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ORIGINAL ARTICLE

Environmental and landscape drivers of domesticated bee-plant interaction networks in tropical agroecosystems of Java, Indonesia

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Key words. Hymenoptera, Apidae, honeybee, stingless bee, plant interaction, pollen composition, pollination network, foraging behavior, landscape composition

Abstract. Landscape composition and environmental conditions may influence pollen resource use by domesticated bees and the structure of bee-plant interaction networks across tropical agroecosystems. This study examined pollen-based interactions of domesticated honeybees and stingless bees across five provinces on Java Island, Indonesia. We also assessed associations between landscape characteristics, environmental variables, and network metrics. Bee and pollen samples were obtained from beekeepers in Banten (17 persons), West Java (9), Central Java (18), Yogyakarta (19), and East Java (10). Landscape characteristics were quantified within a 500 m radius of each sampling site using class area (CA) and number of patches (NP) for agricultural and tree-covered areas, alongside elevation and precipitation. We identified 11 bee species, comprising two honeybee species and nine stingless bee species, that collected pollen from 37 plant families. Pollen composition varied among provinces. Heatmap patterns showed distinct regional pollen profiles among provinces, with high pollen grain counts for several plant families in Yogyakarta, particularly Caricaceae. Beta regression indicated that connectance was negatively associated with elevation and positively associated with precipitation, whereas the landscape variables included in the model were not statistically significant. Other network metrics showed distinct relationships with environmental predictors, while nestedness showed no significant overall relationship with the predictors examined. These findings highlight regional variation in pollen resource use and suggest that environmental gradients are associated with different aspects of domesticated bee-plant interaction networks.

INTRODUCTION

Bees represent one of the most functionally important and taxonomically diverse groups of pollinators, with more than 20,000 species described worldwide (Klein et al., 2007). In Indonesia, Buchori et al. (2022) documented 22 domesticated bee species, comprising 3 honeybee species and 19 stingless bee species. The ecological significance of bees is underscored by their contribution to the reproductive success of approximately 79% of flowering plant species through pollination services (Rodger et al., 2021), as well as their role in enhancing both the quantity and quality of agricultural production (Khalifa et al., 2021). Beyond their pollination function, bees also provide a range of economically and ecologically valuable ecosystem services, including the production of honey, propolis, bee pollen, royal jelly, and bee venom (Kahono et al., 2018).

However, the ecosystem services provided by bees are increasingly threatened by challenges that may reduce their populations and diversity. Winfree et al. (2009) found that human activities that degrade the environment are a primary cause of habitat loss, leading to declines in both bee abundance and diversity. Key factors contributing to bee population declines include land degradation (Richards, 2001) and the loss of flowering plant communities

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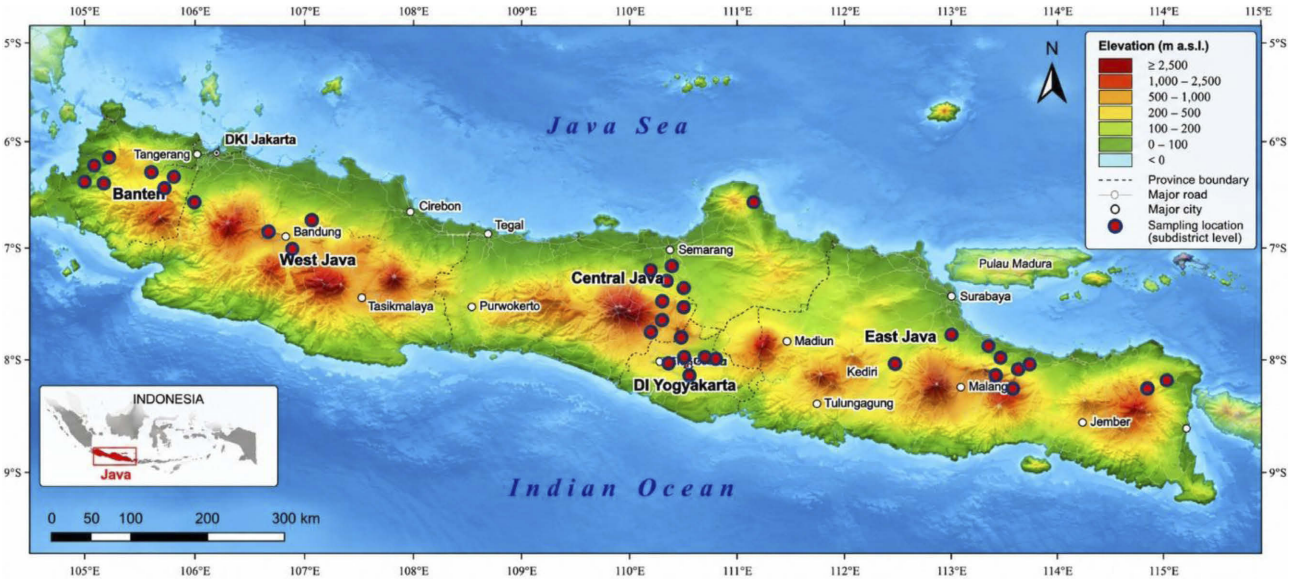


Fig. 1. Elevation and geographic distribution of domesticated bee sampling locations across Java Island, Indonesia. Each dot represents a sampling location at the subdistrict level and may represent 1–3 beekeepers within the same subdistrict.

that provide essential food resources and habitat for bees (Goulson et al., 2008; Senapathi et al., 2015). From the beekeepers' perspective in Indonesia, major constraints include bee mortality driven by climate change, limited food resources, and pesticide exposure (Buchori et al., 2022). Agricultural habitats dominated by monocultures were associated with lower forager abundance and colony weight than in forested and home garden habitats (Buchori et al., 2020). Agricultural systems that rely heavily on chemical inputs and monoculture practices can also decrease honey production in *A. mellifera* colonies (de Groot et al., 2021). Certain classes of insecticides, such as neonicotinoids and pyrethroids, have negative effects on bee health, disrupt foraging behavior, and reduce reproductive function (Mwangi, 2024). Goulson et al. (2015) found that pesticide exposure in bees can impair detoxification mechanisms and immune responses, making them more susceptible to parasites.

