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INSECT POLLINATORS OF COCOA (*Theobroma cacao* L.) IN JATIMULYO, YOGYAKARTA, INDONESIA

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ABSTRACT

Cocoa (Theobroma cacao L.) is an important commercial crop species worldwide. Despite its global significance, the ecology and pollination services of cocoa flowers have received limited attention. Numerous studies have identified Ceratopogonidae flies as the primary pollinators of cocoa, yet the role of other insect species remains insufficiently explored. A comprehensive understanding of cocoa's pollination system is essential to maximize pollination and optimize yield. This study aimed to determine potential insect pollinators associated with cocoa flowers and to investigate the role of stingless bees in cocoa flower pollination. Sampling was conducted at three locations in Jatimulyo, Kulon Progo District, Yogyakarta Province, situated 0 m, 250 m, and 500 m from a meliponary to capture potential variation in pollinator activity. Insects were collected using sweep nets and aspirators, and pollination effectiveness was evaluated based on flower-visiting behavior, pollen load, and pollination dependence. To assess pollination contribution, nine cocoa trees were subjected to two treatments: one group of flower buds was bagged (exclusion treatment) and another group remained open to allow insect visitation (open treatment). The results identified four insect species as potential pollinators, namely Forcipomyia parvula (43% cocoa pollen load), Tetragonula laeviceps (62%), Dasyhelea sylvatica (25%), and Dasyhelea pseudoincisurata (28%). Among them, Tetragonula laeviceps exhibited consistent flower visitation, with the highest rate occurring between 07:00-08:00 and the longest average duration observed between 09:00-10:30, reaching 31.2 seconds per flower. The open-pollination treatment showed a 36.7% increase in fruit formation, indicating a strong dependence of cocoa fruit set on insect visitation. This percentage exceeds values reported in earlier studies that did not include the stingless bee Tetragonula laeviceps. The findings reveal the significant yet previously underappreciated role of stingless bees in cocoa pollination and emphasize their importance for sustainable yield management.

Keywords: Ceratopogonidae; cocoa flowers; fruit set; stingless bees

ABSTRAK

Koko (Theobroma cacao L.) merupakan tanaman komersial yang penting di seluruh dunia. Meskipun mempunyai kepentingan global yang tinggi, ekologi serta perkhidmatan pendebungaan bunga koko masih kurang diberi perhatian. Pelbagai kajian terdahulu telah mengenal pasti bahawa lalat daripada famili Ceratopogonidae merupakan pendebunga utama bagi tanaman ini, namun peranan spesies serangga lain masih belum diterokai secara mendalam. Pemahaman yang menyeluruh tentang sistem pendebungaan koko amat penting bagi memaksimumkan kejayaan pendebungaan serta mengoptimumkan hasil pengeluaran. Kajian ini dijalankan untuk mengenal pasti potensi serangga pendebunga yang berkaitan dengan bunga koko dan meneliti peranan lebah kelulut dalam proses pendebungaan tersebut. Pensampelan telah dilakukan di tiga lokasi berbeza di Jatimulyo, Daerah Kulon Progo, Provinsi Yogyakarta, masing-masing terletak pada jarak 0 m, 250 m dan 500 m dari sebuah meliponari bagi menilai kemungkinan variasi aktiviti pendebunga. Serangga dikutip menggunakan jaring sapuan dan aspirator, manakala keberkesanan pendebungaan dinilai berdasarkan tingkah laku kunjungan bunga, beban debunga, dan tahap kebergantungan terhadap pendebungaan serangga. Bagi menilai sumbangan pendebungaan, sembilan pokok koko telah dikenakan dua jenis rawatan: kumpulan pertama bunga telah dibungkus dengan beg jaring halus (rawatan pengecualian), manakala kumpulan kedua dibiarkan terbuka bagi membolehkan kunjungan serangga (rawatan terbuka). Hasil kajian mengenal pasti empat spesies serangga berpotensi sebagai pendebunga, iaitu Forcipomyia parvula (43% beban debunga koko), Tetragonula laeviceps (62%), Dasyhelea sylvatica (25%) dan Dasyhelea pseudoincisurata (28%). Antara spesies ini, Tetragonula laeviceps menunjukkan kunjungan bunga yang paling konsisten, dengan kadar kunjungan tertinggi direkodkan antara pukul 07:00-08:00 dan tempoh purata kunjungan terpanjang antara pukul 09:00-10:30, mencapai 31.2 saat bagi setiap bunga. Rawatan pendebungaan terbuka menunjukkan peningkatan sebanyak 36.7% dalam pembentukan buah, menandakan tahap kebergantungan yang tinggi terhadap kunjungan serangga pendebunga. Peratusan ini lebih tinggi berbanding nilai yang dilaporkan dalam kajian terdahulu yang tidak melibatkan lebah kelulut Tetragonula laeviceps. Dapatan kajian ini menyerlahkan peranan penting lebah kelulut yang sebelum ini kurang diberi perhatian dalam pendebungaan koko serta menekankan kepentingannya dalam pengurusan hasil yang mampan.

