Received: 21 December 2020 | Revised: 27 July 2021 | Accepted: 31 August 2021

DOI: 10.1111/btp.13023

bioTROPICA ASSOCIATION FOR TROPICAL BIOLOGY AND CONSERVATION WILEY

ORIGINAL ARTICLE

Even small forest patches increase bee visits to flowers in an oil palm plantation landscape

Candice C. Power[1,2] | **Anders Nielsen**[3,4] | **Douglas Sheil**[1,5,6]

[1]Faculty of Environmental Sciences and Natural Resource Management, Norwegian University of Life Sciences (NMBU), Ås, Norway

[2]Department of Biology, Center for Biodiversity Dynamics in a Changing World (BIOCHANGE), Aarhus University, Aarhus, Denmark

[3]Department of Landscape and Biodiversity, Norwegian Institute of Bioeconomy Research (NIBIO), Ås, Norway

[4]Department of Biosciences, Centre for Ecological and Evolutionary Synthesis (CEES), University of Oslo, Oslo, Norway

[5]Wageningen University and Research, Wageningen, The Netherlands

[6]Center for International Forestry Research (CIFOR), Bogor, Indonesia

Correspondence
Douglas Sheil, Wageningen University and Research, 47, 6700AA, Wageningen, Netherlands
Email: douglas.sheil@wur.nl

Funding information
Norges Miljø- og Biovitenskapelige Universitet, Grant/Award Number: TEMNR Field Grant; Centre for International Forestry Research

Associate Editor: Jennifer Powers

Handling Editor: Sofia Gripenberg

Abstract

Pollination sustains biodiversity and food security, but pollinators are threatened by habitat degradation, fragmentation, and loss. We assessed how remaining forest influenced bee visits to flowers in an oil palm-dominated landscape in Borneo. We observed bee visits to six plant species: four crops (*Capsicum frutescens* L. "chili"; *Citrullus lanatus* (Thunb.) Matsum & Nakai "watermelon"; *Solanum lycopersicum* L. "tomato"; and *Solanum melongena* L. "eggplant"); one native plant *Melastoma malabathricum* L. "melastome"; and the exotic *Turnera subulata* Smith "turnera". We made one local grid-based and one landscape-scale transect-based study spanning 208 and 2130 m from forest, respectively. We recorded 1249 bee visits to 4831 flowers in 1046 ten-min observation periods. Visit frequency varied among plant species, ranging from 0 observed visits to *S. lycopersicum* to a mean of 0.62 visits per flower per 10 min to *C. lanatus*. Bee visitation frequency declined with distance from forest in both studies, with expected visitation frequency decreasing by 55% and 66% at the maximum distance from forest in each study. We also tested whether the distance to the nearest oil palm patch, with a maximum distance of 144 m, influenced visitation, but found no such associations. Expected visitation frequency was 70%–77% lower for plants close to a 200 ha forest fragment compared with those near large continuous forests (>400 ha). Our results suggest that, although found throughout the oil palm-dominated landscape, bees depend on remaining forests. Larger forests support more bees, though even a 50 ha fragment has a positive contribution.

Abstract in Indonesian is available with online material.

KEYWORDS
agricultural landscapes, Borneo, Indonesia, remnant forests, Southeast Asia, visitation frequency, wild pollinators

1 | INTRODUCTION

Oil palm plantations (dominated by plantings of the African oil palm *Elaeis guineensis* Jacq.) covered over 18.7 million hectares (Mha) worldwide in 2017 and continue to increase (Meijaard et al., 2018). Much of this expansion has been in Borneo where at least 3.06 Mha of species-rich old-growth forests were converted to industrial plantations between 2000 and 2017 (Gaveau et al., 2018). Such dramatic changes in land cover have major ecological consequences, highlighting the need for research that contributes to the healthy functioning of this important and widespread landscape (Foster et al., 2011). Seeking the best ways to maintain ecological complexity by

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.
© 2021 The Authors. *Biotropica* published by Wiley Periodicals LLC on behalf of Association for Tropical Biology and Conservation.

incorporating forest and other vegetation has become an important issue for plantation owners and planners (Meijaard et al., 2016; Yahya et al., 2017). One motivation for this is to maintain a range of different taxa, including wild pollinators, within the landscape.

Although pollinators are mobile, they can be greatly affected by habitat fragmentation. The conversion of native forests to cultivated land has the potential to cause the loss of both feeding sites (sources of pollen and nectar) and suitable nesting habitat for pollinators (Patrício-Roberto & Campos, 2014). The habitat requirements of pollinators can be complex (e.g., different nesting and foraging habitats; Antoine & Forrest, 2020; Westrich, 1996), which makes them particularly sensitive to habitat loss and fragmentation. Most (an estimated 94%) tropical flowering plants are animal-pollinated (Ollerton et al., 2011). A decline in pollinators thus impacts the reproduction of wild plants and consequently entire ecosystems (Burkle et al., 2013; IPBES, 2016; Potts et al., 2010). Landscape changes, including those within the remnant fragmented areas, may cause loss of genetic variability and population stability, potentially leading to the disappearance of populations (Patrício-Roberto & Campos, 2014; Sodhi et al., 2004) and having severe effects on pollinator services (Potts et al., 2010).

Many food crops require animal pollination to maximize fruit set, size, and quality (Ollerton et al., 2011). Even oil palm is primarily pollinated by African weevils (*Elaeidobius kamerunicus* Faust) that increase fruit set and yield (Caudwell, 2001; Zulkefli et al., 2021). Wild pollinators in particular contribute to the productivity and viability of many crops (Garibaldi et al., 2013) and thus to food security and nutrition (Ellis et al., 2015; Garibaldi et al., 2016). Evidence of this exists for many crops including watermelon (Sawe et al., 2020), tomatoes (Cooley & Vallejo-Marin, 2021; Neto et al., 2013), and chilies (Landaverde et al., 2017). Land-use conversion can disrupt pollination services on which the crops depend (see, e.g., Klein et al., 2003; Ricketts et al., 2008). Such disruptions add to the pollinator declines already seen worldwide, reflecting not just habitat loss but also damaging land-use practices (e.g., pesticide use) and climate change (Potts et al., 2010). While oil palm has raised incomes and living standards in Indonesia (Qaim et al., 2020), there are concerns that diet quality may have declined (Food Security Council et al., 2015; Ickowitz et al., 2016). One possible reason is the difficulty of producing highly nutritional, pollination-dependent food crops in landscapes with insufficient pollination services.

We recognized that a better understanding of pollinator activity may contribute to improved planning and management of the landscape to maintain local pollinators and their beneficial role. Here, we assess bee activity within a landscape of industrial oil palm and remnant forest in West Kalimantan, Indonesia. Our main aim was to determine whether the number of bee visits to flowers is affected by distance to forest. We hypothesize that the frequency of bee visits to flowers of the selected plant species will decrease with distance from forest. A further aim of our study was to test whether flower visitation rates by bees were dependent on the distance to the nearest planted oil palm patch. We expect palm trees to have conditions more similar to forest and to provide more resources for bees than agricultural fields, fallows, and other open land. Therefore, we hypothesize there will be an increase in bee visits when flowers are closer to planted palm compared with non-forested areas. To answer our study questions, we observed bee visits to six plant species and related the visitation frequencies to distance from forest while controlling for weather and time of day. To our knowledge, this is the first study to assess bee visitation frequency to both wild plants and food crops within an oil palm-dominated landscape.

2 | METHODS

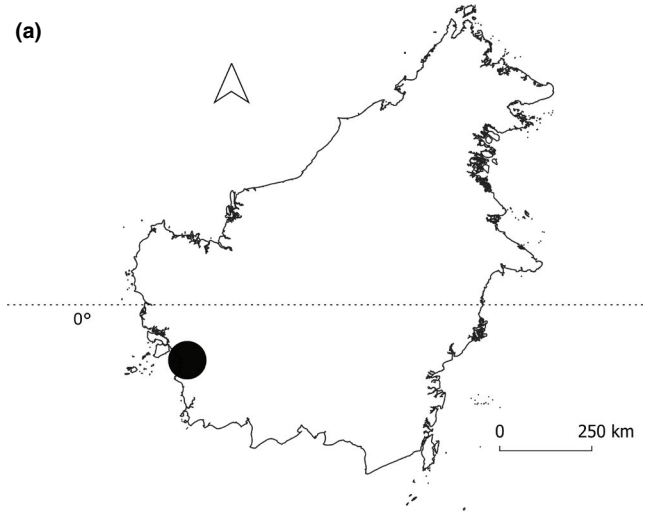
2.1 | Study area

This study was conducted from June to November 2017 within the concession of PT Kayung Agro Lestari (KAL) in Kabupaten Ketapang in the province of West Kalimantan, Borneo, Indonesia (1°26′00.0″S 110°13′00.0″E; Figure 1a). The plantation is owned and managed by PT Austindo Nusantara Jaya (ANJ), a member of the Roundtable on Sustainable Palm Oil (RSPO) (PT Austindo Nusantara Jaya Tbk, 2016). Before conversion to oil palm plantation, the landscape was primarily logged-over natural forest (~8600 ha) and degraded land (Meijaard et al., 2016). Conversion started in 2010 and by 2016, 12,061 ha out of the 17,998 ha had been planted (Meijaard et al., 2016; PT Austindo Nusantara Jaya Tbk, 2016). Here, we use the terms "oil palm plantation" and "plantation" when referring to the entire area inside of the concession and "planted oil palm" when referring to sections of monoculture planted oil palm within the plantation.