As a key factor shaping bee foraging behavior, landscape composition determines the availability, diversity, and spatial distribution of floral resources, thereby influencing resource selection, foraging efficiency, and ultimately the structure of bee-plant interaction networks. Raffiudin et al. (2024) provide an example involving *Apis dorsata*, showing that in heterogeneous landscapes, this species prefers more abundant forage resources compared to those in plantation-dominated monoculture landscapes in Kampar. Similarly, habitat restoration in paddy field areas of Satoyama, Japan, significantly influenced interaction networks and the complexity of bee-plant relationships (Priawandiputra et al., 2017). These studies collectively demonstrate that landscape composition is a key factor shaping the structure and dynamics of bee–plant interaction networks. According to Simla et al. (2022), land-use disturbance influences pollinator communities and the structure of the pollination network at the species level. Sritongchuay et al. (2022) also reported that landscape structure influences pollinator species richness and visitation rates. These effects can subsequently alter plant-pollinator network structure, where community-level specialization increases with higher floral species richness and greater forest cover. In contrast, specialization decreases with increasing proportions of tree plantations, indicating that natural habitats better support specialist species (Sritongchuay et al., 2022). Bees exhibited higher foraging specialization with increasing habitat heterogeneity and visited fewer flowering species (decreased generality) with increasing semi-natural habitat cover (Pardee et al., 2023).

This study aimed to elucidate plant–pollinator interactions involving domesticated bees using pollen-based evidence. Specifically, the objectives were to (1) characterize domesticated bee foraging behavior and its association with interaction network structure, (2) assess the relationship between landscape composition, environmental characterization, and domesticated bee foraging patterns, and (3) evaluate the effects of landscape composition and environmental characteristics on the connectivity and stability of pollination networks.

MATERIAL AND METHODS

Domesticated bees and pollen collections

Bee and pollen samples were collected from domesticated colonies maintained by beekeepers across four provinces on Java Island, namely Banten (17 beekeepers), West Java (9 beekeepers), Central Java (18 beekeepers), East Java (10 beekeepers), and Yogyakarta (19 beekeepers). The study followed the beekeeper selection protocol described by Buchori et al. (2020). The spatial distribution of beekeepers across Java Island, Indonesia, is presented in Fig. 1. Each beekeeper kept at least two bee species. The distribution of beekeepers keeping different bee species is shown in Fig. 2.

Information on the number of domesticated bee colonies maintained by beekeepers was also obtained through interviews. These data were based on colony numbers reported by respondents, with some values representing estimates rather than exact counts. The

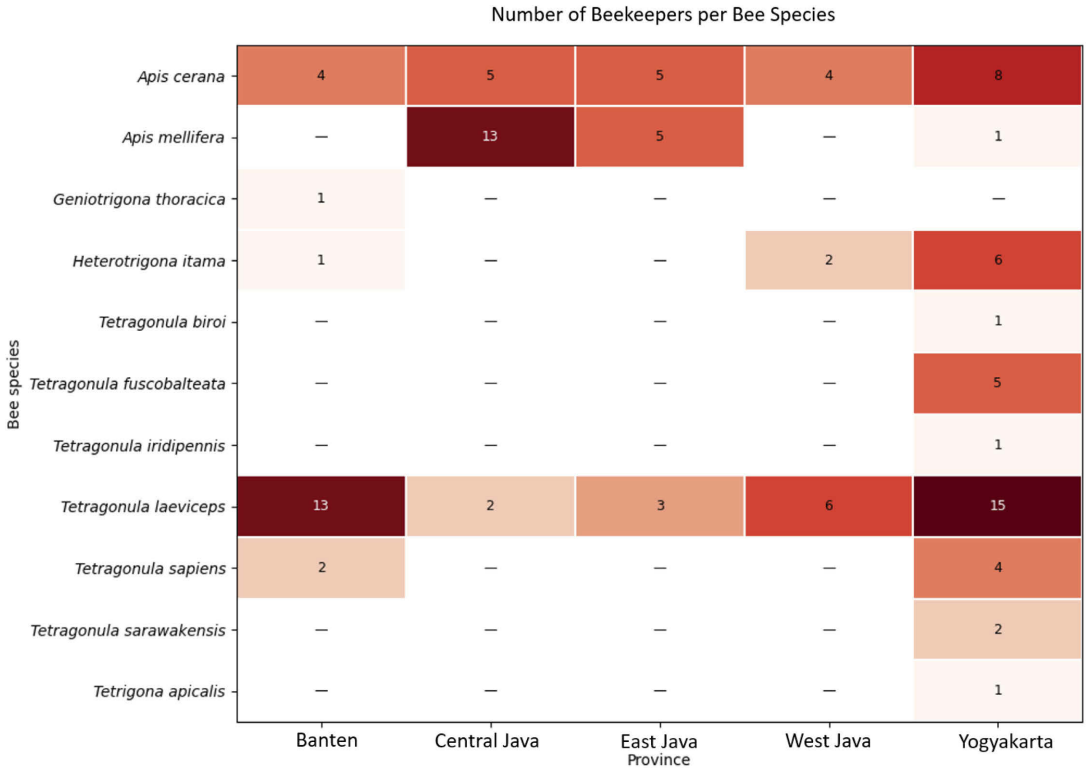


Fig. 2. Number of beekeepers keeping each domesticated bee species across five provinces in Java, Indonesia. Counts are species-specific, and individual beekeepers may be represented in multiple species categories when they keep more than one species. Dashes indicate blank entries in the compiled dataset and should not be interpreted as confirmed zeros.

reported colony numbers were not independently verified by the research team through direct colony counts because the colonies were distributed across a large study area. Therefore, these data were used descriptively to characterize beekeeping activity and the distribution of domesticated bee colonies across provinces, rather than as verified estimates of colony abundance (see Fig. S1).

For each domesticated bee species, five hive boxes were selected as sampling units. Five pollen-laden foragers were collected from each hive as they returned to the colony. Sampling was conducted between 09:00 and 13:00 to coincide with peak foraging activity. Each collected bee was placed in a sterile microtube containing 70% ethanol to preserve the pollen it carried and minimize cross-contamination during subsequent pollen analysis.

Pollen preservation and identification

The pollen analyzed in this study was derived from domesticated bee samples collected from each colony. The analysis included samples from Banten, West Java, Central Java, Yogyakarta and East Java. Pollen samples collected by bees were acetolyzed following the method described by Erdtman (1952). Pollen grains were identified based on polar and equatorial axis morphology and aperture characteristics, following Huang (1972), the Australian Pollen and Spore Atlas (APSA; apsa.anu.edu.au), and the Global Pollen Project (globalpollenproject.org). Data obtained from pollen identification and counting were tabulated in Microsoft Excel for further processing and analysis.