Kata Kunci: Bunga koko; Ceratopogonidae; set buah; kelulut

INTRODUCTION

Cocoa is an agricultural commodity widely traded on international markets, with major global exporters of cocoa beans including the Republic of Côte d'Ivoire, Ghana, Ecuador, Nigeria, Cameroon, and Indonesia (Cruz et al. 2019). Global demand for cocoa has increased by 3% per year over the past 100 years and is projected to grow at a similar rate in the coming years (FAO 2015). This demand benefits Indonesia as one of the world's leading cocoa producers and exporters (Nisa et al. 2023). Cocoa is among Indonesia's top agricultural export commodities (Nisa et al. 2023). It is the third-largest foreign exchange-earning agricultural commodity, after palm oil and rubber, and serves as a primary source of income for 1.7 million farming households (Managanta et al. 2019). However, research by Nisa et al. (2023) indicated that cocoa productivity has declined, as evidenced by the Trade Specialization Index (TSI) results showing an average value nearing 0.5, indicating a downturn in the growth stage of Indonesia's cocoa exports.

Improving cocoa productivity is partly influenced by the success of fruit formation (Fahmid et al. 2018). Fruit formation in plants is preceded by the process of pollination, which involves the transfer of pollen grains onto the stigma (Indriyani et al. 2018). This process is essential for plant reproduction; without pollination, sexual reproduction will not occur, and fruit formation will not happen (Mangena & Mokwala 2018). Bees and other pollinating insects contribute to 87% of fruit formation in global food crops. Moreover, the volume of agricultural production that depends on pollinators has increased by 300% over the past five decades, emphasizing the crucial role of pollinators in supporting global food security and livelihoods (FAO 2018). Furthermore, cocoa plants require cross-pollination due to their self-incompatibility and inability to self-pollinate, making insect pollinators essential for cocoa fruit production (Glendinning 1972).

Globally, about 1,500 insect species have been identified as being associated with cocoa (Entwistle 1972). Among these, several insect species contribute to pollination, with the primary and most effective pollinators of cocoa flowers identified as flies from the family Ceratopogonidae (Anin et al. 2015; Kaufmann 1975; Winder 1978). This is supported by Nugroho et al. (2019) researched cocoa plantations in Lebak, Banten, where a Diptera species from the Ceratopogonidae family, *Forcipomyia* sp., dominated flower visitation, accounting for 79.14% of total visits with an average duration of 6.7 minutes per flower. Hernández et al. (2017) reported that Ceratopogonidae contributed 40.7% and Cecidomyiidae 4.9% to cocoa flower visits in America, West Africa, and Southeast Asia. While Ceratopogonidae is the primary pollinator, Cecidomyiidae also plays a role in cocoa pollination (Vandromme et al. 2019). Members of the Cecidomyiidae family visit cocoa flowers in search of nectar, with females visiting more frequently than males. Both male and female individuals have been observed crawling inside the cocoa anthers (Young 1985b).

While Ceratopogonidae and Cecidomyiidae are widely recognized as the main pollinators of cocoa (Anin et al. 2015), Young (1985a) stated that stingless bees are unable to pollinate cocoa flowers. However, recent studies have shown otherwise, with stingless bees such as *Hypotrigona araujoi*, *Hypotrigona* sp., and *Lasioglossum* sp. observed visiting cocoa flowers and contributing to pollination (Adjaloo & Oduro 2013; Anin et al. 2015). In Jatimulyo Village, Kulon Progo Regency, the local community cultivates stingless bees (Apidae: Meliponini), a group of bees considered vital pollinators in tropical ecosystems (Alebachew 2018; Thomas et al. 2009). Given the small and uniquely structured flowers of cocoa that restrict access to insects under 5 mm, it is plausible that the stingless bee locally known as Klanceng may play a role in cocoa pollination. However, their actual contribution remains underexplored. This study aims to determine potential insect pollinators associated with cocoa flowers and to investigate the presence, foraging behavior, and potential pollination role of stingless bees in cocoa agroforestry systems in Jatimulyo.