The majority of the planted oil palm grows on shallow peat (~63%), with less on mineral soil (~33%) and sands (~4%). The palms are planted about 9 m apart resulting in a mostly closed canopy. Intensive maintenance, including regular physical clearance of ground vegetation and application of herbicides, results in little understory vegetation among the planted palms. Sixteen forested areas (20–2333 ha), 21% (3884 ha) of the concession, have been identified as having High Conservation Value (HCV) and are regularly monitored by the company (Meijaard et al., 2016).

2.2 | Study species

We studied bee visits to six angiosperm species (Table S1). Four of these (*Capsicum frutescens* L. "chili," *Citrullus lanatus* (Thunb.) Matsum & Nakai "watermelon," *Solanum lycopersicum* L. "tomato," and *Solanum melongena* L. "eggplant") are common local crops. The other two, the native *Melastoma malabathricum* L. and the introduced *Turnera subulata* Smith, have a wide distribution throughout the plantation. All the focal species are non-native except *M. malabathricum*, which is a common colonizing plant that occurs in cleared, degraded areas near forest edges within the plantation. *T. subulata* is planted as a method of bio-control for leaf-eating caterpillars (fire- and bagworms), common pests to oil palm (Rashid et al., 2014).



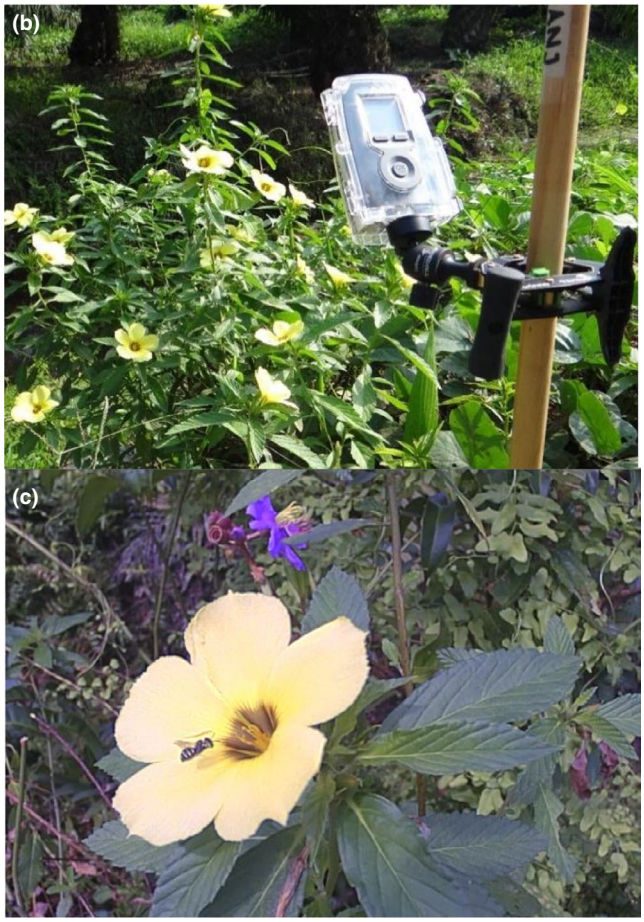


FIGURE 1 (a) Location of the study area on the West coast of Indonesian Borneo. (b) Setup of a Brinno BCC200 Pro camera using a T1 Clamp tripod attached to a wooden pole, to observe planted *Turnera subulata* adjacent to oil palm. (c) An image captured by a Brinno BCC200 Pro camera of a bee visiting a *T. subulata* flower

2.3 | Study design

We conducted two studies: The first (hereafter referred to as the "Grid Study") was a systematically planned study of crop plants within an extensively cleared area of several hectares and the second was a transect study (hereafter referred to as the "Transect Study"). The Grid Study spanned up to a maximum distance of 208 m from forest and 144 m from planted palm (Figure 2a), while the Transect Study spanned from the forest edge up to 2130 m from natural forest.

Transect locations were chosen to represent a range of forest sizes and distances from these (Table S2). Forest 1 is a large, continuous forest that extends beyond the plantation boundary; Forest 2 is a conserved forest within the plantation that extends beyond the boundary; and Forest 3 is an isolated secondary forest hill surrounded by oil palm. The Grid Study was conducted in relation to Forest 4, an isolated hill that has been classified as a high conservation value area.

2.3.1 | Grid Study

We conducted the Grid Study between 22 July and 5 September 2017. In total, we obtained 397 plants, growing in individual poly bags. Due to mortality at the nursery, the number of individuals varied among the species: 134 *C. lanatus*, 108 *S. melongena*, 105 *S. lycopersicum*, and 50 *C. frutescens*. We placed the nursery-grown plants in a grid consisting of twelve plots, with three columns following a gradient from edge of forest and four rows following a gradient from edge of planted oil palm. Each plot had about six columns and six rows of plants, with ~0.5 m spacing between the plants. Plants were assigned randomly to ensure each plot consisted of a representative sample of all study species. The area already had scattered individuals of naturally growing *M. malabathricum* and planted *T. subulata*, allowing assessment of the effect of distance to forest and to planted palm using all six study species.

2.3.2 | Transect Study

We conducted the Transect Study from 15 to 29 October 2017. We observed visits to one plant species, *T. subulata*, within six different transects (Transects A–F). Transects were established in relation to three forested areas (Figure 2b), with each forest having two transects adjacent to it (Figure S1). The transects were located along roadsides where *T. subulata* had been planted, starting as close to the forest edge as possible and continuing for at least 300 m into planted oil palm. Along each transect, we identified four observation points. The *T. subulata* growing closest to the edge of forest was designated as observation point one. We then walked along the transect for about 100 m, measured by a handheld GPS unit, where we located the closest *T. subulata* bush as the second observation point. This process was then repeated for the remaining two observation points. The observation points were selected based on the presence of at least one *T. subulata* bush. The distance between observation points, and the maximum distance from forest (Table S3), varied due to the variation in spacing between the planted *T. subulata*. To