Interaction network and pollen composition analysis

Bee-plant interactions were quantified by integrating pollen data across all sampling locations. A quantitative interaction matrix representing associations between domesticated bee species and plant taxa was constructed and analyzed using the bipartite package in R (Dormann et al., 2008; R Core Team, 2024). Network structure was evaluated and compared among locations using quantitative metrics, including connectance, nestedness, interaction strength asymmetry, and interaction evenness (Blüthgen et al., 2007; Dormann et al., 2009). We also conducted the same analysis at the *family level* using the RStudio package *bipartite.* We focused on three indices at the species level: normalized degree, Paired Difference Index (PDI), and effective partners, to identify the pollen most frequently collected by domesticated bees and to determine whether these pollen sources function as primary or supplementary resources. See Table S1 for details of indices.

To assess variation in pollen composition among the five provinces of Java, non-metric multidimensional scaling (NMDS) ordination was performed using Bray-Curtis dissimilarity (Bray & Curtis, 1957). The ordination was conducted using the *metaMDS* function in the *vegan* package in R (Oksanen et al., 2024). NMDS was used to visualize similarities and dissimilarities in pollen assemblages among provinces. Differences in pollen composition among provinces were statistically evaluated using analysis of similarities (ANOSIM), with 999 permutations (Clarke, 1993). Homogeneity of multivariate dispersion was assessed using *PERMDISP*, implemented through the betadisper function, followed by a permutation test with 999 permutations. Where significant differences in dispersion were detected, Tukey's honestly significant difference (HSD) test was used for pairwise comparisons among provinces (Anderson, 2006). A heatmap was also generated to visualize pollen interaction frequencies and identify dominant pollen types collected by domesticated bees across Java Island.

Characterization of landscape composition and environmental conditions

This study evaluated how landscape composition relates to the interaction networks of domesticated bee species. Landscape

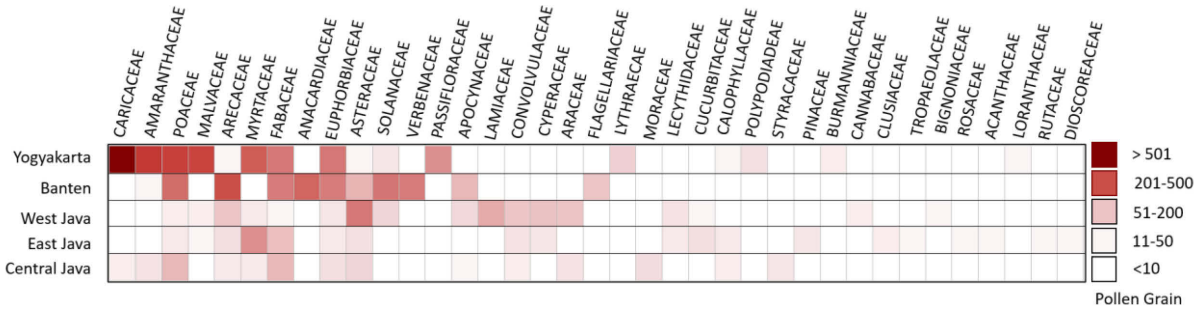


Fig. 3. Heatmap of distribution and abundance of pollen grains from different plant families across five provinces on Java Island, Indonesia. Color intensity represents the number of pollen grains recorded for each plant family in each province. Darker red shades indicate higher pollen counts, whereas white cells indicate low or no recorded counts.

structure was characterized and quantified using QGIS (version 3.34.2). For each sampling location, we delineated a circular buffer with a 500 m radius to characterize the local landscape context that may influence bee foraging and plant-bee interactions. This spatial scale was used to assess landscape composition in the immediate surroundings of the apiaries, where beekeepers also maintained diverse vegetation that could provide locally available floral resources. We acknowledge that *Apis mellifera* and *Apis cerana* can forage over distances exceeding 500 m, depending on resource availability and landscape conditions (Beekman & Ratnieks, 2000; Fox et al., 2022). Thus, the selected buffer represents the local landscape context rather than the full foraging range of these species, and landscape features beyond its boundary may also influence bee foraging activities and plant-bee interactions.

In this study, landscape complexity was operationalized through two dimensions: landscape composition, represented by class area (CA) and proportional land-cover area, and spatial configuration, represented by the number of patches (NP). We quantified these metrics for two main land-cover categories: trees (as a proxy for forested areas) and crops (as a proxy for agricultural areas) (Table S2). Within each buffer, we also calculated the proportional cover of agricultural land and tree vegetation to characterize the relative availability of these habitats. These metrics were used to examine how habitat availability and spatial configuration relate to bee interaction networks. We additionally included elevation and precipitation as environmental variables that may influence floral resource distribution and bee foraging behavior. Precipitation data for the study period were obtained from observation stations of the Meteorology, Climatology, and Geophysics Agency (BMKG) nearest to the study locations.

The relationships between landscape composition and network metrics were examined using regression models appropriate to the distributional properties of each response variable. Generalized linear models (GLMs) with a quasi-Poisson error distribution were used for count-based network metrics when overdispersion was present (Hastie & Pregibon, 2017). The quasi-Poisson approach accounts for overdispersion by adjusting the variance structure, thereby improving the estimation of standard errors and statistical inference. Connectance, which is expressed as a proportion bounded between 0 and 1, was analyzed separately using beta regression with a logit link function. This model was selected to account for the bounded nature of connectance and to assess its associations with landscape composition and environmental variables. The remaining network metrics were analyzed using their respective regression models, and model coefficients and associated significance levels were used to evaluate relationships between both landscape and environmental predictors and network structure.

RESULTS

Domesticated bee species composition across five provinces of Java

The number of beekeepers keeping domesticated bee species varied across the five provinces (Fig. 2). *Tetragonula laeviceps* was the most widely represented species, with beekeepers recorded in all five provinces, ranging from 2 beekeepers in Central Java to 15 in Yogyakarta. *Apis cerana* was also reported across all provinces, with the highest number of beekeepers in Yogyakarta (8), followed by Central and East Java (5 each). In contrast, *Apis mellifera* was primarily kept in Central Java (13 beekeepers) and East Java (5), with only one beekeeper recorded in Yogyakarta.