MATERIALS AND METHODS

Study Site

The study of pollinator populations was conducted in an agroforestry area of Menoreh Hills in Jatimulyo Village, Girimulyo Sub-district, Kulon Progo Regency, Yogyakarta, Indonesia (7°46'01" S, 110°06'53" E), at an elevation of over 629 m a.s.l., with a total of six sampling points (Figure 1).

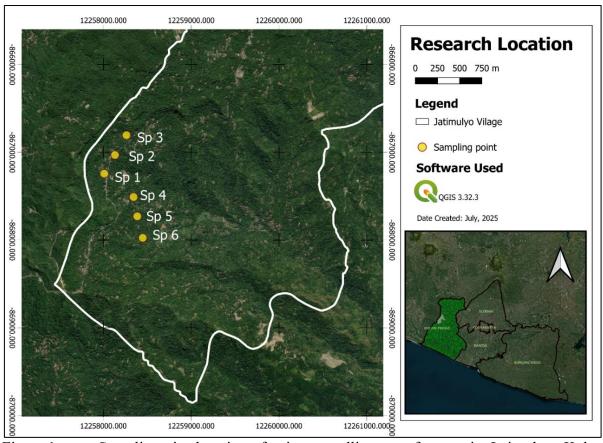


Figure 1. Sampling site locations for insect pollinators of cocoa in Jatimulyo, Kulon Progo District, Yogyakarta, Indonesia. The study area represents an agroforestry landscape where Sampling Point (SP) 1 and SP 6 are located within a meliponary (stingless bee-keeping site) at a 0 meters point. Sampling Points 2 and 5 are situated approximately 250 meters from the meliponary, while SP 3 and SP 4 are located about 500 meters away

Data Collection

Insect Observations and Sampling

Insect observations were conducted from April to May 2024 with time intervals: 07:00-08:30, 09:00-10:30, 12:30-14:00, and 15:00-16:30 at each sampling point (Figure 1). Sampling was carried out using an active method with a sweep net and an aspirator. During the observation, the behavior of insects on cocoa flowers was observed and recorded using images and videos taken with an iPhone 13 camera.

At each sampling point, observations were conducted on seven cocoa trees with nine replicates. Insect samples collected were examined using a stereo microscope and OptiLab® at the Laboratory of Entomology, Faculty of Biology, Universitas Gadjah Mada. Insect identification was based on McAlpine et al. (1981), Goulet and Huber (1993), Shattuck (1999), Triplehorn & Johnson (2005), as well as scientific articles that provide identification keys and support the identification process.

Behaviour of pollinator insects

Pollinator insect activity was observed during flower visits. This study particularly focused on investigating stingless bees' visits to cocoa flowers to evaluate their role in cocoa pollination.

Observations included the number of flowers visited (foraging level) and the duration of each visit (handling time in seconds per flower)

Pollen Identification

Pollen was collected from the insect body and then identified using the acetolysis method, which included the stages of fixation, heating, washing, staining, mounting, and labeling (Warcup et al. 2023). The pollen preparations were then observed using a light microscope at 100X magnification. The morphological analysis of pollens consisted of length (P), diameter (D), shape, and size. The observed preparations were then documented using OptiLab® to be classified into cocoa or non-cocoa pollen.

Measurement of pollination effectiveness

Pollination effectiveness was evaluated by comparing fruit set between flowers exposed to open pollination and those subjected to exclusion treatments. Two distinct groups of flower buds on each tree were designated. One group was allowed natural insect visitation, while the other was enclosed to prevent pollinator access. This experiment was carried out on nine cocoa trees, and pollination effectiveness was quantified using the formula proposed by Leksikowati et al. (2018).

$$PE\% = \frac{Number\ of\ fertilized\ flowers\ (or\ fruits\ set)}{Total\ number\ of\ pollinated\ flowers} X100\%$$

RESULT AND DISCUSSION

Potential Insect Pollinators

Insect pollinators are a component of biodiversity closely related to food crops and agriculture. About 80% of wild flowering plant species are specialized for insect pollination (FAO 2007). The study found four insect species that most frequently visited cocoa flowers. They have special morphological characters such as body length less than 5 cm, have setae on the body, and exhibit flower-visiting behavior with the potential to carry cocoa pollen (Table 1; Figure 2).