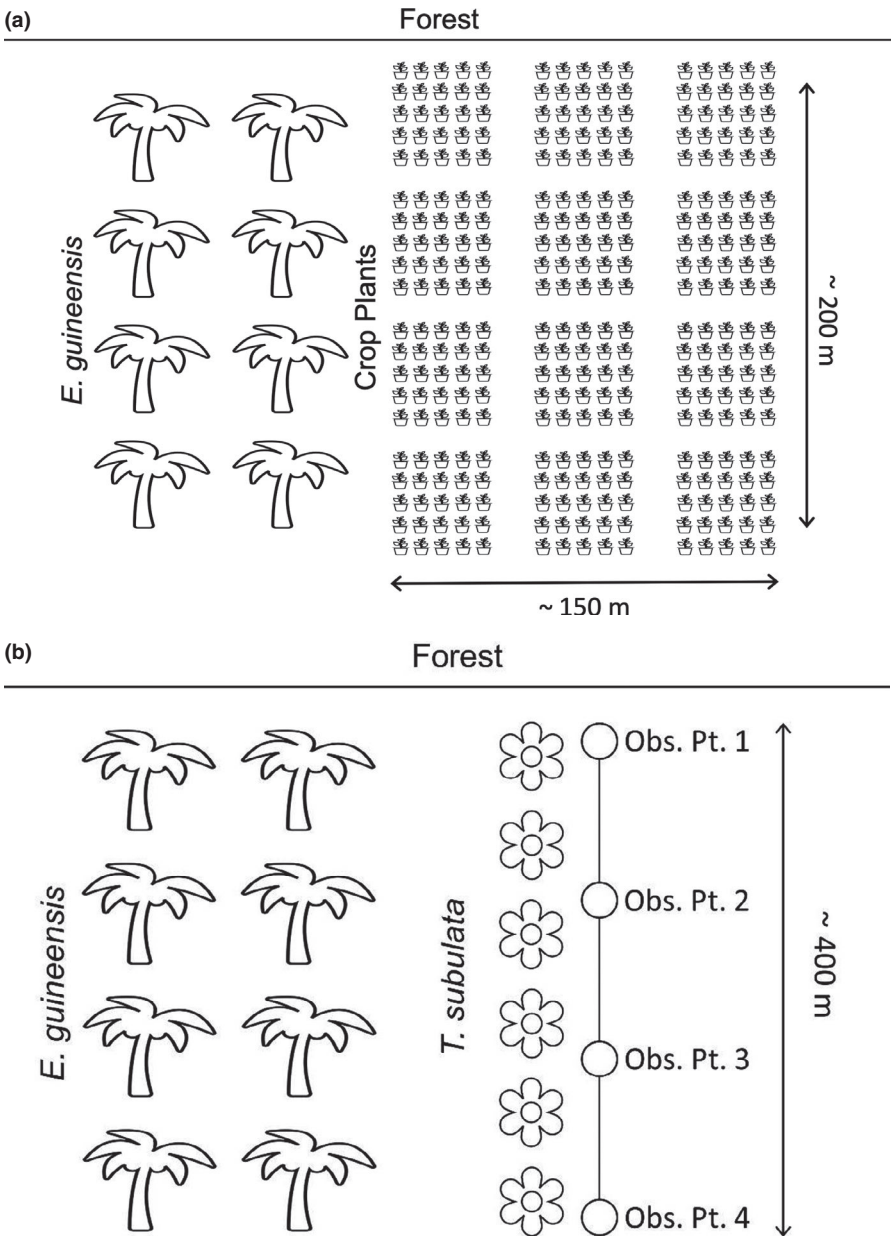


FIGURE 2 (a) Schematic (not to scale) of the grid layout of the crop plant plots for the Grid Study. The observed plants were the crop species (*Citrullus lanatus*, *Solanum melongena*, *Capsicum frutescens*, and *Solanum lycopersicum*), as well as some *Solanum malabathricum* and *Turnera subulata* growing at the study site. (b) Schematic (not to scale) of the transect layout for Transects A, B, C, D, E, and F in the Transect Study. The figure shows one representative transect. *T. subulata* was the only observed plant species

assess pollinator activity further within planted oil palm, we established four additional observation points located more than 800 m from the forest (with a range from 824 to 2130 m) (Figure S1). Final distances between each observation point and the edge of the nearest forest, observed from satellite imagery, were measured using Google Earth.

2.4 | Data collection for both Grid and Transect Studies

2.4.1 | Direct flower visit observations

To estimate flower visitation frequencies, we observed pollinator visits to flowers on all the above-mentioned plant species. We define a visit as a pollinator making apparent contact with the stigma or anthers of the preselected flowers. Each observation period lasted 10 min, and all were conducted by the same observer. During the observation period, all observed pollinator visits were recorded, but later we focused on analyzing only the bee data. Due to taxonomic challenges and the low numbers of visits from some morpho-species, we analyzed all bees as one group. Specimens in an adjacent study were collected and photographed (Hessen, 2020), and visual identification of these specimens was carried out by John S. Ascher based on diagnostic characters documented in Soh and Ascher (2020).

The number of observed flowers for each observation varied, depending on how many flowers were open and their aggregation (ensuring the observer, or the camera, could adequately monitor all flowers simultaneously; range: 1–36, mean: 4.6). The sequence and starting point of which the transects, and plots along the transects, were observed was chosen at random. Observations were conducted between 05:30 and 18:00 h (mean: 1000 h), with most being

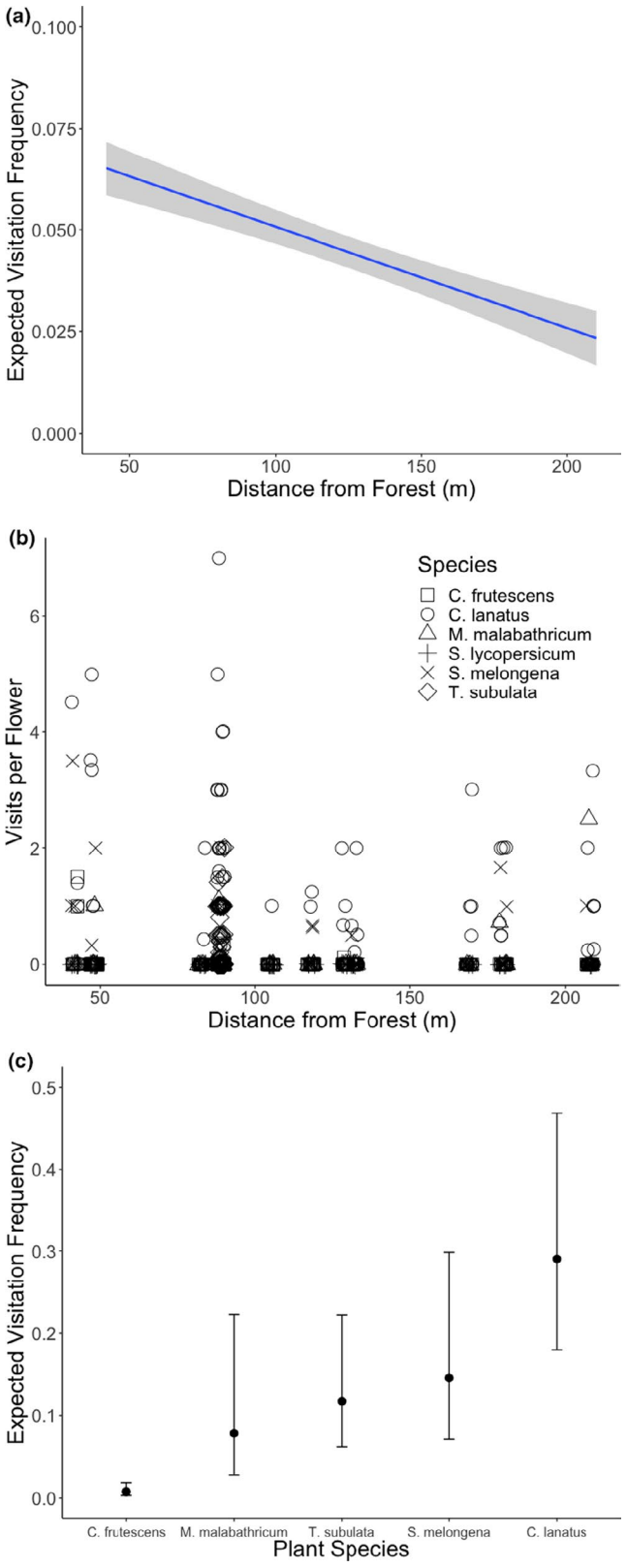


FIGURE 3 (a) Expected visitation frequency per flower per 10-min observation period in the Grid Study in relation to distance from forest (m), with all other variables remaining constant. Expected visitation frequencies are based on Model 1 estimates, and shaded area represents upper and lower estimates ($n = 667$). (b) Bee visits per flower per 10-min observation period in the Grid Study, in relation to distance from forest (m). Points represent raw observed bee visits per flower per 10-min observation period ($n = 723$). (c) Expected visitation frequency per flower per 10-min observation period to each study species, with all other variables remaining constant. Points represent Model 1 estimates, and error bars represent upper and lower estimates (*Melastoma malabathricum* $n = 32$, *Turnera subulata* $n = 75$, *Solanum melongena* $n = 94$, *Citrullus lanatus* $n = 186$, and *Capsicum frutescens* $n = 280$)

during morning hours when most flowers were open. Observations were not conducted during rain.

2.4.2 | Flower visit observations with cameras

We used Brinno BCC200 Pro cameras to perform additional flower visit observations. We used a T1 Clamp tripod to attach the camera to a wooden pole that would stand vertically when placed into the ground (Figure 1b). We adjusted the focus of the cameras manually during each setup. The cameras were set to have a frame rate of one picture per second and with a resolution of 1280 × 720 pixels (Figure 1c). The individual recordings lasted longer than 10 min, but to keep the observations comparable with the direct observations, we treated every 10 min as a separate observation. To count the number of flower visits recorded with the camera, we later viewed the videos on a computer using the Brinno Video Player. Camera observations were conducted in both studies and took place on the same observation days as the direct observations. The percentage of observations conducted with the cameras varied per transect from 0% to 60% (Table S3). The photographs did not allow for identification of pollinators below order level.

2.4.3 | Environmental variables

For each observation period, we recorded time of day, temperature, and relative humidity with a Suncare thermo-hydrometer (model 303C). We subjectively categorized wind, wetness of the vegetation, and sun exposure (Table S4). We also obtained data on daily rainfall from a weather station at the plantation, and we used a weather logger (UA-002 HOBO) placed at a fixed point within the plantation to record light intensity and air temperature at 3-hour intervals. We obtained additional weather data from a meteorological station in Ketapang (~50 km from the study site) and in Pontianak (~188 km from the study site; Table S4).

In the Grid Study, the mean temperature of the observation periods was 28.8°C (23.8–34.0°C) and the mean humidity was 72.4% (50%–96%). In the Transect Study, the mean temperature of the observation periods was 28.5°C (25–32.4°C) and the mean humidity was 79.4% (60%–94%).