Other stingless bee species were reported by fewer beekeepers and showed more geographically restricted distributions. In Yogyakarta, these included *Heterotrigona itama* (6 beekeepers), *Tetragonula fuscobalteata* (5), and *Tetragonula sapiens* (4). *Geniotrigona thoracica* was reported only in Banten, whereas *Tetragonula biroi*, *T. iridipennis*, *T. sarawakensis*, and *Tetrigona apicalis* were recorded only in Yogyakarta. The reported number of colonies showed a partly different pattern from the distribution of beekeepers (Fig. S1). *Apis mellifera* had the highest colony count in Central Java (3,650 colonies), reported by 13 beekeepers, whereas *T. laeviceps* showed comparatively high reported colony numbers across all five provinces, ranging from 117 in West Java to 759 in Banten. *Apis cerana* also had a high reported colony count in Central Java (1,115 colonies). These patterns suggest that the number of beekeepers keeping a species did not necessarily correspond directly to the reported number of colonies. However, colony numbers were obtained through beekeeper interviews and were not independently verified by the research team; some values were estimates provided by respondents. Therefore, these figures should be interpreted as descriptive information on reported beekeeping activity rather than verified estimates of colony abundance.

Pollen composition across provinces in Java Island

The distribution and abundance of pollen grains from different plant families carried by domesticated bees varied among the five provinces of Java Island, Indonesia (Fig. 3). Yogyakarta showed relatively high pollen counts across several plant families, particularly Caricaceae, Amaran-

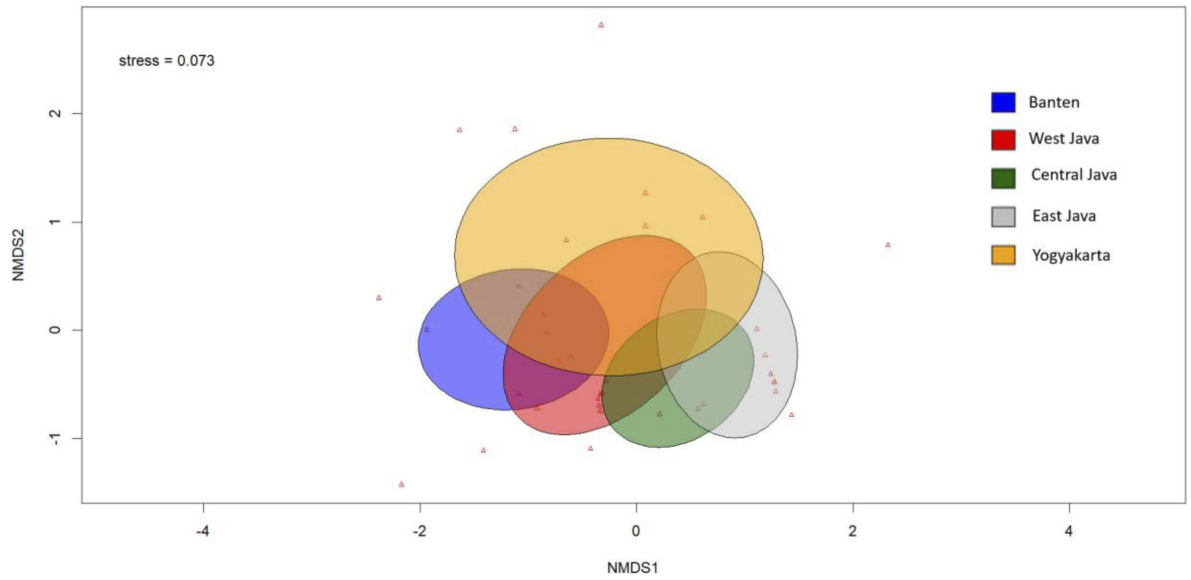


Fig. 4. Non-metric multidimensional scaling (NMDS) ordination based on Bray-Curtis dissimilarity, illustrating variation in pollen composition collected by domesticated bees across five provinces in Java, Indonesia. Points represent individual pollen samples, and colored ellipses indicate the distribution of samples within each province. The stress value (0.073) indicates a good representation of the dissimilarity structure in two dimensions.

thaceae, Poaceae, Malvaceae, and Fabaceae. Caricaceae exhibited the highest pollen count in this province, with more than 500 pollen grains. This pattern suggests that these plant families contributed substantially to the pollen collected by domesticated bees in Yogyakarta.

In Banten, relatively high pollen counts were recorded for several families, including Poaceae, Arecaceae, Anacardiaceae, Euphorbiaceae, Asteraceae, Solanaceae, and Verbenaceae. The relatively high representation of Arecaceae in Banten may be associated with the availability of coconut (*Cocos nucifera*) and other palm species in coastal and lowland landscapes, including home gardens, cultivated areas, and urban green spaces. However, this potential association requires further confirmation using local vegetation data. West Java exhibited a distinct pollen distribution among plant families, with relatively high counts in Asteraceae and detectable pollen from families such as Apocynaceae, Lamiaceae, and Convolvulaceae. In East Java and Central Java, pollen counts were generally lower across most families, although some families, including Myrtaceae and Fabaceae, showed comparatively higher counts. Arecaceae pollen was also detected beyond Banten, indicating that pollen from this family was not restricted to a single province.

Non-metric multidimensional scaling (NMDS) ordination based on Bray-Curtis dissimilarity revealed substantial overlap in pollen composition among the five provinces of Java (Fig. 4). Nevertheless, differences in the relative positions of the provincial centroids indicated geographic variation in pollen composition. The stress value of 0.073 indicated that the dissimilarity structure was well represented in two dimensions. ANOSIM detected significant differences in pollen composition among provinces ($R = 0.1859$, $p = 0.001$). This pattern suggests that some plant families represented in the pollen collected by bees occurred across multiple provinces, although overall pollen composition still exhibited geographic variation.

Multivariate dispersion also differed significantly among provinces (PERMDISP: $F_{4,73} = 4.7913$, $p = 0.002$). Yogyakarta exhibited the highest mean distance to its centroid (0.666), whereas Central Java had the lowest (0.469). Tukey's HSD test revealed a significant difference in dispersion between these two provinces (adjusted $p = 0.000486$). These findings indicate that pollen composition heterogeneity among bee samples varied geographically. The observed patterns may be associated with differences in the availability and distribution of flowering plants across provinces, although these mechanisms cannot be established from pollen composition data alone.

Provincial differences in pollen composition occurred alongside variation in the structural properties of bee-plant interaction networks (Table 1). Connectance was highest in Central Java (0.55) and Banten (0.54), whereas Yogyakarta exhibited the lowest value (0.22). Nestedness was highest in East Java (46.16) and Central Java (45.13), while specialization asymmetry was highest in Central Java (0.475) and West Java (0.41). These differences suggest that the interaction networks varied in their structural organization

Table 1. Domesticated bee-plant interaction network metrics across Java and its provinces.

