




RESEARCH ARTICLE

Insufficient native pollinators during artificially induced early flowering decrease yield and long-term economic viability of a tropical fruit crop

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Abstract

1. The management of crops outside the regular cropping calendar can improve profits when supply is low and prices are high, but we do not know how induced, early flowering impacts the pollination services that crops require.
2. This study examines the effects of flowering time and pollinator management, including managed honeybee colonies and ground flower cover, on the pollination of the tropical fruit tree, longan (*Dimocarpus longan* Lour.), comparing between in-season flowering (naturally) and off-season flowering (chemically induced) in Northern Thailand.
3. Visitation rates of flower visitor groups significantly differed among treatments: for in-season flowering, wild bees were the most frequent pollinator group, whereas in the off-season flowering, there were no wild bees, and instead dipterans were the most frequent pollinator group. Some off-season plantations have honeybee hives present and in this situation honeybees were the most frequent pollinator group.
4. We show that temporal variation in the pollinator community significantly alters the pollination efficiency of longan crops. Consequently, longan production from off-season longan farms generates lower net profit in the absence of managed bees and wild bees, and wild bees produced higher seed-sets than either honeybees or dipterans.
5. *Synthesis and applications.* Wild bees were the main pollinator group of longan in the in-season flowering resulting in high fruit production; whereas in the off-season flowering honeybees and dipterans were the main pollinator group. Longan production from off-season longan farms without managed bee produced less net profit. The farmers practicing off-season with honeybee hives management gain the largest net profit. Developing mechanisms to promote and maintain pollinator abundance and diversity is likely to increase the resilience of the system in

addition to profit in the long term; thus, efforts should be made to provide more nesting habitat and reduce pesticide use.

KEYWORDS

economic value, ecosystem services, honeybees, Longan pollination, off-season flowering, pollination importance, temporal variation, wild bees

1 | INTRODUCTION

Pollinator declines affect biodiversity, ecosystem functioning and human welfare worldwide (Potts et al., 2016). Approximately 75% of all food crops globally depend on animal pollination (Klein et al., 2007), and over past 50 years, disproportionate increases in land area used for animal-pollinated crops means agriculture has become increasingly dependent on pollinators (Aizen et al., 2008). However, with pollinator loss, the production rate of pollinator dependent crops is lower and tends to be more uncertain than the production of wind-pollinated crops (Garibaldi et al., 2011).

Changes in phenology can alter ecological interactions and have significant effects on species reproduction and survival (Rafferty et al., 2015; Thomson, 2010), and changing flowering phenology can have particularly high, typically negative, impacts on plant reproduction (Kudo & Ida, 2013). Underlying this, changed phenology may cause plant-pollinator phenological mismatches because they may time their activities based on different environmental cues. However, the causes and consequences of phenological mismatches in mutualisms such as plants and pollinators, where lose-lose negative outcomes are expected, have been less addressed (Chmura et al., 2019; Forrest & Miller-Rushing, 2010), and empirical field data investigating phenological mismatches between plants and their pollinators are rare (Forrest, 2015).

Honeybees are among the most important crop pollinators in both temperate and tropical areas, and are increasingly managed to enhance pollination services and crop production (Aebi et al., 2012). When temporal mismatches exist between crop plants and potential native pollinators, pollination services may be supplemented by the introduction of managed honeybees. Although many farmers use managed honeybees *Apis mellifera* to enhance crop pollination, there is strong evidence that wild bees are crucial, especially in pollinating tropical crops (Garibaldi et al., 2013; Gibbs et al., 2016; Ricketts, 2004). For some crops, native bees show higher pollinator effectiveness than honeybees, transferring more pollen grains per single visit to flower stigmas (Nicholson & Ricketts, 2019). Honeybees and wild bees can complement each other in providing pollination services (Blitzer et al., 2016; Garibaldi et al., 2011; Greenleaf & Kremen, 2006), and crops can still benefit from native pollinators although honeybees are abundant (Button & Elle, 2014; Garibaldi et al., 2013).

Though many studies have explored pollination dynamics in temperate systems, tropical systems remain understudied, despite

the great importance of sustainable agriculture for food security in these developing regions. Longan (*Dimocarpus longan* Lour.) is an economically important and important fruit for Thailand (2 billion THB or 65 million USD in 2016; Kaewsompong et al., 2019). Northern Thailand is the primary area of longan production (162,132 ha; Sudswang et al., 2018), where it is largely grown in monocultures with chemical fertilizers. However, some farmers have longan trees intercropped with vegetables on raised beds (Limnirankul & Gypmantasiri, 2010). The pollinator efficiency of longan visitors in Southeast Asia has previously been assessed based on the relative abundance of different insects, the amount of longan pollen that each visitor carried and the duration of floral visits (Pham, 2012). The pollination of longan during flowering season is largely dependent on flower visitation from both wild and managed bee species to set fruit, especially from the Asian honeybee *Apis cerana* and from stingless bees (*Trigona* spp.; Blanche et al., 2006; Pham, 2012). Pollination is necessary for 4–6 months before harvesting time. During the peak harvest season, there is always a risk of low prices due to the high availability and market saturation. As the main harvest season in Northern Thailand lasts around 1.5 months, this often causes serious economic losses for the longan-growing farmers that are forced to sell longan produce at low prices. Thus, there is an economic incentive to produce fruit when prices are higher and the cultivation of crops outside the regular cropping calendar through chemical inducement is becoming more common in the region. When supply is low and prices are high, farmers gain better profits and consumers have more choice. However, there is likely to be a trade-off in terms of fruit set and increased costs due to mismatches with native pollinators, and possibly poorer growing conditions, so understanding the costs and benefits is crucial for informing productive management.

We do not currently know how phenological shifts in flowering changes pollinator communities or how this impacts yield, all of which is vital to optimize production and ensure food security. In this study, we evaluated pollination services to the highly pollinator-dependent longan in Northern Thailand. The goal of this study was to investigate the changes in pollinator community composition and pollinator importance for fruit production of longan across two seasons, including in-season flowering (naturally flowering) and off-season flowering (chemically induced flowering), both with and without supplemental pollination from managed honeybees *A. mellifera*. We predicted that during the in-season flowering time, the pollinator community of longan crops would be dominated mainly by native bees with higher pollinator importance.

