. *Intl J Entomol Res* 9 (5): 1-3.
- Waghmare AS, Khandekar RG, Salvi BR, Pethe UB, Malshe KV. 2022. Studies on floral biology and nut set in Areca nut (*Areca catechu* L.) cvs. Shrivardhan and Mangala. *The Pharm Innov J* 11 (12): 6146-6152.
- Wang Y, Yang Y, Zhang M. 2024. The influence of climate change on the potential distribution of *Ageratum conyzoides* in China. *Ecol Evol* 14 (10): e11513. DOI: 10.1002/ece3.11513.
- Widyastuti DE, Sianturi UJ, Arinah H. 2023. Identification of types, flowering of bee plants, and honey production of *Apis cerana* in Aornakan I and Kutatinggi villages, Pakpak Bharat Regency, North Sumatra. *Glob For J* 1 (01): 60-71. DOI: 10.32734/gfj.v1i01.13255.
- Windyarini E, Hasnah TM, Adinugraha HA, Leksono B. 2020. Flowering and fruiting period of *Calophyllum inophyllum* at the provenance seed stand in Wonogiri. *Jurnal Penelitian Sosial dan Ekonomi Kehutanan* 14 (2): 111-120. DOI: 10.20886/jpth.2020.14.2.111-120. [Indonesian]
- Wondracek-Lüdke DC, Custodio AR, Simpson CE, Valls JFM. 2015. Crossability of *Arachis valida* and the B genome *Arachis* species. *Genet Mol Res* 14 (4): 17574-17586. DOI: 10.4238/2015.December.21.30.
- Wróblewska A, Stawiarz E, Masierowska M. 2016. Evaluation of selected ornamental Asteraceae as a pollen source for urban bees. *J Apic Sci* 60 (2): 179-192. DOI: 10.1515/jas-2016-0026.
- Wulandari I, Husodo T, Kusmoro J, Megantara EN, Shanida SS, Amalia CA, Azzahra HR. 2025. Seasonal foraging gaps and floral resource enhancement opportunities for *Apis cerana* in a tropical conservation forest. *Biodiversitas* 26: 4201-4219. DOI: 10.13057/biodiv/d260847.
- Yakupova A, Svetlakov A. 2025. Innovative beekeeping strategies for sustainable rural employment: Addressing socio-ecological contradictions. *E3S Web Conf* 614: 03015. DOI: 10.1051/e3sconf/202561403015.

Yolanda V, Sukarsa, Hidayah HA. 2020. Identification of pollen characteristics as *Apis cerana* feed sources in honeycomb in Serang,

Purbalingga. BioEksakta: Jurnal Ilmiah Biologi Unsoed 2 (1): 42-48. DOI: 10.20884/1.bioe.2020.2.1.1814.