Interaction matrics	Java Island	Banten	West Java	Central Java	East Java	Yogyakarta
Domesticated bee species	11	5	3	3	3	10
Plant families	37	11	17	15	19	16
Connectance	0.27	0.54	0.43	0.55	0.40	0.22
Nestedness	16.5	21.94	40.41	45.13	46.16	28.7
Interaction strength asymmetry	–0.27	–0.17	–0.54	–0.4	–0.56	–0.17
Specialisation asymmetry	0.1	0.22	0.41	0.475	0.37	0.15

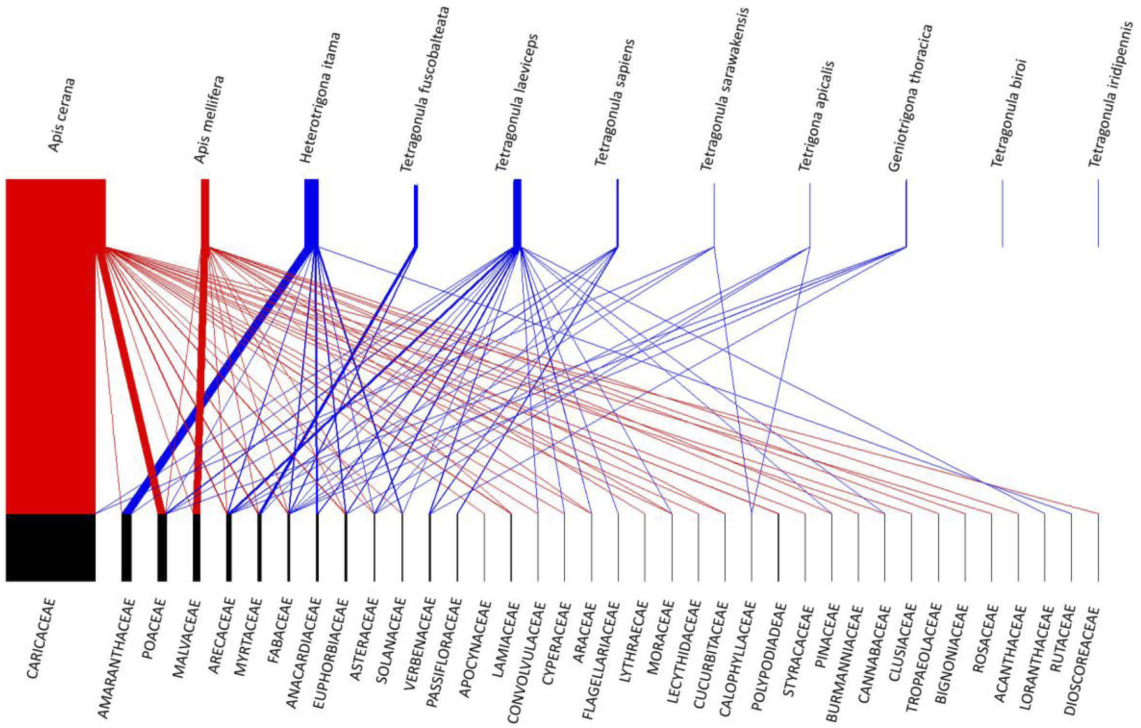


Fig. 5. Pollen interaction network illustrating the plant families represented in pollen collected by different domesticated bee species across Java, Indonesia. The width of the bars and connecting lines represents interaction frequency or pollen abundance, according to the original visualization settings. Different colors distinguish bee groups or interaction categories.

across provinces, despite the substantial overlap observed in the NMDS ordination. However, the network metrics describe interaction structure rather than pollen compositional dissimilarity itself, and their potential relationships with the observed ordination patterns require further statistical testing.

Domesticated bee-plant interactions across provinces in Java Island

The interaction network analysis revealed variation in the composition of pollen resources collected by different bee species across Java Island. At the island scale (Fig. 5), *Apis cerana* collected the highest proportion of pollen from the family Caricaceae, which was identified in the laboratory as originating from *Carica papaya*. In contrast, *Apis mellifera* predominantly collected pollen from the family Malvaceae. Pollen identification from individual worker bees showed that each examined *A. cerana* and *A. mellifera* worker carried only one pollen type, a finding consistent with the concept of floral constancy, whereby bees tend to visit flowers of the same plant species during a foraging bout.

Pollen collection patterns among stingless bees differed from those observed in honeybees. Individual stingless bee workers were found to carry multiple pollen types, suggesting that they may collect pollen from different plant taxa within a single foraging trip. *Heterotrigona itama* collected pollen from several plant families, whereas *Tetragonula fuscobalteata* was recorded collecting pollen from Myrtaceae and Fabaceae. In contrast, the pollen identified from *Tetragonula laeviceps* in a particular dataset belonged exclusively to Euphorbiaceae, while *Tetragonula sapiens* was recorded carrying pollen only from Passifloraceae. No pollen was identified in the samples of *Tetragonula iridipennis* and *Tetragonula biroi*.

At the provincial scale, pollen collection patterns varied geographically. In Banten, *A. cerana* collected the highest proportion of pollen from Arecaceae, whereas *H. itama* collected pollen from several families, including Anacardiaceae, Solanaceae, Euphorbiaceae, Fabaceae, Arecaceae, and Poaceae. A similarly diverse pollen collection pattern was observed in *T. laeviceps*, which carried pollen from Arecaceae, Anacardiaceae, Poaceae, Fabaceae, and Solanaceae. In Central Java, *A. cerana* and *A. mellifera* collected pollen from several plant families, including Poaceae, Fabaceae, Asteraceae, and Cucurbitaceae, whereas *T. laeviceps* collected pollen from Caricaceae and Convolvulaceae. In West Java, *A. cerana* collected the highest proportion of pollen from Apocynaceae, while *T. laeviceps* predominantly collected pollen from Asteraceae. In East Java, *A. cerana* collected pollen primarily from Myrtaceae and Fabaceae, whereas no clear dominance of a particular pollen family was observed for *A. mellifera* or *T. laeviceps*.

The interaction network across Java Island comprised 11 domesticated bee species and 37 plant families, with a connectance of 0.27, nestedness of 16.50, interaction strength asymmetry of −0.27, and specialization asymmetry of 0.10 (Table 1). These metrics provide an overview of the structure of bee-plant interactions at the island scale. Regional comparisons revealed considerable variation in network structure. Central Java had the highest connectance (0.55) and specialization asymmetry (0.475), whereas Yogyakarta had the lowest connectance (0.22), despite recording 10 domesticated bee species. East Java exhibited the

highest nestedness (46.16) and the strongest interaction strength asymmetry (−0.56), while Banten had the lowest nestedness (21.94). These patterns indicate that regional differences in bee-plant interaction networks are not determined solely by the number of interacting species or plant families, but also by the distribution and organization of interactions. The contrasting values of connectance, nestedness, and asymmetry highlight the structural variability of these networks across Java, although further interpretation should account for the specific definitions of these metrics and the completeness of regional sampling.