During the off-season flowering, we predicted that less-important managed pollinators and few native species are abundant due to the lack of floral resources and poorer environmental (climatic) conditions. Ultimately, we expect that this will make the off-season flowering treatment less economically viable in the long term.

2 | MATERIALS AND METHODS

2.1 | Study site

This study was primarily conducted in monocultural longan orchards in Chiang Mai province, Northern Thailand (18°47'43"N 98°59'55"E) from November 2018 to July 2019. The altitude in this region ranges from 310 to 3,565 m a.s.l. The range of temperature and humidity from November 2018 to July 2019 was 24–31°C and 47%–72%, respectively, and monthly temperature and humidity are presented in Figure 1 and Table S1. A total of nine longan orchards of the cultivar E-Daw with similar size (2.5–3.2 ha) were selected, minimally 10 km apart. Each orchard included planted longan and native herbaceous species. Spacing of the longan trees was generally 6 m × 6 m for the selected cultivar. All nine orchards produce longan for in-country consumption, and three longan orchards were used for each treatment (off-season with honeybee hives; off-season without honeybee hives and in-season without honeybee hives). In off-season treatments, potassium chlorate was applied as a pure chemical soil drench (99% active ingredient) in a ring on the cleared soil surface under the tree, which was irrigated afterwards. The amount of the applied chemical ranged from 80 to 150 g depending on the size of the tree as the diameter of the ring depended on the diameter of the canopy of the tree (Manochai et al., 2005). Potassium chlorate induced flowering 20–30 days after the application (Figure 1). Flower

visitation for off-season flowering time was recorded in November and December 2018, whereas in-season visitation was recorded in January and February 2019. Fruits were harvested from April to May 2019 for off-season treatments and from June to August 2019 for in-season treatments.

2.2 | Floral biology

Longan inflorescences are compound dichasia that generally appear in three waves. The overlap of three waves depends on cultivar and environmental conditions. The first wave (M1) consists of 1,000–2,000 staminate flowers per inflorescence, followed by the second wave (F) of 200–1,000 functionally female hermaphrodite flowers and the third wave (M2) of 1,000–4,000 functionally male hermaphrodite flowers (Pham et al., 2015). The female phase usually lasts 3–5 days (Pham, 2012). The M1 and M2 flowers are yellow-light-brown with eight long stamens. The M2 flowers consist of underdeveloped ovaries and stigmas. The stamen filaments of M2 flowers are longer than filaments of the M1 flowers. The anthers dehiscent occur around noon, in both M1 and M2 flowers (Pham, 2012). After dehiscence, the male flowers drop within days (Pham, 2012).

The female flowers consist of a bicarpellate ovary. Only one locule will usually develop into a fruit (Menzel & Waite, 2005). Typically, flowers open late at night. The stigmas are most receptive and pollination often occurs in the morning (Menzel & Waite, 2005; Pham, 2012). However, stigma receptivity lasts for several days, until the flowers senesce (Pham, 2012). The duration from flowering to harvest lasts 4–6 months depending on the specific cultivar and environmental conditions. After fertilization, two fruit waves usually happen and each inflorescence produces 60–80 fruits (Menzel & Waite, 2005). The edible part of the longan fruit is a fleshy aril (Wong, 2000). Pollination is

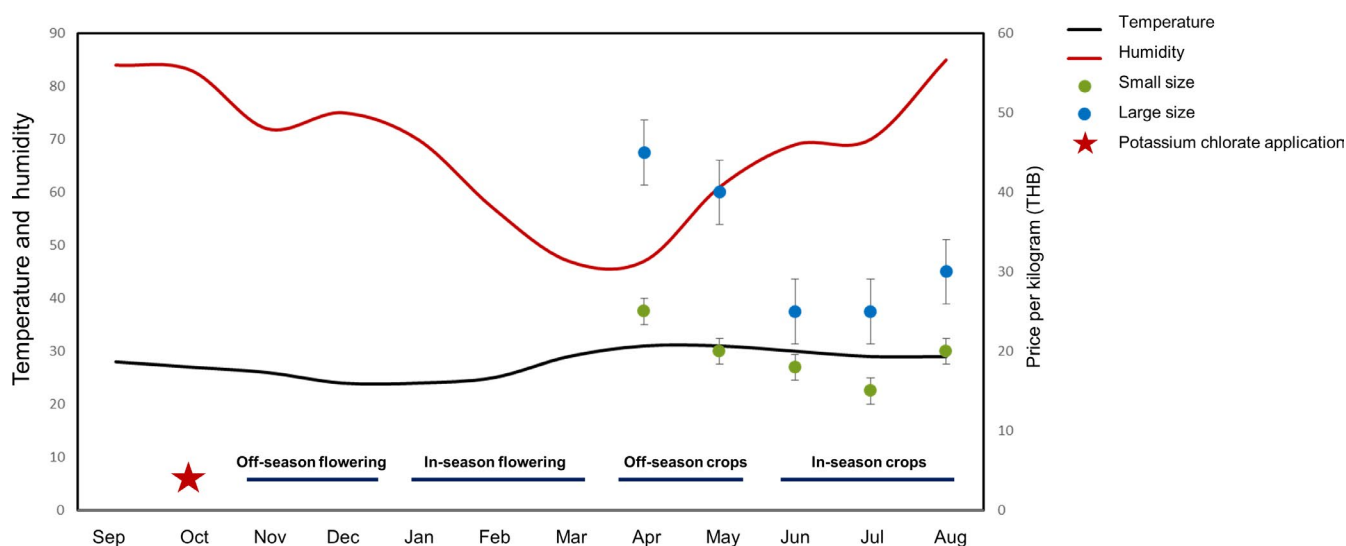


FIGURE 1 Trends of temperature and humidity in Chiang Mai province from September 2018 to August 2019. Mean (\pm SD) values of price of small and large size of longan crops in each month for off-season and in-season crops. Potassium chlorate applications took place in October, one month before induced flowering time. Link for temperature and humidity data: <https://www.timeanddate.com/weather/thailand/chiang-mai/historic?month=7%26;year=2019>

required for fruiting and unpollinated flowers drop 9 days after anthesis. The flowers were pollinated by different insects, but mainly honeybees (Pham, 2012). The few fruits obtained in the nocturnal pollination treatment suggest that nocturnal insect visitors are insignificant (Pham, 2012). In open and hand-cross pollination treatments, only 7% of the female flowers became fruits, which is significantly greater than the number of mature fruits obtained from wind and self-pollination treatments (Pham, 2012).