Table 1. Insect pollinator visit data on cocoa (*Theobroma cacao* L.) flowers

No	Order	Famili	Spesies	Number of individual
1	Diptera	Ceratopogonidae	Forcipomyia parvula	62
2	Hymenoptera	Apidae	Tetragonula laeviceps	51
3	Diptera	Ceratopogonidae	Dasyhelea silvatica	50
4	Diptera	Ceratopogonidae	Dasyhelea pseudoincisurata	34

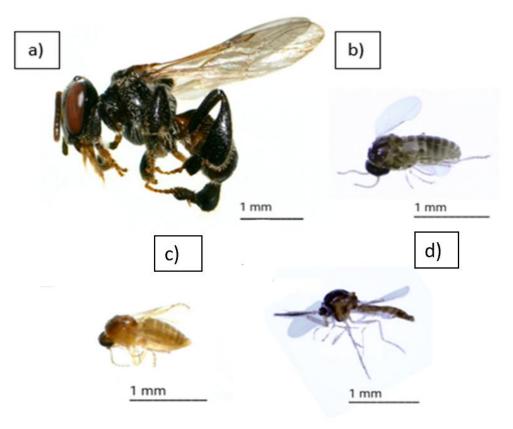


Figure 2. Insect species identified as potential pollinators of cocoa flowers: (a) Tetragonula laeviceps, (b) Forcipomyia parvula, (c) Dasyhelea silvatica, and (d) Dasyhelea pseudoincisurata

Behavior of Insects

This study analyzed pollen loads from four insect species were *Forcipomyia parvula*, *Tetragonula laeviceps*, *Dasyhelea silvatica*, and *Dasyhelea pseudoincisurata*. Based on existing literature and their morphological characteristics, these species demonstrate strong potential as effective pollinators of cocoa flowers and exhibited the highest frequency of occurrence among all observed insects (Figure 3). Other recorded species primarily comprise predators, pests, parasitoids, and non-pollinating floral visitors. These findings align with previous studies that identify midges from the family Ceratopogonidae as the primary pollinators of cocoa (Entwistle 1972; Nugroho et al. 2019; Tscharntke et al. 2011; Young 1985b). Pollen adheres to various parts of Dipteran bodies, particularly on hairy structures such as legs, antennae, and the thoracic region during foraging activities as they seek nectar or other nutritional resources (Raguso 2020). Moreover, banana stumps and cocoa pod husk have been shown to support higher breeding success of *Forcipomyia* spp. (Bakar et al. 2019), Both of which were also naturally found surrounding the cocoa farms in our study site. The availability of these substrates may therefore enhance the presence of these small midges (*Forcipomyia* sp.) and support their role as cocoa pollinators.

Tetragonula laeviceps, a member of the Apidae family, was the second most frequent floral visitor after Forcipomyia parvula. T. laeviceps has strong potential as an effective cocoa flower pollinator due to its morphological traits that facilitate pollen adhesion, particularly on the dorsal thorax, scutum, frons (front of the head), and mid-legs, which are covered in dense hairs (Pangestika et al. 2017; Roubik 1992). These body parts often come into direct contact

with the flower's anthers during nectar foraging, yet are difficult for the bee to groom, making them ideal "safe sites" for passive pollen transfer (Neff & Simpson 1992; Westerkamp 1996). Moreover, the flower constancy exhibited by *T. laeviceps* on cocoa blossoms further highlights its reliability as a pollinator contributing to the reproductive success of the plant (Figure 3).



Figure 3. Activity of Ceratopogonidae (Forcipomyia parvula, Dasyhelea silvatica, and Dasyhelea pseudoincisurata) and Apidae (Tetragonula laeviceps) on cocoa flowers

The presence of *Tetragonula laeviceps* was highest in the morning at 07:00-08:30 with 20 individuals observed, then gradually declined in the afternoon (Figure 4). In contrast, the presence of Ceratopogonidae midges (*Forcipomyia parvula*, *Dasyhelea silvatica*, and *Dasyhelea pseudoincisurata*) showed the opposite trend, with their highest activity recorded in the late afternoon (15:00–16:30), and very low presence during the morning (Figure 4).

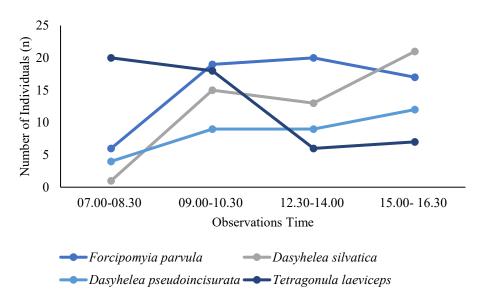


Figure 4. Comparison of the presence of potential pollinator insects at different observation times

Tetragonula laeviceps, family Apidae, is a diurnal ectothermic insect that relies on external temperatures to regulate body heat. *T. laeviceps* is most active in the morning to early afternoon when temperatures are warmer and sunlight facilitates navigation. Due *T. laeviceps* compound eyes being poorly adapted to dim light, *T. laeviceps* becomes inactive at night (Even et al. 2020; Siefert et al. 2021).