Landscape effects on domesticated bee-plant interaction networks

The regression analyses revealed metric-specific associations between both landscape composition and environmental variables, and domesticated bee-plant interaction networks (Table 2). For connectance, beta regression with a logit link showed a significant negative association with elevation (\beta = –0.00114, p < 0.001) and a significant positive association with precipitation (\beta = 0.00160, $p < 0.001$). The other landscape predictors, including tree-cover area, cropland area, and the number of patches in both habitat categories, were not significantly associated with connectance ($p > 0.05$). These findings indicate that environmental conditions were more strongly associated with network connectance than the individual landscape-composition metrics included in the model.

For nestedness, the overall multiple linear regression model was not significant (R^2 = 0.426, adjusted R^2 = 0.197, p = 0.155), although elevation showed a marginal positive association (\beta = 5.070, $p = 0.086$). Interaction strength asymmetry was negatively associated with elevation ((\beta = –0.110), $p = 0.003$; (R^2 = 0.750), adjusted (R^2 = 0.650), $p < 0.001$), while cropland area ((\beta = 0.081), $p = 0.078$) and cropland patch number ((\beta = –0.050), $p = 0.078$) showed marginal trends. Specialization asymmetry was positively associated with precipitation (\beta= 0.102), p = 0.002; (R^2 = 0.698), adjusted (R^2 = 0.577), p = 0.003, whereas the other predictors were not significant.

Table 2. Generalized Linear Model (GLM) analysis of domesticated bee-plant interaction network metrics in relation to landscape and environmental variables.

		Estimate	Std.Error	t-value	Pr(>|t|)
Connectance	(Intercept)	–1.317	0.1867	–7.055	1.72E-12
	CA.trees	0.0026	0.0019	1.328	0.184
	CA.crops	–0.0042	0.0080	–0.528	0.597
	NP.trees	–0.0096	0.0090	–1.062	0.288
	NP.crops	0.00046	0.0020	0.227	0.82
	Elevation	–0.0011	0.0001	–11.238	< 2e-16
	Precipitation	0.0015	0.0001	14.586	< 2e-16
Nestedness	(Intercept)	37.475	1.87	20.039	3.07E-12
	CA.trees	–2.755	2.77	–0.995	0.3357
	CA.crops	–2.654	3.828	–0.693	0.4987
	NP.trees	1.544	3.166	0.488	0.6327
	NP.crops	1.327	2.371	0.56	0.5838
	Elevation	5.07	2.76	1.837	0.0861
	Precipitation	1.544	2.851	0.542	0.596
Interaction strength assymmetry	(Intercept)	–0.366	0.0207	–17.637	1.93E-11
	CA.trees	–0.002	0.0307	–0.067	0.94756
	CA.crops	0.0805	0.0424	1.895	0.07758
	NP.trees	–0.047	0.0351	–1.357	0.19473
	NP.crops	–0.049	0.0263	–1.892	0.07802
	Elevation	–0.109	0.0306	–3.589	0.00269
	Precipitation	–0.0068	0.0316	–0.215	0.83258
Specialization asymmetry	(Intercept)	0.3435	0.0179	19.156	5.89E-12
	CA.trees	–0.030	0.0265	–1.155	0.26604
	CA.crops	–0.010	0.0367	–0.29	0.77591
	NP.trees	0.0041	0.0303	0.137	0.89259
	NP.crops	0.004	0.0227	0.179	0.8603
	Elevation	0.013	0.0264	0.517	0.61274
	Precipitation	0.1017	0.0273	3.721	0.00205

DISCUSSION

Our study identified two domesticated honeybee species and nine domesticated stingless bee (Meliponini) species on Java Island. This indicates that beekeepers have varying preferences for different bee species. Our interviews and bee samples collected showed that a single beekeeper may manage more than one bee species. Beekeepers who began with a small number of hives (fewer than 20 or 20–50 hives) tended to substantially expand their colonies to scale up their operations, whereas those who started with larger numbers (51–150 hives or more than 150 hives) generally did not increase their hive numbers (Buchori et al., 2022). Beekeepers acquire bees from multiple sources, including purchasing them from marketplaces, domesticating colonies from wild forest populations, and exchanging them with, or receiving them from, fellow beekeepers. Some beekeepers reported purchasing several bee species from outside Java Island, including *G. thoracica, T. sarawakensis*, and *T. fuscobalteata.* Salatnaya et al. (2023) reported that *G. thoracica and T. fuscobalteata* are endemic to Sumatra and Kalimantan, whereas *T. sarawakensis* is endemic to Sulawesi. Inter-island colony transfers may influence the foraging behavior of these bees, as they must adapt to new environmental conditions and plant communities. Free et al. (1960) demonstrated that relocating *Apis mellifera* colonies from areas with flowering plants to areas where plants had not yet flowered can reduce their foraging activity. In addition, the proportion of foraging bees visiting plants increases when colony transfer is delayed until after flowering has begun. Windra et al. (2025) also emphasized that relocating colonies of *Tetragonula laeviceps* is more effective when conducted during the flowering season, as it facilitates better habituation to local floral resources.

Our study found that pollen from the family Caricaceae accounted for the largest proportion of pollen collected by *Apis cerana*. This pattern may be explained by the timing of pollen sampling, which coincided with the flowering season of papaya (*Carica papaya*) around the bee colonies. Similarly, Priawandiputra et al. (2025) found that *Carica papaya* pollen was the most abundant pollen type collected by *Tetragonula laeviceps* at one of their study sites, potentially because the papaya flowering season coincided with the sampling period. Pollen composition in this study was also influenced by bee foraging behavior. Foraging behavior in honeybees (*Apis cerana* and *A. mellifera*) often shows floral constancy, with individual foragers typically focusing on a single plant species during a for-

aging trip. Flower constancy is an adaptive behavior that allows bees to minimize unnecessary energy expenditure when switching between plant species (Grüter & Ratnieks, 2011). Roubik (1980) reported that Africanized honeybees exhibit superior competitive ability at high-reward floral resources due to efficient recruitment, large colony size, and flexible foraging behavior, whereas stingless bees rely more on resource partitioning and avoidance strategies to coexist. This behavior is influenced by several floral cues, including scent or chemical signals, as well as flower color and morphology (Grüter & Ratnieks, 2011).