2.3 | Sampling flowers, flower-visitors and flower-visitor interactions

To identify flower visitors and understand how pollinator visitation frequency is influenced by local floral resource variability and treatment factors, we marked a 10 × 20 m plot in each orchard and we identified the plant species and counted the number of flowers in bloom of ground flora and noted the percent covered with flowers in each study plot. Visitor frequency and richness were recorded in fair weather (i.e. sunny and without rain, with the temperature ranging from 26°C to 28°C) between 07:00 and 11:00. We only collected data on insects when they came into contact with the flower. We sampled the number of floral visitors from the flowers of 10 longan trees in each orchard. For each observed longan tree, we used 15-min pollinator observation sessions within four 1 m × 1 m quadrats placed at a height of the midpoint of the tree facing each of the four cardinal directions of the tree (north, south, east and west). We categorized visitors into four groups: (a) western honey bees *A. mellifera*; (b) Asian honey bees *A. cerana*; (c) wild bees (stingless bees and other wild bees) and (d) flies. We classified *A. mellifera* and *A. cerana* into different groups as *A. mellifera* is obligately managed and non-native and *A. cerana* is used as a managed bee only in parts of the region outside of our study sites, so is a native, sometimes-managed species rather than an obligately wild species or a purely imported, non-native species.

2.4 | Reproductive success of longan

To assess the effect of flowering time on reproductive success, we measured fruit-set and yield resulting from 10 open-pollinated (marked with twist-ties) and 10 control inflorescences per tree, 10 trees per orchard. Each chosen inflorescence had a similar number of flower buds (3,000–3,500 buds). For the control, 10 inflorescences from each tree were covered with a light fabric bag pre-flowering (30 cm × 30 cm). After all flowering ceased, the bags were removed and fruit weights were recorded when fruits ripened. As the first flowers/fruits drop wave occurred 2–4 weeks after flowering (Pham et al., 2016), we counted the number of fruits per inflorescence for each study tree c. 14 days after flowering period (so that our measure of pollination success was not affected by any potential effects of resource limitation). We also counted the number of mature fruit at the same time as the farmer harvested the longans.

2.5 | Single-visit pollen deposition (SVD) and role in pollination

We recorded SVD (our measure of pollinator effectiveness; PE) following the method from Willmer et al. (2017), with a minimum of 30 individual flowers per tree. To examine SVD, inflorescences were bagged in the evening with fine mesh, then opened carefully for pollination trials when blooming. Individual flowers were observed until they received their first visit, usually between 07:00 and 11:00. Where possible, insect visitors to flowers were identified to species or morphotype in the field; if this was not possible, a visitor was collected for later identification. Insects were allowed to visit the flower freely before being disturbed, unless the visit took longer than 5 min. The stigma was removed with clean forceps and put on a fuchsin agar gel, after each insect visit. Gels were melted on microscope slides under coverslips, and all conspecific and hetero-specific pollen grains deposited on stigma were counted under light microscope (400× magnification). In all, 10 control stigmas were also investigated, by removing stigmas from bagged flowers before a visit occurred and examining pollen presence in the same way, to account for pollen found on stigmas due to opening of flower and/or handling and bagging procedures. Mean control values for each visitor species were subtracted from SVD values obtained from individual visits.

Following De Medeiros et al. (2019), we calculated the pollinator importance value index (PI) as the product of visitation frequencies (V) to flowers and the pollen load per single visit, by species ($PI = V \times PE$). The relative importance (RI) of each species as a pollinator is the fraction of PI for each species over the sum of PI across species.

2.6 | Economic valuation

Initially, yield and cost data for longan production were obtained from orchard owners during our survey. An interview was conducted with longan orchard owners to analyse the costs and market price. In all, 10 orchard owners from each practice (off-season and in-season) were interviewed. Questionnaires for interviewing growers were formulated based on typical activities of longan growers and included plantation preparation, cultivation, orchard management as well as the factors of production and profit such as seedling, organic fertilizer, chemical fertilizer, herbicide, fungicide, logistic cost, yield and market price. The questionnaire used for assessing cost and market price is provided in S4.

To estimate the value of pollination to longan crops, we used a method based on the economic loss that would occur in the absence of any insect pollinators. The net profit of the crop was then calculated per rai (1 ha = 6.25 rais) by calculating the costs per rai (material, machinery and miscellaneous costs) and subtracting them from returns (per rai). The average production costs were variable costs such as human costs of plantation preparation, planting, fertilizer, pesticide application and potassium chlorate application to stimulate early flowering, planting

materials, organic and chemical fertilizers, fuel or electricity costs and costs of repairing agricultural equipment. Fixed costs included agricultural equipment depreciation. Costs of honeybee hive maintenance do not need to be accounted for, as beekeepers pay farmers to allow bees to forage in their backyard gardens during the off-season.

2.7 | Statistical analyses

First, a probability distribution which best fits the response variables was identified by computing skewness and the kurtosis index in the package *rBASICS* (Wuertz et al., 2017). We verified that assumptions of normality and heteroscedasticity were met and that Poisson models were not over-dispersed. Treatments, flower abundance and pollinator groups were included as explanatory variables. Study sites and tree ID were included as a random effect, as every study site does not show a significant effect on the average of response variables. The Poisson distribution and log-link function were used for the following response variables: pollinator richness, visitation rate (number of visits per 15 min) and number of mature fruits (as all response variables were counts).

To test the effect of treatments and flower abundance on pollinator variables, the response variables (pollinator richness, visitation rate, fruit set) were examined using a GLMM with a Poisson distribution. Treatments (off-season with honeybee hives, off-season without honeybee hives and in-season) and flower abundance were included as explanatory variables. All explanatory variables of interest were fitted in the model and afterwards variables with a p value over 0.10 were removed from the models. The interactions between explanatory variables that contribute at least marginally to the model ($p < 0.10$) were also added. We used sample size corrected Akaike information criterion (AICc) to determine the best candidate model. The GLMM with the lowest AIC was selected (Burnham & Anderson, 2004). Akaike weights (wAICc) to quantify the probability by which a given model is the best within the candidate models set (Table S2). GLMMs were analysed using the package *LME4* (Bates et al., 2018). The 'glht' within 'multcomp' package was used to conduct post hoc Tukey's tests after GLMM (Hothorn et al., 2015). All statistical analyses were conducted with R 3.6.1 (R Core Team, 2018).