In contrast, Ceratopogonidae midges are active throughout the day but exhibit peak activity in the late afternoon and evening. This behavior is influenced by lower ambient temperatures, reduced wind speeds, and higher humidity, which help prevent dehydration. Additionally, many of their hosts (e.g., mammals and birds) rest during these hours, making it easier for females to obtain blood meals for reproduction. Their compound eyes are sensitive to low light levels, allowing them to orient toward artificial or moonlight sources at night, aided by sensory mechanisms like CO₂ detection (Sarwar 2020; Zhang & Derrick 2022).

The highest presence of *Tetragonula laeviceps* was observed at point zero meters close to the meliponaries, and less at points 250 meters and 500 meters away from the meliponaries (Figure 5). The home range of stingless bees is influenced by several factors, such as the availability of food sources (nectar and pollen), environmental conditions, and certain species. According to Smith et al. (2016), the Stingless bee cruising distance can be up to 300 m with a maximum of 712 m when needed. Greenleaf et al. (2007) state that the stingless distance ranges from 175 m to 562 m. The farther away from the nest, the less stingless bees are found. As the distance of the observation point increases, the presence of Diptera also increases. This may be related to competition among organisms in the community.

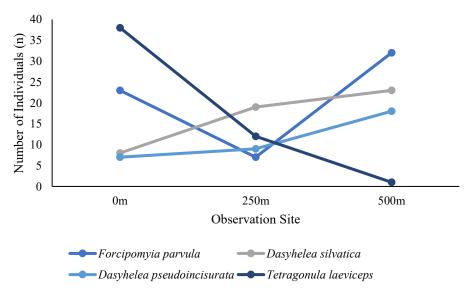


Figure 5. Comparison of the presence of potential pollinator insects at each observation site

The report states that an insect with a body length of 3 mm, such as Ceratopogonidae flies, is the primary pollinator of cocoa (Entwistle 1972; Tscharntke et al. 2011; Young 1985b; Young 1986). In this study, it was stated that insects with a size of 4 – 5 mm could also help pollination as *Tetragonula laeviceps* routinely visits cocoa flowers and moves to several other cocoa flowers, based on observations of stingless bees moving to a maximum of five flowers and a minimum of one flower. (Figure 3) When the head of the stingless bee enters the base of the flower, its feet come into contact with the pollen, allowing the stingless bee to obtain nectar. In addition, stingless bees tend to exhibit foraging behavior consistently on the same flowers, so they tend to visit the same flowers repeatedly (Putra et al. 2016). *Tetragonula laeviceps* consistently visited cocoa flowers every day, with the most visits was at 07:00-08:00 Western Indonesian Time (WIT), but the longest visit duration was at 09:00–10:30 WIT with an average of 31.2 seconds/flower. Following the cocoa receptive time, the sepals of cocoa flowers split

during the day and continue to open at night. The next morning, the flowers are open fully and the anther releases the pollen. The style matures slightly later, which is a good time for pollination (Wood & Lass 2001). In Figure 6, it can be seen that *Tetragonula laeviceps* visitation is negatively correlated and significant with a P 4.7 e^{-08} <0.05. In contrast, Ceratopogonidae (*Forcipomyia parvula*, *Dasyhelea silvatica*, and *Dasyhelea pseudoincisurat* visitation is positively correlated but not significant at any point with a P 0.17>0.05 (Figure 6).

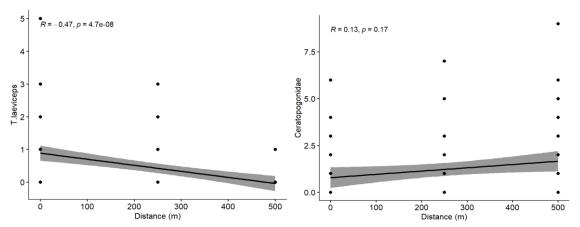


Figure 6. Spearman correlation of the number of insects and the site distance

Pollen Loads

Forcipomyia parvula carried 43% (n=46) of cocoa pollen, Tetragonula laeviceps carried 62% (n=106), Dasyhelea silvatica carried 25% (n=5), Dasyhelea pseudoincisurata carried 28% (n=42) (Figure 7). Mature pollen has a well-defined morphology that allows for identifying the species of origin (Rahmawati et al. 2019). Cocoa pollen attached to the insect body was acetolyzed and observed under a microscope at 100X magnification and photographed using an optiLab® camera. In general, cocoa pollen is 20 μm in size, spherical to oval, and elongated prolate spheroidal. The surface of the pollen is smooth (psilate) with a thin granularization pattern (Talledo et al. 2019).