According to Heard (1994), stingless bees primarily collected pollen, resulting in frequent and close contact with the stigma, whereas honeybees mainly foraged for nectar and made less frequent contact with the stigma. Stingless bees also predominantly collect pollen from wild plant families such as Arecaceae, Asteraceae, Anacardiaceae, and Poaceae. Flowers belonging to Myrtaceae, Arecaceae, Asteraceae, Malvaceae, and Fabaceae (subfamily Mimosoideae) are characterized by open corollas with abundant stamens and longitudinally opening anthers (Torres & Galetto, 2002), which enhance accessibility to pollen and nectar for bees. In addition, stingless bees can obtain floral resources by perforating the corolla, a behavior known as "nectar robbing" (Barrows, 1976). These findings are consistent with those of Ramadani et al. (2021), who reported that Asteraceae pollen was the dominant taxon collected by both *Lepidotrigona terminata* and *Sundatrigona moorei* in Sumatra.

The interaction network metrics revealed contrasting patterns in bee-plant interactions across Java Island. Central Java exhibited the highest connectance (0.55) and the highest specialization asymmetry (0.475), whereas Yogyakarta showed the lowest connectance (0.22) and the lowest specialization asymmetry (0.15). However, neither metric alone captures generalist foraging behavior at the individual-bee level (Blüthgen et al., 2007). From a behavioral perspective, networks with higher connectance may be consistent with broader resource use at the community level, whereas lower connectance may reflect a more limited set of realized interactions. In Yogyakarta, the combination of low connectance and high dispersion in pollen composition among samples suggests that resource use varied across sampling units, potentially reflecting spatial differences in floral resource availability or foraging choices. Such variation may arise from differences among colonies or locations rather than greater foraging flexibility by individual bees. Pollen use can vary with resource availability, seasonal conditions, and pollen-source preferences (Ghosh et al., 2023), while flexible foraging can shape the structure of plant-pollinator interaction networks (Spiesman & Gratton, 2016). Nevertheless, these interpretations should be treated as hypotheses because network-level metrics and pollen composition data do not directly measure individual foraging behavior.

Landscape composition and environmental conditions may also be associated with the structure of domesticated bee-plant interaction networks, although their relationships may differ among network metrics. Land-use change can reduce species richness and disrupt mutualistic interactions between plants and pollinators (Weiner et al., 2014). In our study, elevation and precipitation emerged as important environmental correlates of network structure. Higher elevations were associated with lower connectance, whereas greater precipitation was associated with higher connectance. Elevation was also associated with lower asymmetry in interaction strength, while precipitation was associated with greater asymmetry in specialization. Increasing elevation may alter the availability and distribution of floral resources, potentially increasing dietary overlap among bee species. However, greater dietary overlap does not necessarily indicate stronger competition, as competition also depends on resource availability and the intensity of resource use (Barthel & Resasco, 2025). These contrasting patterns suggest that environmental gradients may relate differently to network connectivity and the distribution of interactions among bee and plant taxa. Lawson & Rands (2019) reported that changes in rainfall patterns could alter the timing of phenological phases and increase the likelihood of pollen degradation and nectar dilution, each of which has detrimental effects on the fitness of plants, pollinators, or both. Higher temperatures may decrease flower visitation time while increasing flower visitation rate and flight speed in the bumblebee Bombus terrestris (Gerard et al., 2024).

By contrast, nestedness did not show a statistically significant relationship with the predictors considered, indicating that this network property may respond differently to environmental and landscape variation. Previous studies provide additional context for these patterns. Pardee et al. (2023) reported that landscape heterogeneity can promote greater specialization within ecological networks, potentially because such heterogeneity alters resource distributions and species interactions. Blüthgen (2010) likewise discussed how ecological context and resource availability can shape specialization patterns. Redhead et al. (2018) found that generalist pollinators were more abundant in agriculturally dominated landscapes, suggesting that simplified agricultural environments may support distinct pollinator community structures. Raffiudin et al. (2024) reported that *Apis dorsata* tends to utilize richer and more abundant floral resources in heterogeneous landscapes, whereas its foraging is more constrained in plantation-dominated monoculture areas such as those in Kampar. Bogo et al. (2025) reported that landscape heterogeneity enhances pollen diversity and the nutritional quality of honeybee diets, whereas simplified agroecosystems limit resource availability, potentially constraining colony health and forcing bees to expand their foraging range. Land use and landscape heterogeneity influence the composition and nutritional value of pollen collected by *Apis mellifera* (da Silva et al., 2024).

Our findings suggest that environmental conditions, namely elevation and precipitation, are associated with distinct dimensions of domesticated bee-plant interaction networks. Such relationships are ecologically plausible

because elevational gradients can influence temperature regimes, species distributions, and the availability of flowering resources, thereby altering the structure of plant-pollinator interactions (Adedoja et al., 2018; Dzekashu et al., 2023). However, the responses of network metrics to environmental gradients are not necessarily uniform. Dzekashu et al. (2023) found that floral resource diversity and bee diversity were important predictors of several network properties along an elevational gradient, highlighting the potential role of community composition and resource availability in mediating network responses. Similarly, Trøjelsgaard & Olesen (2013) demonstrated that precipitation was associated with variation in pollination network topology at broad spatial scales. In this context, the negative association between elevation and connectance, and the positive association between precipitation and connectance observed in our study, may reflect differences in the availability of potential interaction partners and in the environmental conditions under which interactions occur. Nevertheless, these relationships should be interpreted as associations rather than direct evidence of causal mechanisms.

CONCLUSION

The domesticated bee assemblage across five provinces in Java comprised 11 species, with *Apis cerana* being the most prevalent. Pollen analysis revealed regional variation in floral resource use, with Yogyakarta showing particularly high pollen grain counts in several plant families, especially Caricaceae, while the pollen profiles of other provinces were more variable. These patterns indicate spatial differences in the floral resources collected by domesticated bees. Network analyses further showed that environmental variables, particularly elevation and precipitation, were significantly associated with network structure. Elevation was negatively associated with connectance, whereas precipitation showed a positive association; other network metrics exhibited distinct relationships with these environmental gradients. These findings suggest that local environmental conditions may be important correlates of bee-plant interactions. From an applied perspective, considering regional floral resource availability and environmental conditions may help inform bee-farming management, including the selection and enrichment of forage plants. Future studies should evaluate whether targeted floral enrichment can improve resource availability and colony performance across different landscape and environmental settings.