3 | RESULTS

Overall, a total of 42,727 flower visits by four pollinator groups (western honey bees, Asian honey bees, wild bees and flies) were observed, representing 97 morphospecies. *A. mellifera* honeybees were found at all sites throughout the year as a consequence of the hives placed in plots during the off-season. The most frequent native pollinator was the Asian honeybee, *Apis cerana*, with 43.8%; followed by dipterans with 40.1% and wild bees at 16.2%. The most frequent wild bees were stingless bees, with 62.1% of wild-bee flower visits.

3.1 | Effects of flowering time and flower abundance on pollinator richness and visitation rate

Flowering time and herbaceous flower abundance explained visitation rate and pollinator species richness. Visitation rate of flower visitor groups significantly differed among treatments ($p < 0.05$): for in-season flowering, wild bees were the most frequent pollinator group ($M \pm SD = 18.72 \pm 4.01$ visits/15 min), followed by *A. cerana* (8.53 ± 1.87 visits/15 min), dipterans (8.72 ± 3.91 visits/15 min) and *A. mellifera* (4.99 ± 1.99 visits/15 min); for off-season flowering without honeybees, dipterans (families Syrphidae and Calliphoridae) comprised the most frequent pollinator group (33.98 ± 16.41 visits/15 min), followed by *A. cerana* (6.46 ± 2.58 visits/15 min), *A. mellifera* (2.57 ± 2.09 visits/15 min) and wild bees (2.15 ± 1.74 visits/15 min); for the off-season flowering with honeybee treatment, *A. mellifera* were the most frequent pollinator group (24.29 ± 5.82 visits/15 min), followed by dipterans (19.95 ± 9.70 visits/15 min), *A. cerana* (10.69 ± 5.34 visits/15 min) and wild bees (2.27 ± 1.57 visits/15 min; Figure 2A). The effect of flower abundance on visitation rate depended on pollinator group, as there was a significant interaction between herbaceous flower abundance and pollinator group (GLMM; $\chi^2_3 = 7,977.45$, $p < 0.001$). While we did not detect an effect of flower abundance on visitation rate by dipterans ($\chi^2_3 = 1.03$, $p = 0.32$) and *A. mellifera* ($\chi^2_3 = 2.11$, $p = 0.15$) the visitation of wild bees ($\chi^2_3 = 10.54$, $p = 0.002$) and *A. cerana* ($\chi^2_3 = 741.75$, $p < 0.001$) were significantly impacted by flower abundance. There was also significant interaction effect between herbaceous flower abundance and treatments on visitation rate (Table S3). The effect of herbaceous flower abundance on visitation rate is significantly positive in in-season flowering ($\chi^2_3 = 75.42$, $p < 0.001$), whereas we did not detect an effect of flower abundance on visitation rate in off-season with and without honeybee hives (Table S3).

Species richness of visitors significantly differed by treatment ($\chi^2_3 = 193.40$, $p < 0.001$) but not flower abundance ($\chi^2_3 = 0.78$, $p = 0.38$). The species richness of pollinators was significantly higher during in-season flowering (26.84 ± 2.54 morphospecies) than off-season flowering with honeybees (5.75 ± 1.10 morphospecies) and off-season flowering without honeybees (4.75 ± 0.9 morphospecies; Figure 2B).

3.2 | Visitation rate, pollen loads and pollinator importance

The highest visitation rate was by *Apis cerana* ($M \pm SD = 40.6 \pm 4.96$ visits/15 min, followed by *Apis mellifera* (33.1 ± 6.72 visits/15 min) and *Tetragonilla collina* (32.7 ± 8.67 visits/15 min). On average, *Tetragonula laeviceps* carried the most longan pollen grains to stigmas per single visits (4 ± 1.54 grains), followed by *Heterotrigona itama* (3.5 ± 1.92 grains) and *Tetragonilla collina* (2.6 ± 1.06 grains; Table 1). Pollinator importance indices, based on visitation rate and pollen load, were highest for *Tetragonula laeviceps*, *Heterotrigona itama* and *Tetragonilla collina* (Table 1).