2.5 | Statistical analyses

2.5.1 | Variables

We collected data on various factors that might influence pollinator activity. We placed the variables into five categories: weather (including temperature, humidity, precipitation, and sunlight), temporal

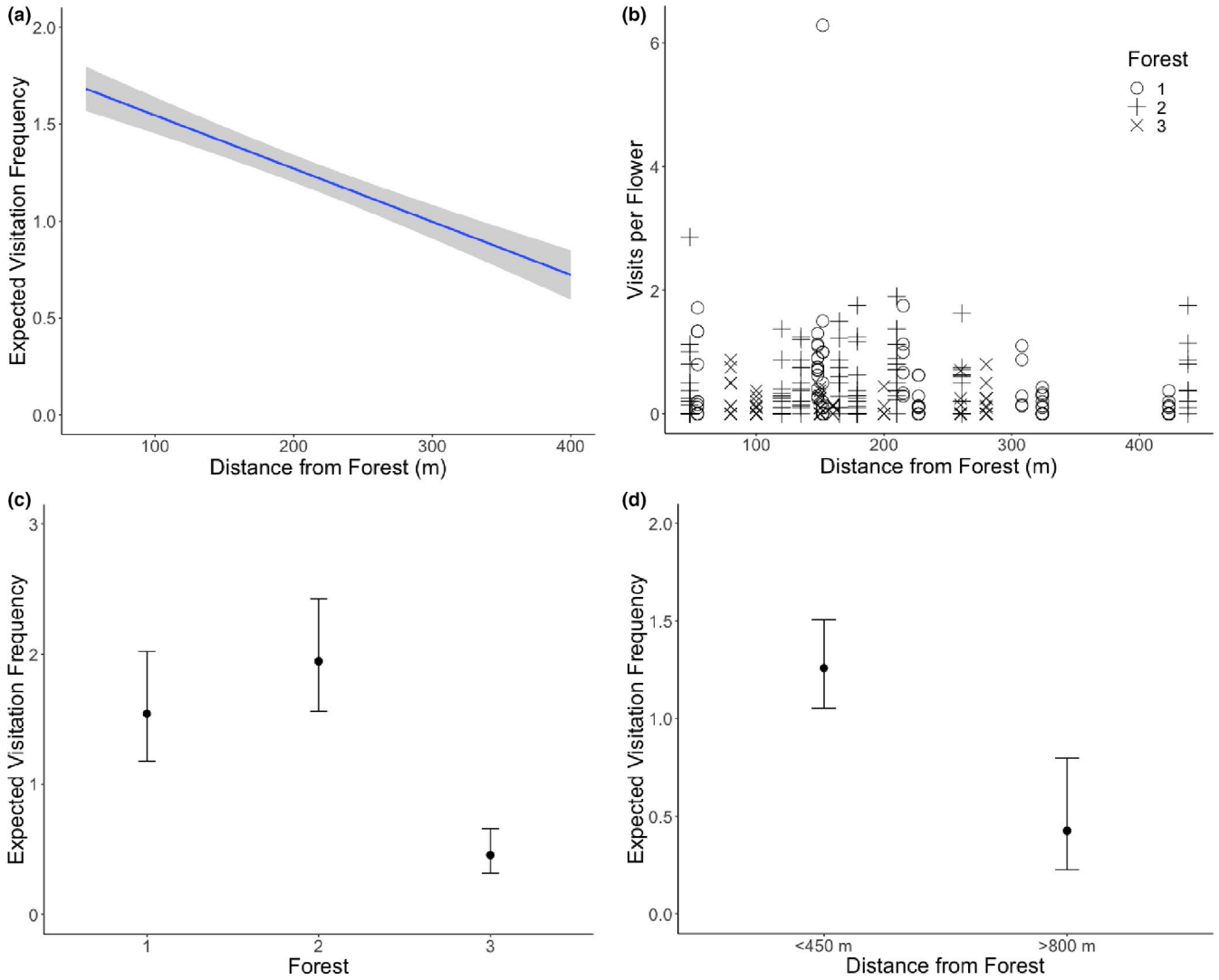


FIGURE 4 (a) Expected visitation frequency per flower per 10-min observation period in the Transect Study in relation to distance from forest (m), with all other variables remaining constant. Expected visitation frequencies are based on Model 2.1 estimates, and shaded area represents upper and lower estimates ($n = 301$). (b) Bee visits per flower per 10-min observation period in the Transect Study, in relation to distance from forest (m). Points represent raw observed bee visits per flower per 10-min observation period ($n = 301$). (c) Expected visitation frequency per flower per 10-min observation period to *Turnera subulata* adjacent to the three study forests in the Transect Study, with all other variables remaining constant. Points represent Model 1.2 estimates, and error bars represent upper and lower estimates (Forest 1 $n = 96$, Forest 2 $n = 125$, and Forest 3 $n = 80$). (d) Expected visitation frequency per flower per 10-min observation period to *T. subulata* <450 m from forest and >800 m from forest in the Transect Study, with all other variables remaining constant. Points represent Model 2.2 estimates, and error bars represent upper and lower estimates (<450 m $n = 301$, >800 m $n = 22$)

(including time of day and day of year), environmental (including forest ID, size of forest, and soil type), spatial (including distance from forest and distance from oil palm), and observed plant (including plant species, number of flowers observed per observation, recording ID and observation method). See Table S4 for more details on all of the variables we identified.

2.5.2 | Analyses

All data analyses were performed using R (version 3.5.1 with macOS version 10.14.6; R Core Team, 2018). We conducted initial data exploration following Zuur et al. (2010) on all variables (Table S4). To analyze the relationship between flower visitation frequencies and a number of explanatory variables, we generated generalized linear mixed models (GLMMs) with a Poisson error (log link) distribution. Number of visits was used as the response variable and the number of flowers observed was included as an offset variable in all models, following Reitan and Nielsen (2016). Observation ID was included in each model as a random effect to account for overdispersion (Harrison, 2014). Other variables considered as random effects include transect, plot, day, and recording ID. All models were generated using the "glmer" function in the R package "lme4" version 1.1-15 (Bates et al., 2015) with the "bobyqa" optimizer. Continuous variables

were centered and scaled using the "scale" function (R Core Team, 2018). We used an information-theoretic approach to identify the most parsimonious model using the Bayesian information criterion (BIC). Variance inflation factors (VIFs) were assessed using the "vif" function in the R package "car" (Fox & Weisberg, 2011). Dispersion, zero-inflation, and uniformity were tested using "testDispersion," "testZeroInflation," and "testUniformity" functions in the R package "DHARMa" version 0.3.2.0 (Hartig, 2020). Confidence intervals were calculated using the Wald method with the "confint.merMod" in the R package "lme4" version 1.1-15 (Bates et al., 2015). Pseudo R^2 values (delta method) were generated for each model using the "r.squaredGLMM" function in the R package "MuMIn" version 1.42.1 (Bartoń, 2018). Figures 3 and 4 were created using "ggplot" function in the R package "ggplot2" version 3.3.2 (Wickham, 2016). Effect of predictors for each model was generated using "allEffects" function in the R package "effects" version 4.1.0 (Fox, 2003, 2019).

3 | RESULTS

The field observations revealed a diversity of flower-visiting insects with bees, the most frequently observed visitor to all species, making up 81.4% of the total number of observed visits (Figure S2a,b). Specimens collected in an adjacent study (Hessen, 2020) show that pollinators in the study site included individuals of the following genera: *Apis* sp., *Ceratina* sp., *Geniotrigona* sp., *Heterotrigona* sp., *Homotrigona* sp., *Lasioglossum* spp., *Lipotriches* sp., *Nomia* spp., *and Xylocopa* spp..

In the Grid Study, we counted 355 bee visits to 2071 flowers during 723 10-min observation periods over 32 days. The mean visits per flower for all plant species combined was 0.23 per 10-min period (0.19 when observed manually and 0.31 when recorded by the cameras [Table 1]). In the Transect Study, we counted 894 bee visits to 2760 flowers during 323 10-min observation periods over 15 days. The overall mean visits per flower were 0.34 per 10-min observation (0.52 when observed manually and 0.16 when recorded by cameras [Table 1]).

As we recorded no visits to *S. lycopersicum* flowers ($n = 56$ observation periods), we excluded this species from further analyses. The flower visits recorded in the two studies were analyzed separately.

3.1 | Factors explaining variation in visit frequency in the Grid Study

Our best model (Model 1) explaining how visitation frequency to flowers varied in the Grid Study (R^2m = 0.520, R^2c = 0.947) included distance from forest, plant species, sun, time of day, and sampling method (camera or manual observation) as fixed effects (Table 2). The estimated relative contribution of explained variation for each variable in the model is listed in Table S5a. The estimated effect of each predictor (based on Model 1) with all other variables being held constant is listed in Table S6a. VIF for each variable is <2.