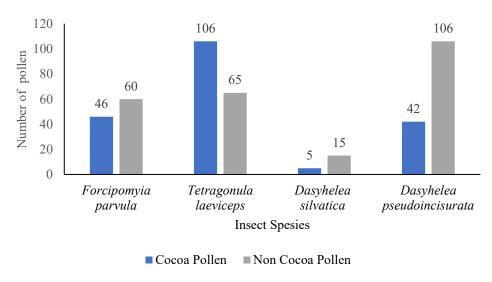


Figure 7. Pollen on the body of the pollinator insect

Pollination of cocoa flowers depends on insect pollinators. Although cocoa trees produce a large number of flowers, fewer than 5% successfully develop into fruit (Wood & Lass 2001; Young 1994). Despite having hermaphroditic flowers, cocoa is predominantly cross-pollinated due to reverse herkogamy, which inhibits self-pollination. This, coupled with both sporophytic and gametophytic incompatibility, results in less than 25% of flowers being fertilized annually, with only up to 2% ultimately developing into harvestable fruits (Gutiérrez 2013).

Self-pollination led to limited success, whereas cross-pollinated plants exhibited a three- to eightfold higher fertilization rate (Vansynghel et al. 2023). Nugroho et al. (2019) reported that open-pollinated flowers increased fruit formation by only 4% compared to closed-pollinated flowers. In contrast, the present study revealed that the combined presence of Ceratopogonidae and stingless bees (*Tetragonula laeviceps*) resulted in a pollination success rate 36.7% higher than previously reported, highlighting the important contribution of these pollinators.

These findings emphasize the critical role of insect pollinators in supporting cocoa production. This insight is particularly valuable for cocoa farmers, as it highlights the potential benefits of managing and cultivating *T. laeviceps* around cocoa plantations to enhance pollination services. Strengthening the role of pollinators in cocoa agroecosystems not only improves yield but also supports the livelihoods of smallholder and family farmers, especially in developing regions where cocoa is a key commodity.

CONCLUSION

This study identified four insect species as potential pollinators of cocoa flowers: Forcipomyia parvula (n=62) carrying 43% cocoa pollen, Tetragonula laeviceps (n=51) carrying 62%, Dasyhelea sylvatica (n=50) carrying 25%, and Dasyhelea pseudoincisurata (n=34) carrying 28%. Among them, T. laeviceps exhibited more consistent foraging behavior, with peak visitation occurring between 07:00–08:00 and the longest average visit duration (31.2 seconds per flower) observed between 09:00–10:30. These time intervals aligned more closely with the cocoa flower's receptive period compared to the three Ceratopogonidae species. Pollination trials further confirmed that cocoa fruit formation is dependent on insect pollinators, with the open pollination treatment increasing fruit set by 36.7%. This success rate, which is notably higher in the presence of T. laeviceps compared to previous studies. These findings emphasize the critical contribution of insects, particularly stingless bees, in enhancing cocoa pollination success and underscore the importance of conserving and managing pollinator populations in cocoa agroecosystems.

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AUTHORS DECLARATION

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Conflict of Interest

The authors declare that they have no conflicts of interest.

Data Availability Statement

The data supporting this study's findings are available on request from the corresponding author.

Authors' Contributions

Syefrina Rosyada (SR) Conceptualization, collected, and analyzed the data, administered the project, and wrote the manuscript. Hari Purwanto (HP) Conceptualization, manuscript review, and supervised all the processes.