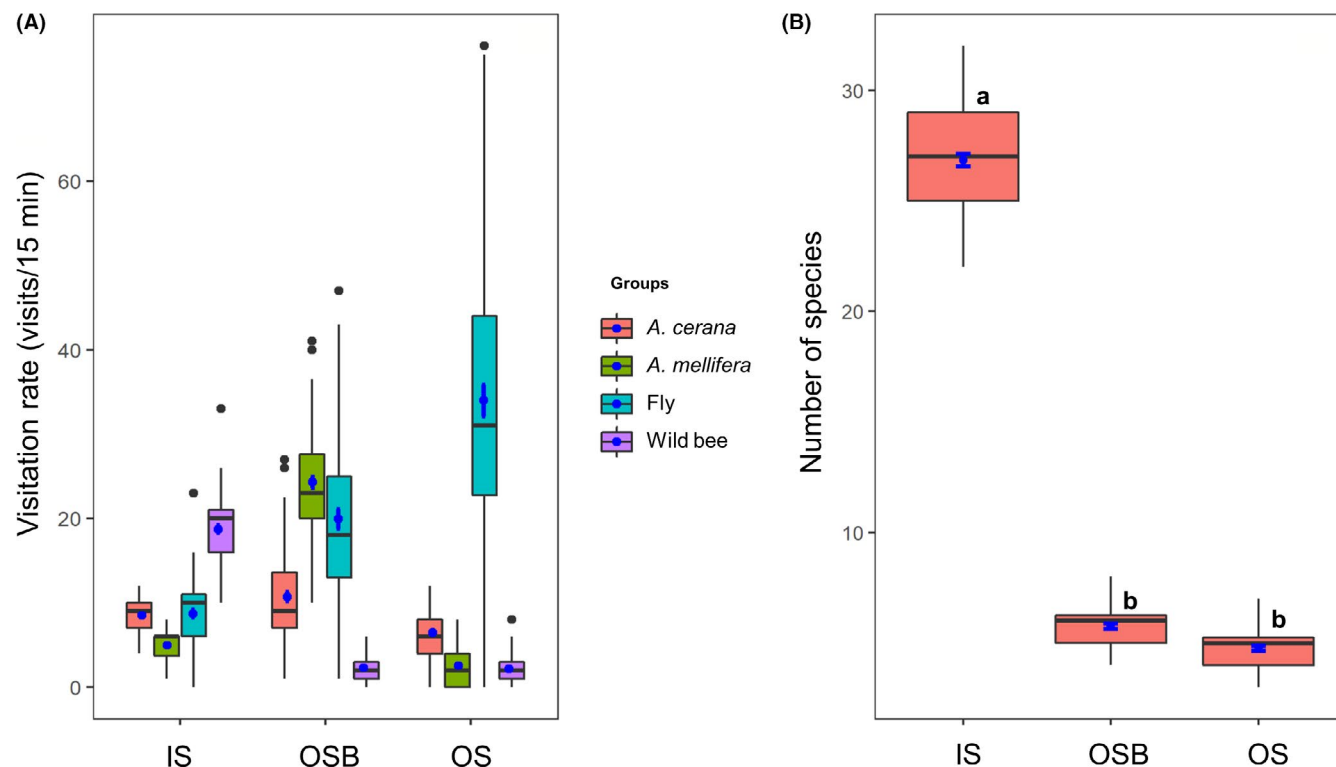


FIGURE 2 (A) The visitation rates of insects from different groups (fly, honeybee, wild bee) to longan flowers within 15 min observations. (B) The mean number of visitor species within 15 min observations during the in-season (IS), off-season with honeybee hives (OSB) and off-season without honeybee hives (OS)

TABLE 1 Mean (\pm SD) values of parameters used to calculate pollinator importance (number of longan pollen grains per single visit \times visitation rate). The relative importance (RI) of each species as a pollinator is the fraction of pollinator importance for each species over the sum of pollinator importance across species. Species with RI > 0.05 are considered important pollinators

	Visitation rate/15 min	#Pollen grains from single visit	Pollinator importance	Relative importance
<i>Tetragonula laeviceps</i>	28.8 \pm 7.25	4 \pm 1.54	115.2	0.20
<i>Heterotrigma itama</i>	28.9 \pm 6.53	3.5 \pm 1.92	101.15	0.17
<i>Tetragonilla collina</i>	32.7 \pm 8.67	2.6 \pm 1.06	85.02	0.15
<i>Apis cerana</i>	40.6 \pm 4.96	1.7 \pm 0.74	69.02	0.12
<i>Apis mellifera</i>	33.1 \pm 6.72	1.5 \pm 0.64	49.65	0.08
<i>Apis florea</i>	24.3 \pm 2.41	1.8 \pm 0.83	43.74	0.07
Calliphoridae (Blow flies)	27.9 \pm 7.59	1 \pm 0.60	27.9	0.05
Syrphidae (Flower flies)	29.1 \pm 11.80	0.8 \pm 0.71	23.28	0.04
<i>Apis dorsata</i>	18.6 \pm 6.48	1.1 \pm 0.79	20.46	0.03
Muscidae (House flies)	19.9 \pm 8.82	1 \pm 0.74	19.9	0.03
Halictidae	8.6 \pm 2.26	1.6 \pm 1.14	13.76	0.02
Megachilidae	9 \pm 1.81	1.2 \pm 0.93	10.8	0.02
Vespidae	5.3 \pm 2.21	1.1 \pm 0.67	5.83	0.01

3.3 | Fruit set

Results of the pollination experiment showed a significant difference across treatments (Figure 3). The average fruit-set in open pollination at 2 weeks was highest for the in-season treatment (83.24 \pm 13.94 fruits per inflorescence), followed by off-season with honeybee hives treatment (54.01 \pm 14.71 fruits per inflorescence) and off-season without honeybee hives treatment (26 \pm 7.99 fruits per inflorescence). The

average initial fruit set in closed pollination at 2 weeks was lower than four fruits in all treatments. Fruit abortion occurred in all treatments for mature fruit, especially in closed pollination. Closed pollination treatments yielded no mature fruit. The average number of mature fruits in open pollination for the in-season treatment (50.20 \pm 16.86 fruits) was significantly greater than the off-season with honeybee hives (35 \pm 10.53 fruits, $p < 0.01$) and off-season without honeybee hives (15.42 \pm 2.80 fruits, $p < 0.01$; Figure 3B).