TABLE 1 Summary of bee visits in both studies during 1046 observation periods between 22 July and 29 October 2017

Species	# Of visits observed	# Of observation periods	# Of observation days	Range of observation dates (dd/mm)	% Of observation periods with zero visits	Max visits/ flower/10 min	Mean visits/ flower/10 min	Study
Citrullus lanatus	184	186	25	24/07–05/09	64.5	7	0.62	1
Turnera subulata	89	75	5	22/07–28/07	53.3	2.0	0.33	1
Melastoma malabathricum	30	32	13	25/07–05/09	78.1	2.5	0.19	1
Solanum melongena	42	94	19	28/07–05/09	85.1	3.5	0.18	1
Capsicum frutescens	10	280	24	28/07–05/09	98.6	1.5	0.01	1
Solanum lycopersicum	0	56	21	30/07–05/09	100	0	0	1
T. subulata	894	323	15	15/10–29/10	39.0	6.3	0.34	2

Note: # of visits observed = total number of bee visits in all 10-min observation periods combined. Study 1 = small-scale grid-based study (Grid Study), Study 2 = large-scale transect study (Transect Study).

TABLE 2 Output for the GLMM (Model 1) that best explains the variation in bee visit frequency to flowers in the Grid Study, based on 667 observation periods

			95% Confidence limits		
Fixed effect	**Estimate**	**SE**	**Lower**	**Upper**	***p*-Value**
Intercept	−6.16	0.485	−7.11	−5.21	<0.001
Forest distance	−0.270	0.134	−0.533	−0.00605	<0.05
Camera (yes)	0.739	0.304	0.143	1.33	<0.05
Species (*Melastoma malabathricum*)	2.37	0.663	1.07	3.67	<0.001
Species (*Solanum melongena*)	2.99	0.529	1.95	4.03	<0.001
Species (*Turnera subulata*)	2.77	0.518	−1.76	3.79	<0.001
Species (*Citrullus lanatus*)	3.68	0.478	2.74	4.61	<0.001
Time of day	−0.397	0.176	−0.741	−0.0525	<0.05
Sun (some)	0.712	0.292	0.141	1.28	<0.05
Sun (yes)	1.17	0.365	0.456	1.89	<0.01

Note: All continuous variables were centered and scaled. Forest Distance = Distance (m) from nearest forest. Camera = Whether observation was observed in field or via camera (factor, 2 levels: yes, no). Species = Plant species observed (factor, 5 levels: *C. lanatus*, *T. subulata*, *M. malabathricum*, *S. melongena*, *and C. frutescens*). Time of day = Minute of the day observation was started. Sun = Presence of direct sunlight on observed flowers (factor, 3 levels: yes, some, no). SE = standard error. Confidence intervals calculated using Wald method. The random effect is "observation ID" ($n = 667$).

TABLE 3 Output for the GLMM (Model 2.1) that best explains the variation in bee visit frequency to *Turnera subulata* in the Transect Study based on 301 observation periods

			95% Confidence limits		
Fixed effect	**Estimate**	**SE**	**Lower**	**Upper**	***p*-Value**
Intercept	−2.18	0.324	−2.81	−1.54	<0.001
Forest distance	−0.249	0.0788	−0.403	−0.0943	<0.01
Forest 2	0.232	0.167	−0.0951	0.559	0.165
Forest 3	−1.21	0.215	−1.64	−0.793	<0.001
Sun (some)	1.37	0.308	0.768	1.98	<0.001
Sun (yes)	1.83	0.326	1.19	2.47	<0.001
Time of day	−0.209	0.0824	−0.371	−0.0479	<0.05
Camera (yes)	−1.59	0.155	−1.89	−1.29	<0.001

Note: All continuous variables were centered and scaled. Forest Distance = Distance (m) from nearest forest. Forest = The closest forest (factor, 3 levels: 1, 2, and 3). Sun = Presence of direct sunlight on observed flowers (factor, 3 levels: yes, some, no). Time of day = Minute of the day observation was started. Camera = Whether observation was observed in field or via camera (factor, 2 levels: yes, no). Confidence intervals calculated using Wald method. SE = standard error. Random effect is "observation ID" ($n = 301$).

There was a significant decrease in visitation frequency with greater distance from forest (Figure 3a), with the expected visitation frequency decreasing by 55.4% at the maximum distance of 208 m from forest. We did not detect any influence of distance from oil palm on visitation frequency. There was variation in visitation frequency among the focal plant species. *C. lanatus* had the highest visit frequency, followed by *T. subulata*, *S. melongena*, *M. malabathricum*, and *C. frutescens* (Figure 3b,c). Expected visitation frequency was positively associated with observed flowers being in direct sunlight. Time of day also showed a positive linear association with visit frequency. Temperature and humidity were highly correlated with time of day, and thus, we were unable to disentangle the effects of these three variables. Therefore, although we expect temperature and humidity to play an important role, they were not included in the best model. We did not anticipate the observation method would influence the number of observed visits. However, analyses showed that the cameras revealed a higher visit frequency than human observations.

3.2 | Factors explaining variation in visit frequency in the Transect Study

We developed two models to describe how visit frequency to *T. subulata* varied in the Transect Study. The first model (Model 2.1) included observation points spanning from the forest edge to 483 m into planted oil palm (and did not include observation points >800 m from forest; R^2m = 0.270, R^2c = 0.445), while the second model (Model 2.2) included data from all observation points as a

TABLE 4 Output for the GLMM (Model 2.2) that best explains the variation in bee visit frequency on *Turnera subulata* in the Transect Study based on 323 observation periods

			95% Confidence limits		
Fixed effect	**Estimate**	**SE**	**Lower**	**Upper**	***p*-Value**
Intercept	−2.20	0.329	−2.84	−1.56	<0.001
>800 m	−1.08	0.317	−1.71	−0.462	<0.001
Forest 2	0.230	0.165	−0.0927	0.553	0.162
Forest 3	−1.16	0.213	−1.57	−0.738	<0.001
Sun (some)	1.34	0.313	0.723	1.95	<0.001
Sun (yes)	1.90	0.331	1.25	2.55	<0.001
Time of day	−0.141	0.0818	−0.302	0.0192	0.0845
Camera (yes)	−1.58	0.160	−1.89	−1.27	<0.001

Note: All continuous variables were centered and scaled. >800 m = over 800 m from any forest. Forest = The closest forest (factor, 3 levels: 1, 2, and 3). Sun = Presence of direct sunlight on observed flowers (factor, 3 levels: yes, some, no). Time of day = Minute of the day observation was started. Camera = Whether observation was observed in field or via camera (factor, 2 levels: yes, no). Confidence intervals calculated using Wald method. SE = Standard Error. Random effect is "observation ID" (n = 323).

2-level fixed factor discriminating between plots situated <450 m or >800 m from forest (R^2m = 0.259, R^2c = 0.451). The estimated relative contribution of explained variation for each variable in each models is listed in Table S5b,c. The estimated effect of each predictor (based on Model 2.1 and 2.2) with all other variables being held constant is listed in Table S6b,c. VIF for each variable is <2.

Model 2.1 included distance from forest, forest ID, sun, time of day, and camera as fixed effects (Table 3). We found a significant decrease in visitation frequency with an increase in distance from forest (Figure 4a). The expected visitation frequency decreased by 52.6% at the maximum distance from forest of 438 m. The best model included forest ID showing that the larger forests (Forests 1 and 2) had similar and higher visitation frequencies compared with the smaller forest (Forest 3; Figure 4b). The expected visit frequency for Forest 3 at any distance was 70.3%–76.5% lower than for Forests 1 and 2, respectively (Figure 4c). Visitation frequency was positively associated with direct sunlight. Time of day had a negative linear relationship with visit frequency, and camera observations unexpectedly had significantly lower observed visitation frequencies.

Model 2.2 included distance from forest (as a factor: <450 m or >800 m from forest), forest ID, sun, time of day, and camera as fixed effects. Visitation frequencies were significantly higher near forests, with expected visitation frequency being 66.2% lower at distances greater than 800m from the forest edge than at distances less than 450 m (Figure 4d). The other fixed effects showed similar patterns as for Model 2.1 (Table 4).

4 | DISCUSSION

Once environmental factors were accounted for, flower visitation frequency by bees was influenced by the distance to the nearest forest. This relationship was observed in both studies despite the difference in spatial scale.

The results from each study indicate expected visitation frequency to decrease by 55.4% at 208 m from forest, and 66.2% at >800 m from forest, respectively. Declines in bee visit frequency with distance from natural habitats have been found in agricultural systems elsewhere, for example, with coffee flowers having higher visitation frequency near native forests in Costa Rica (Ricketts, 2004); mustard and radish flowers having higher bee visitation near natural grasslands within an agricultural landscape in Germany (Steffan-Dewenter & Tscharntke, 1999); and watermelon flowers having higher visitation near oak woodland and chaparral habitat on farms in California (Kremen et al., 2002). The relationship between flower visitation and distance from forest suggests the forests act as a source of pollinators which may forage among the oil palms but reside in more natural habitats. The lack of relationship between flower visitation and distance from planted oil palm suggests the plantation does not provide resources comparable to the native forest.