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REFERENCES

- Adjaloo, M.K. & Oduro, W. 2013. Insect assemblage and the pollination system in cocoa ecosystems. *Journal of Applied Biosciences* 62(1): 4582-4594.
- Alebachew, G.W. 2018. Economic value of pollination service of agricultural crops in Ethiopia: Biological pollinators. *Journal of Apicultural Science* 62(2): 265-273.
- Anin, F.K., Bosu, P.P., Adjaloo, M.K., Braimah, H. Oduro, W. & Kwapong, P. 2015. *Some Facts about Cocoa Pollination*. Ghana: University of Cape Coast Printing Press.
- Bakar, S., Adnan, N.A. & Redzuwan, U. S. A. 2019. Temporal geospatial assessment of cocoa pollinator, *Forcipomyia* in cocoa plantation area. *Serangga* 24(1): 159–172.
- Cruz, A.F., Suwastika, I.N., Sasaki, H., Uchiyama, T., Pakawaru, N.A., Wijayanti, W., Muslimin, Basri, Z., Ishizaki, Y. & Shiina, T. 2019. Cacao plantations on Sulawesi Island, Indonesia: An agro-ecological analysis of conventional and organic farms. *Organic Agriculture* 9(2): 225–34.
- Entwistle, P.F. 1972. Pests of Cocoa. First Edition. London: Longman.
- Even, N., Olivier, B. & Mathieu, L. 2020. *Navigation by Honey Bee. Encyclopedia Of Animal Cognition and Behavior*. USA: Springer Cham.
- Fahmid, I.M., Harun, H., Fahmid, M.M., Saadah, & Busthanul, N. 2018. Competitiveness, production, and productivity of cocoa in Indonesia. *IOP Conference Series: Earth and Environmental Science* 157(1): 1-6.
- FAO. 2007. The State of the World's Biodiversity for Food and Agriculture. Rome: FAO Commission on Genetic Resources for Food and Agriculture.
- FAO. 2015. Statistical Pocket Book 2015 World Food and Agriculture. Rome: Food and Agriculture Organization of the United Nations.
- FAO. 2018. Why Bees Matter: The Importance of Bees and Other Pollinators for Food and Agriculture. Rome: Food and Agriculture Organization of the United Nations.
- Glendinning, D.R. 1972. Natural pollination of cocoa. *New Phytologist* 7: 719–729.
- Goulet, H. & Huber, J.T. 1993. *Hymenoptera of The World: An Identification Guide to Families*. Ottawa (CA): Agriculture Canada.
- Greenleaf, S., Williams, N., Winfree, R. & Kremen, C. 2007. Bee foraging ranges and their relationship to body size. *Oecologia* 153: 589–596.
- Gutiérrez, G.S.P. 2013. Plan de negocios para la exportación de cacao producido en la región 7 (Loja, Zamora y El Oro). Master thesis, Universidad de Cuenca, Ecuador.

- Hernández, M.T., Wanger, T.C. & Tscharntke, T. 2017. Neglected pollinators: Can enhanced pollination services improve cocoa yields? A review. *Agriculture, Ecosystems and Environment* 247: 137-148.
- Indriyani, S., Ekowati, G. & Widoretno, W. 2018. *Petunjuk Parktikum Biologi Reproduksi Tumbuhan*. UB: Malang.
- Kaufmann, T. 1975. Studies on the ecology and biology of a cocoa polinator, *Forcipomyia squamipennis* I. And M. (Diptera, ceratopogonidae), in Ghana. *Bulletin of Entomological Research* 65: 263–268.
- Leksikowati, S.S., Putra, E.R., Rosmiati, M. Kinasih, I. Husna Z., Novitasari., Setiyarni, E. & Rustam, F.A. 2018. Aplikasi *Trigona (Tetragonula) laeviceps* sebagai agen penyerbuk pada sistem tumpang sari buncis dan tomat di dalam rumah kaca. *Jurnal Sumberdaya HAYATI* 4(2): 63–70.
- Managanta, A.A., Sumardjo, D. Sadono, P. & Tjitropranoto. 2019. Faktor-faktor yang berpengaruh terhadap kompetensi petani kakao di Provinsi Sulawesi Tengah. *Jurnal penyuluhan* 15(1): 120-133.
- Mangena, P. & Mokwala, P.M. 2018. *Introductory Chapter: Pollination. Pollination in Plants*. London: IntechOpen.
- McAlpine, J.F., Peterson, B.V., Shewell, G.E, Teskey, H.J., Vockeroth, J.R. & Wood, D.M. 1981. *Manual of Nearctic Diptera*. Ottawa: Research Branch Agriculture Canada.
- Neff, J.L. & Simpson, B.B. 1992. Indices of pollen exposure in bees: The pollen load analysis. *Journal of the Kansas Entomological Society* 65(4): 504–525.
- Nisa, D.P.J.I.N., Darsono. & Antriyandarti, E. 2023. Comparative analysis of Indonesian cocoa competitiveness in the international market. *AIP Conference Proceedings*, pp. 2583.
- Nugroho, A., Atmowidi, T. & Kahono, S. 2019. Diversitas serangga penyerbuk dan pembentukkan buah tanaman kakao (*Theobroma cacao* L.). *Jurnal Sumberdaya Hayati* 5(1): 11–17.
- Pangestika, N.W., Atmowidi, T. & Kahono, S. 2017. Pollen load and flower constancy of three species of stingless bees (Hymenoptera, Apidae, Meliponinae). *Tropical Life Sciences Research* 28: 179–187.
- Putra, D.P., Dahelmi, Salmah, S. & Swasti, E. 2016. Pollination in chili pepper (*Capsicum annuum* L.) by *Trigona laeviceps* and *T. minangkabau* (Hymenoptera, Meliponini). *Journal of Entomology and Zoology Studies* 4(4): 191-194.
- Raguso, A.R. 2020. Don't forget the flies: Dipteran diversity and its consequences for floral ecology and evolution. *Applied Entomology and Zoology* 55: 1–7.
- Rahmawati, L.U., Purwanti, E., Budiyanto, M.A.K., Zaenab, S., Susetyarini, R.E. & Permana, T.I. 2019. Identification of pollen grains morphology and morphometry in Liliaceae. *IOP Conference Series: Earth and Environmental Science* 276(1): 012031.