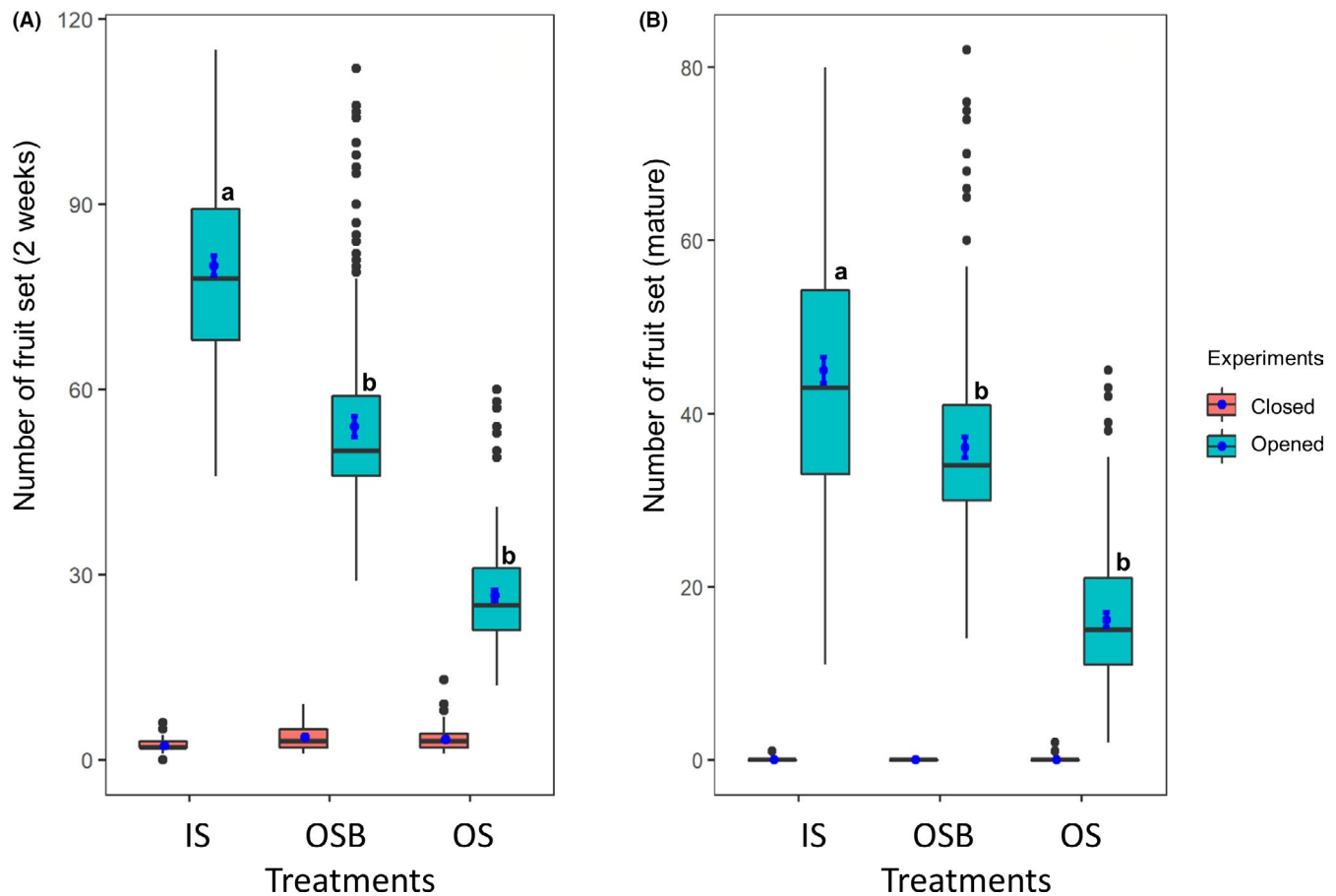


FIGURE 3 (A) The fruit set within 2 weeks and (B) mature fruits from closed and open pollination experiments from the in-season, off-season with bee and off-season without bee treatments. Different letters above the columns indicate significant differences between different treatments ($p < 0.05$), as revealed by GLMM followed by post hoc Tukey's tests for multiple comparisons

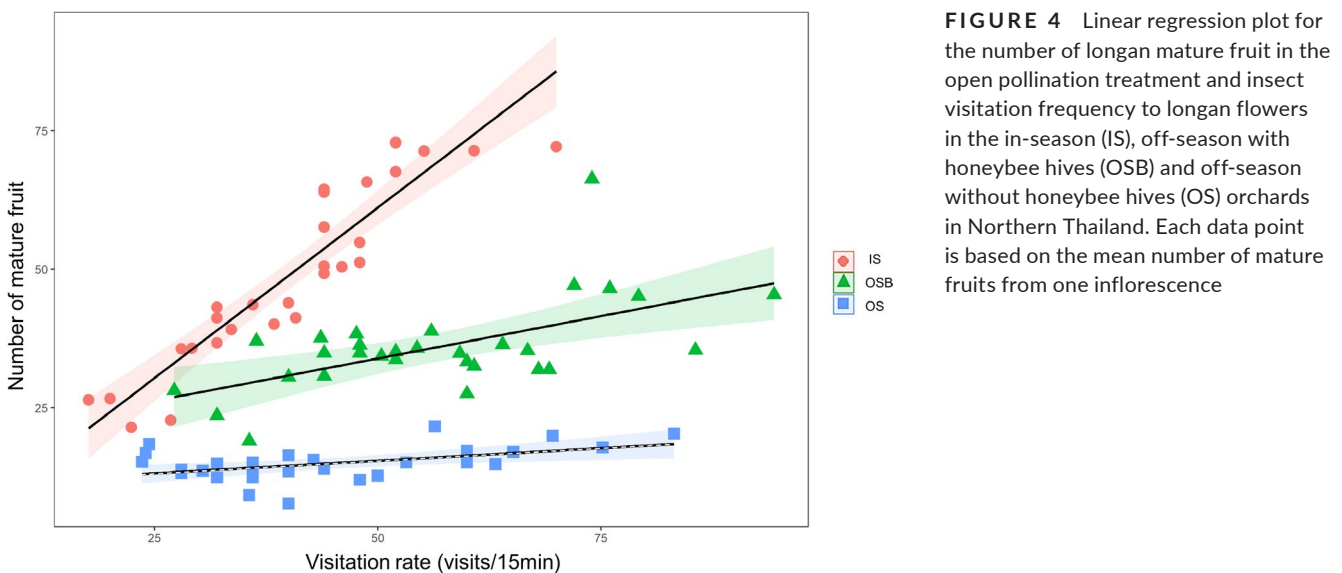


FIGURE 4 Linear regression plot for the number of longan mature fruit in the open pollination treatment and insect visitation frequency to longan flowers in the in-season (IS), off-season with honeybee hives (OSB) and off-season without honeybee hives (OS) orchards in Northern Thailand. Each data point is based on the mean number of mature fruits from one inflorescence

The effect of visitation rate on the number of mature fruit depended on the treatment (Figure 4). There was a significant interaction between visitation rate and treatments (Figure 4, GLMM; $\chi^2_3 = 301.95$, $p < 0.001$). The number of mature fruits in the in-season (GLMM, $\chi^2_3 = 1,003.1$, $p < 0.001$) and off-season

with honeybee hives (GLMM, $\chi^2_3 = 82.256$, $p < 0.001$) were significantly affected by visitation rate, while we did not detect an effect of visitation rate on the number of mature fruits in off-season without honeybee hives beekeeping (GLMM, $\chi^2_3 = 0.687$, $p = 0.407$).