Flower visitation frequency was affected by the nearest forest as seen in the Transect Study, where flowers in proximity to Forest 3 (the smallest fragment) had an expected visitation frequency 70.3% lower than flowers near Forest 1 and 76.5% lower than flowers near Forest 2 (the larger forests). Studies elsewhere have indicated that various pollinators are more abundant in or near large primary forests than small forest fragments and plantations (Beck et al., 2002; Liow et al., 2001; Lucey & Hill, 2011; Mayfield, 2005). Despite this, we found that even a 54 ha forest patch boosts flower visitations in the surrounding plantation landscape. Similar findings of small forest fragments positively affecting potential pollinators have been observed in other landscapes, for example with forests as small as 0.24 ha supporting a diverse bee assemblage in an agricultural landscape in Costa Rica (Brosi et al., 2008). Although conserving large intact forests remains crucial (Edwards et al., 2011), small damaged forests should also be protected where practical as this will help maintain bees and other taxa (Benedick et al., 2006).

Automatic cameras have been used in many ecological studies to observe various taxa including pollinators (for example, see [Steen,

2017]). The use of simple, low-cost automatic cameras here was valuable for increasing sample size but had an unexpected effect on observed visitation frequency. In the Grid Study, more visits were observed with the camera compared with direct observations, while in the Transect Study, fewer visits were observed with the camera. This was likely due to the height-biased selection of observed flowers (due to *T. subulata* bushes being taller than the camera setup), camera placement, and more observations outside of peak activity time. These findings suggest results are highly dependent on camera setup and flower selection.

The variation in visit frequency among the plant species indicate their differing levels of attraction for available pollinators. Strikingly, *S. lycopersicum* – from a genus known for its pollen-only, nectar-free flowers that rely on specialized "buzz-pollination" (Vallejo-Marín, 2019) – received no visits. This plant originates in the Americas where there appear to be effective pollinators (Franceschinelli et al., 2013; Rosi-Denadai et al., 2020). In addition, *C. frutescens* – another neotropical Solanaceae, known for effective self-pollination (though also pollinated by bees in the Americas [Knapp, 2010]) – had the lowest visitation aside from *S. lycopersicum*. In contrast, *C. lanatus*, though also an exotic (originating in Africa), is less specialized and had the highest visit frequency.

However, fruit set and quality were not assessed in this study due to high plant mortality, partly as a result of the harsh conditions that emerged in the study site (high temperatures and droughts). We, therefore, can only make conclusions about visits and not pollination adequacy, since visits may not translate into effective pollination events. Here, we compare our observed visits to the known requirements of *C. lanatus* to speculate about the pollination adequacy of our study location. It has previously been shown that *C. lanatus* flowers require 6–8 honey-bee visits, or just one bumble bee visit, in order to achieve optimum fruit set (Adlerz, 1966; Bomfim et al., 2016). This translates to a visit frequency of at least 0.11 visits per 10 min per flower for the day the flower is open, which is lower than our observed mean visit frequency for *C. lanatus* (0.62) (mean at <50 m distance from forest: 0.83 visits per 10 min per flower, mean at >200 m from forest: 0.36 visits per 10 min per flower). This suggests sufficient visits in our study for optimum fruit set and quality for *C. lanatus*. In contrast, *S. lycopersicum* clearly receives insufficient visits to achieve optimum yields (zero visits in the entire study), but this is not linked to distance from forest. We stress that pollination adequacy for crops within the oil palm dominated landscape requires further investigation.

As mentioned above, the study period was dry and hot with plants requiring watering twice a day to avoid wilting and death. Temperatures reached 34°C during the observations and there was an average of three days with no rainfall before each observation (max: 17), with a total of 930 mm of rain from July to September (max: 127 mm/day, with 64 out of 92 days having 0–4 mm). Such factors reflect the greater heat and higher vapor pressure deficit in oil palm plantations (and neighboring open areas) versus forest (Hardwick et al., 2015; Luskin & Potts, 2011; Ramdani et al., 2014) and the increased heat and reduced rain already seen across the island of Borneo (McAlpine et al., 2018). These climate-driven impacts are making small-scale agriculture harder and riskier. The local and island level impacts are likely to become more severe as plantations spread, forest cover declines, and the global climate gets warmer and less predictable (Meijaard et al., 2018). This may ultimately impact not only small holder agriculture but also the plantations themselves (Meijaard et al., 2018).

Pollinator density and richness have been shown to improve yields in various pollinator-dependent crop systems across different ecosystems, with flower-visitor density being the most important predictor of crop yield globally (Garibaldi et al., 2016). Land-use intensification can disrupt pollinators and pollinator services by causing declines in both pollinator species and functional richness (Rader et al., 2014). A wide range of Southeast Asian taxa including bees (Liow et al., 2001), butterflies (Koh & Sodhi, 2004), and moths (Beck et al., 2002) are experiencing declines in species richness and population density due in part to increasing forest disturbance (Sodhi et al., 2004). Protecting native forests and incorporating forest patches into agricultural land provides increased habitats for a variety of pollinators, as well as other wildlife and beneficial insects. Thus, diverse agricultural landscapes can positively affect the abundance and diversity of pollinators as well as plant–animal interactions (Horner-Devine et al., 2003; Klein et al., 2003; Ricketts et al., 2008) and should be considered in the management of such landscapes.

While pollination limitation is a concern, especially for specialized crops such as *S. lycopersicum*, adequate pollination is more likely for crops grown sufficiently close to natural forests (Klein et al., 2003). In this study, bees were found throughout the oil palm plantation, but with significantly higher bee visitation to flowers near forests. This relationship was observed even with the smallest forest fragment, though flowers near the larger forests had the highest visitation frequency. Our results emphasize the importance of maintaining as much native forest as possible within and around the agricultural landscape to sustain pollinator availability. We encourage further research to focus on pollination adequacy within oil palm landscapes.

ACKNOWLEDGEMENTS

Funding was provided by USAID's Forestry and Biodiversity Office via CIFOR (Amy Ickowitz and Terry Sunderland) and NMBU's TEMNR Field grant. We thank Erik Meijaard (Borneo Futures), Yves Laumonier (CIFOR and CIRAD), Gusti Hardiansyah, and Farah Diba (Tanjungpura University) for support with the collaborations in Kalimantan. We are thankful to everyone at PT Austindo Nusantara Jaya Agri (ANJ) and PT Kayung Agro Lestari (KAL) who supported our research and stay at KAL. We especially thank the KAL Conservation Team, in particular Ero Prasetyo, for field assistance; the KAL fire team for watering the plants; Johannes Terang for providing the crop plants; and Nardiyono, Hendriyana Rahman, and Viktor Terang for assistance with setting up and running the studies. We thank Ronny Steen for guidance with cameras and GPS equipment; Miriam van Heist, Lindawaty (Lahuka Services), Dilla Trianti

(Indonesian embassy in Oslo), and Dwi Yoga for administrative and logistical assistance; and Nia Atmadja (CIFOR) for translating the abstract. CP thanks Knut Hessen and Lynn Jørgensen for logistical and scientific support; Lisa Fagerli, Ingvild Asmervik, and Ross Whetherbee for statistical advice; Luc Le Grand and Jonas Anderson for constructive comments on the text; and John S. Ascher (National University of Singapore) for bee identifications.

CONFLICT OF INTEREST

The project was developed as a formal cooperation with PT Austindo Nusantara Jaya Agri. The company hosted and facilitated our work on the basis that we would have freedom to publish our results without interference. We agreed in advance that they could, based on their review of our drafted articles, request us to withhold any specific details judged sensitive for commercial reasons. This review has been completed, and no such requests were made.

AUTHOR CONTRIBUTIONS

DS conceived the project in close cooperation with CIFOR, PT Austindo Nusantara Jaya Agri, Tanjungpura University and Borneo Futures. DS and AN designed, managed, and supervised the larger project. DS, AN, and CP designed the specific study described here. CP collected and analyzed the data and wrote the original manuscript with DS and AN providing supervision and critical inputs. All coauthors reviewed and edited the final manuscript and approve the final version.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in the Dryad Digital Repository: https://doi.org/10.5061/dryad.s4mw6m96h (Power et al., 2021).

ORCID

Candice C. Power https://orcid.org/0000-0002-9677-2587
Anders Nielsen https://orcid.org/0000-0002-3294-6234

REFERENCES

Adlerz, W. C. (1966). Honey bee visit numbers and watermelon pollination. *Journal of Economic Entomology*, *59*, 28–30.