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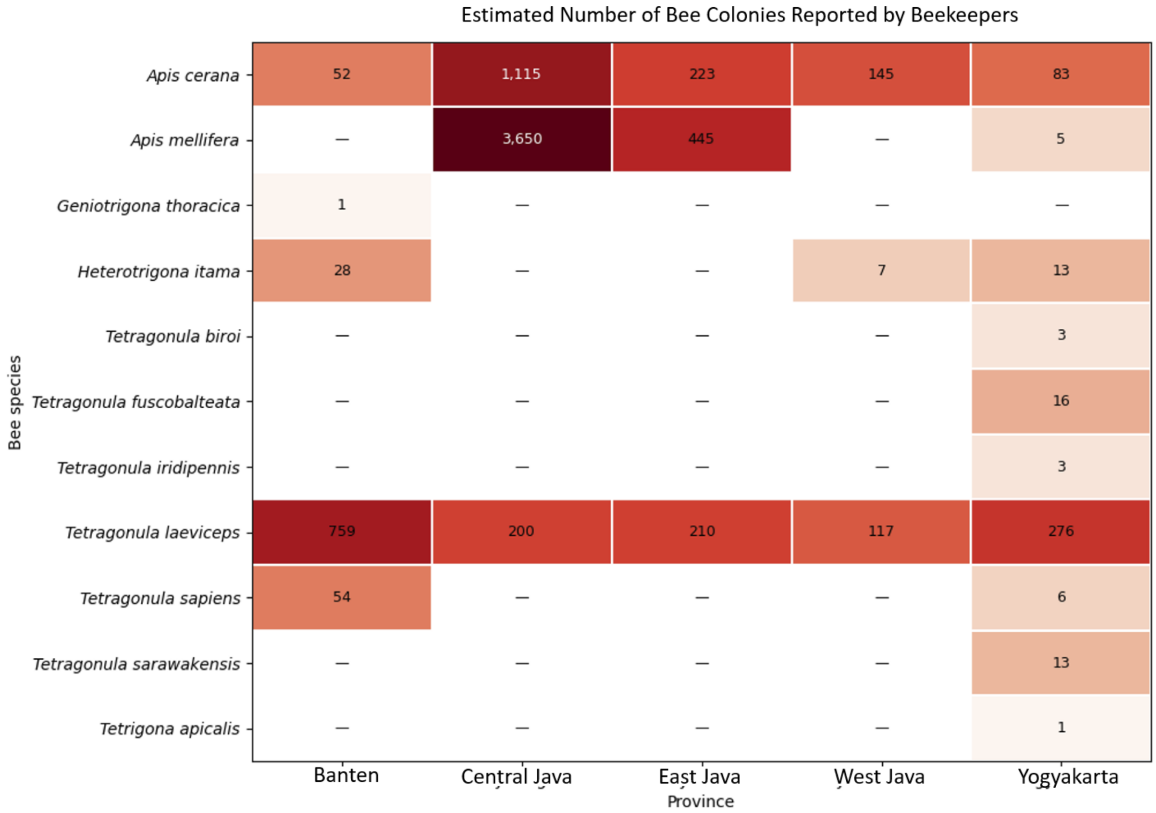


Fig. S1. Beekeeper-reported numbers of domesticated bee colonies across five provinces in Java, Indonesia.

Table S1. Network and species level indices used for bipartite analysis of plant-bee interactions from Dormann et al. (2009) (34,65) and Blüthgen (2010) (35).

Network level indices	Definition	Value range	Value scale
Connectance (C)	Proportion of all possible interactions within a network that are achieved	0–1	Low (<0.2), Medium (0.2–0.5), High (>0.5)
Nestedness	Specialist species to interact with subsets of the partners of more generalist species	0–100	Low (<20), Medium (20–50), High (>50)
Specialization asymmetry	A metric that reflects the difference in specialization levels between two groups in a bipartite network	–1–1	Negative (<0), Neutral (≈0), Positive (>0)
Interaction strength asymmetry	A metric that quantifies the imbalance in interaction strength between two trophic groups in a bipartite network, indicating which group is more dependent on the other		Negative (<0, stronger dependence of pollinators on plants), Neutral (≈0, balanced interaction), Positive (>0, stronger dependence of plants on pollinators)
Normalised degree	Proportion of realized interactions of a species relative to all possible interactions available in the network, indicating the relative generalization level		Low (<0.3), Medium (0.3–0.7), High (>0.7)
PDI (Paired Difference Index)	Measure of interaction specialization based on the unevenness of interaction distribution across partners	0–1	Low (<0.3), Medium (0.3–0.7), High (>0.7)
Effective Partners	Number of interaction partners weighted by interaction strength, representing functionally important partners in the network	1–N	Low (<25% of potential partners), Medium (25–75%), High (>75%)

Table S2. Landscape composition across four provinces in Java Island.

Province	Elevation (m a.s.l.)	Precipitation (mm/year)	No. patch of trees	No. patch of crops	Class area of trees (ha)	Class area of crops (ha)
Banten	80.2	949.22	4	22	65.93	5.47
Banten	41.4	949.22	7	9	62.88	7.47
Banten	120.7	949.22	5	14	68.66	1.90
Banten	80.3	949.22	2	18	61.04	9.36
West Java	1337.7	1587.3	4	18	73.33	2.34
West Java	1351.3	1587.3	2	10	78.61	0.35
West Java	1331.2	1587.3	5	11	75.67	1.41
Central Java	421.2	1202.35	2	0	79.37	0
Central Java	406.2	1202.35	3	32	61.03	7.90
Central Java	545.9	1202.35	2	4	70.79	5.74
Central Java	248	1202.35	10	13	25.01	2.12
Central Java	407.5	1202.35	0	53	0	3.11
Central Java	244.5	1202.35	24	32	26.45	25.08
Central Java	641.8	1202.35	3	10	66.29	8.77
East Java	758.2	933.4	2	0	68.47	0
East Java	568	933.4	3	19	71.98	0.31
East Java	856.5	822.66	1	11	78.98	0.19
East Java	408.5	822.66	9	79	49.56	9.69
Yogyakarta	87.2	239.025	7	28	30.7	18
Yogyakarta	250	208.0833	12	22	48	15
Yogyakarta	140	237.6083	11.6	25	43.3	16.6
Yogyakarta	147.6	276.2417	9	26.6	39.3	19.3