TABLE 2 Comparison mean \pm SE of cost and net margin of longan production from the three treatments. Production costs consisted of variable and fixed costs, including fertilizer, spray (stimulate), weeding, harvest, logistic, agricultural equipment depreciation. All costs and benefits are in Thai Baht. Here, 'bee' refers to honeybee *Apis mellifera* management specifically

	Off-season without Bee		Off-season with Bee		In-season	
	Large	Small	Large	Small	Large	Small
Marketable yield (kg/rai)	227 \pm 97	176 \pm 61	385 \pm 28	352 \pm 36	419 \pm 2	321 \pm 20
Price (THB/kg)	40 \pm 4	23 \pm 2	40 \pm 4	23 \pm 2	30 \pm 8	20 \pm 3
Bee payment from bee keeper (THB/rai)	0	0	750	750	0	0
Income (THB/rai)	9,067 \pm 369	4,032 \pm 431	15,400 \pm 714	8,096 \pm 78	12,579 \pm 380	6,420 \pm 262
Cost (variable + fixed costs, per rai)	3,245 \pm 608		3,245 \pm 608		2,751 \pm 187	
Net profit (THB/rai)	9,854 \pm 2,635		20,250 \pm 2068		16,248 \pm 2,890	

3.4 | Economic valuation

The average production cost for off-season longan management (3,245.31 THB/rai) was higher than the cost of in-season management (2,751.77 THB/rai; Table 2). Fruit were higher valued in the off-season, with large and small size class longan ranging from 35 to 45 THB/kg and 20 to 25 THB/kg, respectively (Figure 1). In off-season longan without beekeeping, the farmers produced a yield of 402 ± 50.13 kg/rai ($M \pm SD$) with 226.67 ± 96.67 kg/rai of the large size class and 175.33 ± 61.07 kg/rai of the small size class, while in off-season longan with beekeeping the farmers produced yield of 737 ± 11.43 kg/rai, with 385 ± 28.17 kg/rai of large size class fruits and 352 ± 36.02 kg/rai of small size class fruits. In-season longan were less expensive; the price per kg of longan in big and small size classes in the off-season ranged from 20 to 40 THB/kg and 14 to 20 THB/kg, respectively. In-season, farmers produced a yield of 740.33 ± 18.57 kg/rai with 419.33 ± 1.70 kg/rai of large size class fruits and 321 ± 20.05 kg/rai of small size class fruits.

The contribution of insect pollinators to the economic value of longan varied in different management types, providing net profits (after both variable and fixed cost are accounted for) of $9,854.08 \pm 2,635.31$ THB/rai for the off-season without honeybee hives treatment, $20,250.69 \pm 2068.19$ THB/rai for off-season with honeybee hives treatment and $16,248.13 \pm 2,890.40$ THB/rai for in-season treatment.

4 | DISCUSSION

This study highlights the critical role of temporal variation for pollination services in longan. There are two important results. First, temporal variation in the pollinator community significantly impacted the pollination efficiency of longan crops and, thus, the economic benefits vary across the year, with off-season crops strictly requiring managed pollinators. Second, the visitation rate of wild bees and honeybees to longan flowers increased with the number of non-crop flowers in the orchards. We will discuss each of these elements, including economic valuation and implications for conservation.

4.1 | Pollination services in longan orchards

Our results demonstrate that pollination rates in longan, as represented by both initial fruit-set and mature fruit-set, are substantially enhanced by pollinators, especially native pollinators. Similar to previous studies (e.g. Blanche et al., 2006; Pham et al., 2016), we found a diverse range of insects in longan orchards, with a total of 97 bee and fly morphospecies. As expected, pollinators differed in their crop pollination efficiencies (Rader et al., 2019). Stingless bees (*Tetragonula laeviceps*, *Heterotrigona itama* and *Tetragonilla collina*) and honeybees (*A. cerana* and *A. mellifera*) were the most useful pollinators of longan based on the amount of pollen deposited to the stigma per visit and their visitation rates.

Previous studies have found that high diversity of insect communities improve the pollination efficiency of both wild plants and crops by complementarity, where the pollinator species with higher and lower abundance can help enhancing a yield threshold (Hoehn et al., 2008; Winfree et al., 2018). However, species turnover is also crucial for reaching this threshold (Winfree et al., 2018). In some agricultural systems, the frequency in fluctuations of the most abundant pollinator species may have greater effect on temporal variation in pollination services than changes in species richness (Genung et al., 2017). This study shows that temporal variation in the pollinator community significantly alters the pollination efficiency of longan crops between off-season and in-season flowering in cultivated areas. In November, the early flowering period, bees were scarce and flies of the family Syrphidae (flower flies) were instead the most frequent visitors, but provided little contribution in pollen deposition, surprisingly, despite their importance in other systems (Rader et al., 2016, 2019). In contrast, in the January and February flowering season, stingless bees and native honeybees *A. cerana* became the main visitors of longan crops, providing superior pollination services. These primary pollinators are similar to those from both a prior study on longan (Blanche et al., 2006) and other crops from the same region such as rambutan (Sritongchuay et al., 2016), lychee (Rai et al., 2017) and guava (Hansen et al., 2020). The pollination efficiency results of our study indicate that the fruit set of open

pollination was significantly different in the three treatments; the average number of mature fruits in open pollination was greatest for the in-season treatment, followed by off-season with honeybee hives. Moreover, the positive relationship between the number of visits to longan with initial fruit set and mature fruit in the off-season with honeybee hives and in-season treatments suggests that bees (wild and managed) are the major pollinating insects of longan flowers. In contrast, the number of mature fruits was not affected by the visitation rate in the off-season without honeybee hives treatment because longan flowers were being visited by flies that were not effective pollinators. Therefore, in the early flowering period without honeybee management, fly visitation is insufficient for economically viable fruit production in longan crops.

Temporal variation in pollinator visitation and efficiency determined the reproductive success of longan. During the in-season flowering period, stingless bees visit longan flowers early in the day, removing and depositing more viable pollen than other pollinators; furthermore, stingless bees had four times greater pollen deposition to longan flowers than honeybees, blow flies and flower flies. These results suggest that stingless bees are the most effective pollinators of longan. As key pollinators, the phenology of stingless bees in seasonal environments is an important determinant of these temporally variable pollinator assemblages. Previous studies indicate that the activity of stingless bees is influenced by both abiotic factors, such as temperature or rainfall and differences in floral resource availability (Aleixo et al., 2017; Eltz et al., 2002). However, the temperature and humidity during off-season (November and December 2018) and in-season (January and February 2019) are in the same range. In addition, Phankaew (2016) found that the life-cycle of stingless and other bee activity in the Northern Thailand is synchronized with the natural blooming period of both important crops like longan and lychee as well as native herbaceous species from January to March.