Antoine, C. M., & Forrest, J. R. K. (2020). Nesting habitat of ground-nesting bees: A review. *Ecological Entomology*, *46*, 143–159. https://doi.org/10.1111/een.12986

Bartoń, K. (2018). *MuMIn: Multi-model inference*. R package version 1.42.1.

Bates, D., Machler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using (lme4). *Journal of Statistical Software*, *67*, 1–48. https://doi.org/10.18637/jss.v067.i01

Beck, J., Schulze, C., Linsenmair, K., & Fiedler, K. (2002). From forest to farmland: Diversity of geometrid moths along two habitat gradients on Borneo. *Journal of Tropical Ecology*, *18*, 33–51. https://doi.org/10.1017/S026646740200202X

Benedick, S., Hill, J. K., Mustaffa, N., Chey, V. K., Maryati, M., Searle, J. B., Schilthuizen, M., & Hamer, K. C. (2006). Impacts of rain forest fragmentation on butterflies in northern Borneo: Species richness, turnover and the value of small fragments. *Journal of Applied Ecology*, *43*, 967–977. https://doi.org/10.1111/j.1365-2664.2006.01209.x

Bomfim, I. G. A., Freitas, B. M., Aragão, F. A. S. d., & A., Walters. (2016). Pollination in cucurbit crops. In M. Pessarakli (Ed.), *Handbook of cucurbits: Growth, cultural practices, and physiology* (pp. 181–200). CRC Press. https://doi.org/10.1201/b19233

Brosi, B. J., Daily, G. C., Shih, T. M., Oviedo, F., & Durán, G. (2008). The effects of forest fragmentation on bee communities in tropical countryside. *Journal of Applied Ecology*, *45*, 773–783. https://doi.org/10.1111/j.1365-2664.2007.01412.x

Burkle, L. A., Marlin, J. C., & Knight, T. M. (2013). Plant-pollinator interactions over 120 years: Loss of species, co-occurrence, and function. *Science*, *339*, 1611–1615. https://doi.org/10.1126/science.1232728

Caudwell, R. W. (2001). Insect pollination of oil palm-time to evaluate the long-term viability and sustainability of *Elaeidobius kamerunicus*? *Planter*, *77*, 181–190.

Cooley, H., & Vallejo-Marin, M. (2021). Buzz-pollinated crops: A global review and meta-analysis of the effects of supplemental bee pollination in tomato. *Journal of Economic Entomology*, *114*, 505–519. https://doi.org/10.1093/jee/toab009

Edwards, D. P., Fisher, B., & Wilcove, D. S. (2011). High conservation value or high confusion value? Sustainable agriculture and biodiversity conservation in the tropics. *Conservation Letters*, *5*, 20–27. https://doi.org/10.1111/j.1755-263X.2011.00209.x

Ellis, A. M., Myers, S. S., & Ricketts, T. H. (2015). Do pollinators contribute to nutritional health? *PLoS One*, *10*, e114805. https://doi.org/10.1371/journal.pone.0114805

Food Security Council, Ministry of Agriculture, & World Food Programme (2015). *Food Security and Vulnerability Atlas of Indonesia Dewan Ketahanan Pangan, Kementerian Pertanian and World Food Programme (WFP)*.

Foster, W. A., Snaddon, J. L., Turner, E. C., Fayle, T. M., Cockerill, T. D., Ellwood, M. D. F., Broad, G. R., Chung, A. Y. C., Eggleton, P., Khen, C. V., & Yusah, K. M. (2011). Establishing the evidence base for maintaining biodiversity and ecosystem function in the oil palm landscapes of South East Asia. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *366*, 3277–3291. https://doi.org/10.1098/rstb.2011.0041

Fox, J. (2003). Effect displays in R for generalised linear models. *Journal of Statistical Software*, *8*, 1–27. https://doi.org/10.18637/jss.v008.i15

Fox, J. (2019). *An R companion to applied regression* (3rd ed.). Sage. https://socialsciences.mcmaster.ca/jfox/Books/Companion/

Fox, J., & Weisberg, S. (2011). *An R companion to applied regression* (2nd ed.). Sage.

Franceschinelli, E. V., Silva Neto, C. M., Lima, F. G., Gonçalves, B. B., Bergamini, L. L., Bergamini, B. A. R., & Elias, M. A. (2013). Native bees pollinate tomato flowers and increase fruit production. *Journal of Pollination Ecology*, *11*, 41–45. https://doi.org/10.26786/1920-7603(2013)4

Garibaldi, L. A., Carvalheiro, L. G., Vaissière, B. E., Gemmill-Herren, B., Hipólito, J., Freitas, B. M., Ngo, H. T., Azzu, N., Sáez, A., Åström, J., An, J., Blochtein, B., Buchori, D., García, F. J. C., Oliveira da Silva, F., Devkota, K., Ribeiro, M. D. F., Freitas, L., Gaglianone, M. C., … Zhang, H. (2016). Mutually beneficial pollinator diversity and crop yield outcomes in small and large farms. *Science*, *351*(6271), 388–391. https://doi.org/10.1126/science.aac7287

Garibaldi, L. A., Steffan-Dewenter, I., Winfree, R., Aizen, M. A., Bommarco, R., Cunningham, S. A., Kremen, C., Carvalheiro, L. G., Harder, L. D., Afik, O., Bartomeus, I., Benjamin, F., Boreux, V., Cariveau, D., Chacoff, N. P., Dudenhoffer, J. H., Freitas, B. M., Ghazoul, J., Greenleaf, S., … Klein, A. M. (2013). Wild pollinators enhance fruit set of crops regardless of honey bee abundance. *Science*, *339*, 1608–1611. https://doi.org/10.1126/science.1230200

Gaveau, D. L., Locatelli, B., Salim, M. A., Yaen, H., Pacheco, P., & Sheil, D. (2018). Rise and fall of forest loss and industrial plantations in Borneo (2000–2017). *Conservation Letters*, *12*(3), e12622. https://doi.org/10.1111/conl.12622

Hardwick, S. R., Toumi, R., Pfeifer, M., Turner, E. C., Nilus, R., & Ewers, R. M. (2015). The relationship between leaf area index and microclimate in tropical forest and oil palm plantation: Forest disturbance drives changes in microclimate. *Agricultural and Forest Meteorology*, *201*, 187–195. https://doi.org/10.1016/j.agrformet.2014.11.010

Harrison, X. (2014). Using observation-level random effects to model overdispersion in count data in ecology and evolution. *PeerJ*, *2*, e616. https://doi.org/10.7717/peerj.616

Hartig, F. (2020). *DHARMa: Residual diagnostics for hierarchical (multi-level/mixed) regression models*. R package version 0.3.2.0.

Hessen, K. O. V. (2020). *The influence of native forest patches on the insect pollinator community within an oil palm plantation landscape*. M.Sc. Thesis. University of Oslo, Department of Biosciences. http://urn.nb.no/URN:NBN:no-82800

Horner-Devine, M. C., Daily, G. C., Ehrlich, P. R., & Boggs, C. L. (2003). Countryside biogeography of tropical butterflies. *Conservation Biology*, *17*, 168–177. https://doi.org/10.1046/j.1523-1739.2003.01310.x

Ickowitz, A., Rowland, D., Powell, B., Salim, M. A., & Sunderland, T. (2016). Forests, trees, and micronutrient-rich food consumption in Indonesia. *PLoS One*, *11*, e0154139. https://doi.org/10.1371/journal.pone.0154139

IPBES (2016). Summary for policymakers of the assessment report of the intergovernmental science-policy platform on biodiversity and ecosystem services on pollinators, pollination and food production. In S. G. Potts, V. L. Imperatriz-Fonseca, H. T. Ngo, J. C. Biesmeijer, T. D. Breeze, L. V. Dicks, L. A. Garibaldi, R. Hill, J. Settele, A. J. Vanbergen, M. A. Aizen, S. A. Cunningham, C. Eardley, B. M. Freitas, N. Gallai, P. G. Kevan, A. Kovács-Hostyánszki, P. K. Kwapong, X. L. J. Li, D. J. Martins, G. Nates-Parra, J. S. Pettis, R. Rader, & B. F. Vian (Eds.), (pp. 1–36). Secretariat of the intergovernmental science-policy platform on biodiversity and ecosystem services.