- Roubik, D.W. 1992. *Ecology and Natural History of Tropical Bees*. Cambridge University Press.
- Sarwar, M. 2020. *Typical Flies: Natural History, Lifestyle, and Diversity of Diptera*. London: IntechOpen.
- Shattuck, S.O. 1999. Australian Ants: Their Biology and Identification. Monographs on Invertebrate Taxonomy. Volume 3. Collingwood (AU): CSIRO Publishing.
- Siefert, P., Buling, N. & Gru newald, B. 2021. Honey bee behaviours within the hive: Insights from long-term video analysis. PLoS ONE 16(3): 1-14.
- Smith, J.P., Tim, A.H., Madelaine, B. & Ros. G. 2016. Flight range of the Australian stingless bee *Tetragonula carbonaria* (Hymenoptera: Apidae). *Austral Entomology* 56: 1-4.
- Talledo. G.B., Bazurto, Z.A. & García Cruzatty, L. 2019. Morphology, viability, and longevity of pollen of national type and trinitarian (CCN-51) clones of cocoa (*Theobroma cacao* L.) on the Coast of Ecuador. *Brazilian Journal of Botany* 42(3): 441–448.
- Thomas, S.G., Rehel, S.M., Varghese, A., Davidar, P. & Potts, S.G. 2009. Social bees and plant associations in the Nilgiri Biosphere Reserve, India. *Tropical Ecology* 50: 79-88.
- Triplehorn, C.A. & Johnson, N.F. 2005. *Borror and Delong's Introduction to the Study of Insect*. 7th Edition. Belmont (USA): Thompson Brooks/Cole
- Tscharntke, T., Clough, Y., Bhagwat, S.A., Buchori, D., Faust, H., Hertel, D., Hölscher, D., Juhrbandt, J., Kessler, M., Perfecto, I., Scherber, C., Schroth, G., Veldkamp, E. & Wanger, T.C. 2011. Multifunctional shade-tree management in tropical agroforestry landscapes A review. *Journal of Applied Ecology* 48(3): 619–29.
- Vandromme, M., Trekels, H., Sepúlveda, R.N., Somarriba, E. & Vanschoenwinkel, B. 2019. Exploring the suitability of bromeliads as aquatic breeding habitats for cacao pollinators. *Hydrobiologia* 828(1): 327–337.
- Vansynghel, J., Thomas, E., Ocampo-Ariza, C., Maas, B., Ulloque-Samatelo, C., Zhang, D., Tscharntke, T. & Steffan, D.I. 2023. Cross-pollination with native genotypes improves fruit set and yield quality of Peruvian cacao. *Agriculture, Ecosystems & Environment* 357: 108671.
- Warcup, K., Bethany, R., Katherine, K.O. & Jason, H. 2023. Acetolysis modifications to process small pollen samples swabbed from live bees. *Journal of Insect Science* 23(6): 1-6.
- Westerkamp, C. 1996. Pollen in bee–flower relations: Some considerations on melittophily. *Botanica Acta* 109(4): 325–332.
- Winder, J.A. 1978. The role of non-dipterous insects in the pollination of cocoa in Brazil. *Bulletin of entomological research* 68: 559-574.
- Wood, G.A.R. & Lass R.A. 2001. Cocoa: Fourth Edition. USA: John Wiley and Sons.

- Young, A.M. 1985a. Pollen-collecting by stingless bees on cacao flowers. *Experientia* 41(6): 760–62.
- Young, A.M. 1985b. Studies of cecidomyiid midges (Diptera: Cecidomyiidae) as cocoa pollinators (*Theobroma cacao* L.) in Central America. *Proceedings of the Entomological Society of Washington* 87: 49–79.
- Young, A.M. 1994. The Chocolate Tree. Washington: Smithsonian Institution Press.
- Zhang, X. & Derrick. K.M. 2022. The effects of light wavelength and trapping habitat on surveillance of *Culicoides* biting midges (Diptera: Ceratopogonidae) in Alabama. *Journal of Medical Entomology* 59(6): 2053–2065.