4.2 | Effects of non-crop flowers on wild insects and managed honeybees

The visitation rates of wild bees and honeybees to longan flowers increased with the number of non-crop flowers in the orchards, suggesting that non-crop plants which flower year-round enhanced local populations of wild pollinators (mainly wild bees) in longan orchards and surrounding natural habitats. To maintain large populations in agricultural landscapes, wild pollinators require sufficient nesting and food resources (Kremen et al., 2004; Sritongchuay et al., 2016, 2019). For highly eusocial species such as stingless bees, resources must also be present well beyond the primary crop flowering period. Conventionally managed orchards represent partial or sub-optimal habitats for these pollinators due to lacking floral resources in periods outside of crop bloom. Therefore, the positive trends observed in visitation rates (wild and managed bees) with the number of non-crop flowers are expected to be a consequence of additional floral

resources in the period following crop bloom supporting local insect populations with higher fitness benefits relative to populations without them (although lacking floral resources may also correspond to other intensive management strategies like tilling that can also be detrimental to bees; Roulston & Goodell, 2011). Our findings add to the growing body of evidence that pollinator-friendly management schemes at local scales can boost wild pollinator populations on farms (Garibaldi et al., 2016).

4.3 | Economic valuation and conservation implications

Our estimate of the value of longan pollination to the economy is comparable but slightly lower than the only previous estimate in Thailand (Boonyaritthongchai et al., 2015) which valued intensively managed longan in eastern Thailand at about 25,000 THB/rai (higher than the values for longan produced for domestic consumption here). Here, we estimate the net value of insect pollination after costs are deducted for off-season longan without beekeeping at 9,854 THB/rai, whereas at 20,250 THB/rai for off-season with honeybee hives and 16,248 THB/rai for in-season. Our study indicates that longan production from off-season longan farms, where early flowering is induced using potassium chlorate to produce off-season fruit, gains significantly less net profit in the absence of managed bees and wild bees. The farmers practicing off-season with honeybee hives management gain the largest net profit, indicating that use of honeybees in the off-season is an effective method for increasing crop yields and farm profits. Although practicing off-season longan with honeybee *A. mellifera* management increases farm profit, local bee species management such as *A. cerana*, *Tetragonula pagdeni* (Schwarz) and *T. laeviceps* Smith could possibly avoid the issue of using exotic pollinator species, as in these environments they may be more suitable and profitable managed pollinators.

In addition, we found that beekeepers in Chiang Mai province often pay longan farmers a fee to let their colonies forage longan nectar on their farms, consistent with some other studies (Narjes & Lippert, 2019). Interestingly, Narjes and Lippert (2019) predicted that the farmers will allow beekeepers to place bee hives for free for optimum pollination services, but that beekeepers are required to pay farmers for exclusive right to floral resource if beekeepers add more hives, as excessive visits can be bad for production. However, if many farmers adopted off-season management with honeybees, this would shift supply and demand such that beekeepers might instead charge for use of their bees, depleting the profits of practicing off-season longan with managed honeybees. Moreover, beekeepers in some parts of Thailand avoid placing their honeybee colonies in off-season longan farms because it is difficult for beekeepers to protect their colonies from pesticide exposure at that time (Phankaew, 2016). Beekeepers may only be prepared to pay longan farmers because of scarce natural flowers in the winter, thus when native flowers are abundant there is no incentive for them to pay for a free service, and with native pollinators available during

this period it is unlikely longan producers would pay for the service in-season; thus, though the concept is interesting, it is economically not supported in the current season, whereas mechanisms to increase native pollinator abundance carry little long-term cost.

Wild bees are the primary pollinators of longan fields, but in the early flowering period these insects are at low abundance in large fields, perhaps due to insufficient nesting sites (Olliff-Yang & Mesler, 2018) or competition for resources with honeybees (Rafferty et al., 2015). Our findings highlight the dependence of commercial fruit producers on honeybees and suggest that increasing the pollination contribution of other bees, particularly stingless bees, will encourage that growers adopt wild-bee conservation strategies or install managed colonies in their fields (Garibaldi et al., 2014). Although farmers are presently paid for allowing honeybees in their crops, this could change with market conditions, making wild bees a more stable option. The effects of availability of mass-flowering crops on bees and their colonies are difficult to discern because visiting such crops often exposes bees to pesticide residues so that positive effects of increased food availability may be offset by negative effects of the pesticides (Goulson et al., 2015). Moreover, practices that intercrop different agronomic species (where one of them is likely to provide shelter) and allowing non-crop vegetation around field borders will preserve, or even enhance, wild-bee pollination services.

Our study did not include an in-season with honeybee hives treatment, as honeybees are removed during this period because of pesticide use. Thus, studies to investigate the competition of honeybees and wild bees, and including how a landscape context (i.e. proximity to forest) influences wild-bee abundance would also be useful to understand how to enhance the provision of natural pollination services. Further research will also be needed to explore the impacts of changes of climate as a driver of phenological asymmetry and how the ability of natural systems to continue to provide services is impacted by their diversity.

In summary, our findings suggest that pollination of crops by wild bees relies on our ability to maintain or create a natural area providing food and nest resources for wild pollinators within agricultural matrixes and optimal management of off-season longan for maximum yield and net profit. We show the importance of native pollinators to the viable economic production of tropical tree crops. The study also demonstrates the sensitivity of these systems to climatic change, which could also cause phenological shifts in flowering. Developing means to promote and maintain pollinator abundance and diversity is likely to increase the resilience of the system in addition to profit in the long term; thus, efforts should be made to provide more nesting habitat and reduce pesticide use (through enhanced provision of natural alternatives).

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AUTHORS' CONTRIBUTIONS

T.S., K.W., M.C.O. and A.C.H. conceived the ideas and designed methodology; T.S. collected the data; T.S. analysed the data; T.S. and A.C.H. led the writing of the manuscript; T.S., K.W., M.C.O. and A.C.H. contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data available via the Figshare Digital Repository <https://doi.org/10.6084/m9.figshare.13088930> (Sritongchuay, 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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