Klein, A. M., Steffan-Dewenter, I., & Tscharntke, T. (2003). Pollination of *Coffea canephora* in relation to local and regional agroforestry management. *Journal of Applied Ecology*, *40*, 837–845. https://doi.org/10.1046/j.1365-2664.2003.00847.x

Knapp, S. (2010). On 'various contrivances': pollination, phylogeny and flower form in the Solanaceae. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*, 449–460. https://doi.org/10.1098/rstb.2009.0236

Koh, L. P., & Sodhi, N. S. (2004). Importance of reserves, fragments, and parks for butterfly conservation in a tropical urban landscape. *Ecological Applications*, *14*(6), 1695–1708. https://doi.org/10.1890/03-5269

Kremen, C., Williams, N. M., & Thorp, R. W. (2002). Crop pollination from native bees at risk from agricultural intensification. *Proceedings of the National Academy of Sciences of the United States of America*, *99*, 16812–16816. https://doi.org/10.1073/pnas.262413599

Landaverde, P., Quezada-Euan, J. J. G., Theodorou, P., Murray, T., Husemann, M., Ayala, R., Moo-Valle, H., Vandame, R., & Paxton, R. (2017). Sweat bees on hot chillies: Provision of pollination services by native bees in traditional slash-and-burn agriculture in the Yucatán Peninsula of tropical Mexico. *Journal of Applied Ecology*, *54*, 1814–1824. https://doi.org/10.1111/1365-2664.12860

Liow, L. H., Sodhi, N. S., & Elmqvist, T. (2001). Bee diversity along a disturbance gradient in tropical lowland forests of south-east Asia. *Journal of Applied Ecology*, *38*, 180–192. https://doi.org/10.1046/j.1365-2664.2001.00582.x

Lucey, J. M., & Hill, J. K. (2011). Spillover of insects from rain forest into adjacent oil palm plantations. *Biotropica*, *44*, 368–377. https://doi.org/10.1111/j.1744-7429.2011.00824.x

Luskin, M. S., & Potts, M. D. (2011). Microclimate and habitat heterogeneity through the oil palm lifecycle. *Basic and Applied Ecology*, *12*, 540–551. https://doi.org/10.1016/j.baae.2011.06.004

Mayfield, M. (2005). The importance of nearby forest to known and potential pollinators of oil palm in southern Costa Rica. *Economic Botany*, *59*(2), 190–196.

McAlpine, C. A., Johnson, A., Salazar, A., Syktus, J., Wilson, K., Meijaard, E., Seabrook, L., Dargusch, P., Nordin, H., & Sheil, D. (2018). Forest loss and Borneo's climate. *Environmental Research Letters*, *13*, 044009. https://doi.org/10.1088/1748-9326/aaa4ff

Meijaard, E., Garcia-Ulloa, J., Sheil, D., Wich, S. A., Carlson, K. M., Juffe-Bignoli, D., & Brooks, T. M. (2018). *Oil palm and biodiversity. A situation analysis by the IUCN Oil Palm Task Force* (xiii+116 pp.). IUCN.

Meijaard, E., Rahman, H., Husson, S., Sanchez, K. L., & Campbell-Smith, G. (2016). Exploring conservation management in an oil-palm concession. *International Journal of Nature Resource Ecology and Management*, *1*(4), 179–187.

Ollerton, J., Winfree, R., & Tarrant, S. (2011). How many flowering plants are pollinated by animals? *Oikos*, *120*, 321–326. https://doi.org/10.1111/j.1600-0706.2010.18644.x

Patrício-Roberto, G., & Campos, M. (2014). Aspects of landscape and pollinators—What is important to bee conservation? *Diversity*, *6*, 158. https://doi.org/10.3390/d6010158

Potts, S. G., Biesmeijer, J. C., Kremen, C., Neumann, P., Schweiger, O., & Kunin, W. E. (2010). Global pollinator declines: trends, impacts and drivers. *Trends in Ecology & Evolution*, *25*(6), 345–353. https://doi.org/10.1016/j.tree.2010.01.007

Power, C. C., Nielsen, A., & Sheil, D. (2021). Pollinator visits to six plant species in an oil palm landscape. *Dryad*, *Dataset*. https://doi.org/10.5061/dryad.s4mw6m96h

PT Austindo Nusantara Jaya Tbk (2016). *About us: Location map*. https://anj-group.com/en/location-map

Qaim, M., Sibhatu, K. T., Siregar, H., & Grass, I. (2020). Environmental, economic, and social consequences of the oil palm boom. *Annual Review of Resource Economics*, *12*, 321–344. https://doi.org/10.1146/annurev-resource-110119-024922

R Core Team (2018). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.

Rader, R., Bartomeus, I., Tylianakis, J. M., Laliberté, E., & van Kleunen, M. (2014). The winners and losers of land use intensification: Pollinator community disassembly is non-random and alters functional diversity. *Diversity and Distributions*, *20*, 908–917. https://doi.org/10.1111/ddi.12221

Ramdani, F., Moffiet, T., & Hino, M. (2014). Local surface temperature change due to expansion of oil palm plantation in Indonesia. *Climatic Change*, *123*, 189–200. https://doi.org/10.1007/s10584-013-1045-4

Rashid, Y., Che Salmah, M. D. R., Ahmad, A. H., & Hamid, N. H. (2014). Diversity and distribution of natural enemies (predators and parasitoids) of bagworms (Lepidoptera: Psychidae) on selected host plants in an oil palm plantation. *Planter*, *90*(1055), 91–101.

Reitan, T., & Nielsen, A. (2016). Do not divide count data with count data; A story from pollination ecology with implications beyond. *PLoS One*, *11*(2), e0149129. https://doi.org/10.1371/journal.pone.0149129

Ricketts, T. H. (2004). Tropical forest fragments enhance pollinator activity in nearby coffee crops. *Conservation Biology*, *18*, 1262–1271. https://doi.org/10.1111/j.1523-1739.2004.00227.x

Ricketts, T. H., Regetz, J., Steffan-Dewenter, I., Cunningham, S. A., Kremen, C., Bogdanski, A., Gemmill-Herren, B., Greenleaf, S. S., Klein, A. M., Mayfield, M. M., Morandin, L. A., Ochieng', A., & Viana, B. F. (2008). Landscape effects on crop pollination services: Are there general patterns? *Ecology Letters*, *11*, 499–515. https://doi.org/10.1111/j.1461-0248.2008.01157.x

Rosi-Denadai, C. A., Araújo, P. C. S., Campos, L. A. D. O., Cosme, L., & Guedes, R. N. C. (2020). Buzz-pollination in Neotropical bees: Genus-dependent frequencies and lack of optimal frequency for pollen release. *J Insect Science*, *27*, 133–142. https://doi.org/10.1111/1744-7917.12602

Sawe, T., Eldegard, K., Totland, O., Macrice, S., & Nielsen, A. (2020). Enhancing pollination is more effective than increased conventional agriculture inputs for improving watermelon yields. *Ecology and Evolution*, *10*, 5343–5353. https://doi.org/10.1002/ece3.6278

Sodhi, N. S., Koh, L. P., Brook, B. W., & Ng, P. K. L. (2004). Southeast Asian biodiversity: An impending disaster. *Trends in Ecology and Evolution*, *19*, 654–660. https://doi.org/10.1016/j.tree.2004.09.006

Soh, Z. W. W., & Ascher, J. S. (2020). *A guide to the bees of Singapore*. National Parks Board.

Steen, R. (2017). Diel activity, frequency and visit duration of pollinators in focal plants: In situ automatic camera monitoring and data processing. *Methods in Ecology and Evolution*, *8*, 203–213. https://doi.org/10.1111/2041-210X.12654

Steffan-Dewenter, I., & Tscharntke, T. (1999). Effects of habitat isolation on pollinator communities and seed set. *Oecologia*, *121*, 432–440. https://doi.org/10.1007/s004420050949

Vallejo-Marín, M. (2019). Buzz pollination: Studying bee vibrations on flowers. *New Phytologist*, *224*, 1068–1074. https://doi.org/10.1111/nph.15666

Westrich, P. (1996). Habitat requirements of central European bees and the problems of partial habitats. In A. Matheson, S. I. Buchmann, C. O'Toole, P. Westrich, & I. Williams (Eds.), *The conservation of bees* (pp. 2–16). Academic Press.

Wickham, H. (2016). *ggplot2: Elegant graphics for data analysis*. Springer-Verlag.

Yahya, M. S., Syafiq, M., Ashton-Butt, A., Ghazali, A., Asmah, S., & Azhar, B. (2017). Switching from monoculture to polyculture farming benefits birds in oil palm production landscapes: Evidence from mist netting data. *Ecology and Evolution*, *7*, 6314–6325. https://doi.org/10.1002/ece3.3205

Zulkefli, M. H. H., Jamian, S., Adam, N. A., Jalinas, J., Mohamad, S. A., & Mohd Masri, M. M. (2021). Beyond four decades of *Elaeidobius kamerunicus* Faust (Coleoptera: Curculionidae) in the Malaysian oil palm industry: A review. *Journal of Tropical Ecology*, *36*(6), 282–292. https://doi.org/10.1017/S026646742000022X

Zuur, A. F., Ieno, E. N., & Elphick, C. S. (2010). A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution*, *1*, 3–14. https://doi.org/10.1111/j.2041-210X.2009.00001.x

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

How to cite this article: Power, C. C., Nielsen, A., & Sheil, D. (2021). Even small forest patches increase bee visits to flowers in an oil palm plantation landscape. *Biotropica*, 00, 1–13. https://doi.org/10.1111/btp.13023