

Norwegian University
of Life Sciences

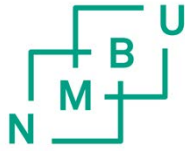
Master's Thesis 2018 60 ECTS

Faculty of Environmental Sciences and Natural Resource Management
Douglas Sheil

The effect of proximity to forest on bee visit frequency to six plant species in an oil palm landscape in Borneo

Candice Casandra Power

Master of Science in Ecology
Faculty of Environmental Sciences and Natural Resource Management



The effect of proximity to forest on bee visit frequency to six plant species in an oil palm landscape in Borneo

Candice Casandra Power

Supervisors: Douglas Sheil (NMBU) and Anders Nielsen (UiO)

Ås, Norway

July 2 2018



This project was a collaboration led by the Norwegian University of Life Sciences,

in partnership with:

the Centre for Ecological and Evolutionary Synthesis (CEES) at the University of

Oslo,

Tanjunpura University in Pontianak,

PT Austindo Nusantara Jaya Agri near Ketapang,

and the Center for International Forest Research in Bogor

Acknowledgments

Thank you to my two supervisors Douglas Sheil (NMBU) and Anders Nielsen (UiO) for giving me the opportunity to be part of this project. I appreciate all the advice, patience, and guidance from the both of you throughout the whole process. I also want to express my gratitude to CIFOR and NMBU for funding this project.

Special thanks go to Lynn and Knut for sharing in the experience of traveling to and working in Indonesia. It would not have been the same without you. An important thank you goes to Miriam for organizing all of the paper work for us, you made the fieldwork possible.

I would like to express my great appreciation to everyone at ANJ who went above and beyond to support this research. Though I can't list everyone who helped, I'd like to say a special thanks to Pak Yohannes for growing the crop plants; Pak Viktor and family for the amazing hospitality; Pak Nardiyono and Pak Hendriyana for always answering my questions and providing everything I needed; Pak Artisto for all of the help at the office; Pak Bashar and Ibu Susy for the amazing fishing trip; Pak Briandy; Ibu Ratna; and Pak Dawid. Thanks to everyone at the mess who made us feel at home. Special thanks to the conservation team for being my field assistants and friends, especially Ero who worked many long hours to help with the field work. Thanks to the University of Tanjungpura, especially Dr. Farah Diba and Pak Dwi Yoga, for helping with logistics and showing us your city. Terima kasih to everyone else that I met in Indonesia that made me feel so welcome. Thanks to Kat for your advice and translating. A huge thank you goes to Ronny for providing all the camera and GPS equipment. Special thanks to Helena, Marthe, and Silvia for visiting me in Indonesia.

I want to express huge thanks to Ross, Lisa, and Ingvild for all of the statistical advice. I'm thankful to Lisa, Silvia, Pali, and Luc for reading my thesis and giving such helpful feedback. I'd also like to thank Thomas for all of the advice. Special thanks to Kristian, Rhia, and Silvia who made days at Sørhellinga enjoyable and memorable. Thanks to Pali for being a supportive classmate and friend throughout our time at NMBU. Thanks to Silvia, Luc, Tali, and Jonas for being my unconventional Norwegian family. Thanks to Christian for all of the encouragement and conversations about oil palm. Thanks to all the other amazing people from all over the world I've met while studying at NMBU. Special thanks to Silvia, I'm so grateful for our friendship and experiences we've shared while exploring Indonesia and Norway, and writing our theses.

Thank you to my lovely roommates on the Royal 8th Floor for being understanding and supportive while I've been writing this thesis; I'm so thankful for our friendship and memories. Special thanks goes out to Anna for delivering food to me during the most stressful times.

Thanks to my loving family back at home. You support me no matter what I decide to do, even when it brings me far away and on the road less traveled. Thank you for instilling in me the value of nature and family. I would not be the person I am today without the guidance and unconditional love you have always shown me.

In loving memory of Garfield Young (1949-2016).

Abstract

Pollination is critical for global food security as it ensures the reproduction of many wild and crop plants. Pollination services may be at risk as tropical rainforests are rapidly being destroyed and degraded, largely due to agricultural expansion.

In this study I assessed the ability of a mixed forest and oil palm landscape in West Kalimantan, Borneo, Indonesia to sustain bees. I quantified bee visitation frequency by observing visits to four crop plants, *Citrullus lanatus* (watermelon), *Capsicum frutescens* (chili), *Solanum lycopersicum* (tomato), and *Solanum melongena* (eggplant); one native colonizing plant *Melastoma malabathricum*; and one exotic species *Turnera subulata*. I examined the relationships between visitation frequencies and distance from forest; distance from oil palm; size of the nearest forest; and environmental conditions. I also assessed the feasibility of using automatic cameras to observe pollinator visits and whether visitation rates varied among plant species. My observations combine two studies: Study 1 was a small scale grid-based study with six plant species observed in a cleared area at distances up to 208m from natural forest and 144m from oil palm. Study 2 was a large scale transect study with observations conducted on *T. subulata* planted within oil palm at distances up to 2130m from natural forests.

In Study 1 I recorded 355 bee visits in 723 ten-minute observation periods from July 22nd to September 5th, 2017. In Study 2 I recorded 894 bee visits in 323 observation periods from October 15-29th, 2017. Analyses revealed a positive relationship with visit frequency and temperature in Study 1. In both studies there were positive relationships between visit frequency and sunlight while there was a negative relationship with time of day. The use of cameras had a negative relationship, when compared to direct observations, with observed visitation frequency in Study 1 but a slightly positive relationship in Study 2. Visitation frequency varied among the observed plant species (ranging from 0 observed visits to *S. lycopersicum* to an average of 0.62 visits/flower/per ten minutes to *C. lanatus*), with *C. frutescens* and *S. lycopersicum* receiving significantly lower visitation frequencies than the other species. In both studies bee visit frequency declined with increasing distance from forest. In Study 1, there is a decrease in expected visitation frequency of about 72% at the maximum distance from forest, and in Study 2, the decrease of expected visitation frequency is about 94% at the maximum distance. In Study 2, visitation frequency was positively related to the size of the nearest forest, with flowers near the smallest forest expected to have a visitation frequency about 67% lower than flowers near the larger forest. I detected no relationship with distance from oil palm.

My results suggest that though bees forage in the planted oil palm, the majority, if not all, remain dependent on the natural forests. The low visitation frequencies observed for some plant species suggest there may be a lack of essential pollinators. Conserving large forests provides the most benefit to bees, though I show that forests as small as 50ha can have a positive effect. Along with conserving forests, managing the agricultural matrix to maintain suitable floral resources can lead to a more heterogenous landscape which may support more bees and thus pollinator services. More studies are required to better understand the effect of oil palm plantations on pollinator communities and the services they provide.

Table of Contents

INTRODUCTION	2
TROPICAL FORESTS.....	3
<i>Forest Fragmentation and Degradation</i>	<i>3</i>
PALM OIL INDUSTRY	4
POLLINATOR IMPORTANCE AND THREATS	5
FOOD SECURITY.....	6
POLLINATORS IN A FRAGMENTED LANDSCAPE	6
OBJECTIVES	8
METHODS	9
STUDY AREA.....	9
<i>Description of general area</i>	<i>9</i>
<i>PT Kayung Agro Lestari</i>	<i>10</i>
STUDY SPECIES.....	12
STUDY DESIGN.....	14
<i>Study 1.....</i>	<i>14</i>
<i>Study 2.....</i>	<i>16</i>
<i>Distance from forest.....</i>	<i>18</i>
DATA COLLECTION	20
<i>Observations</i>	<i>20</i>
<i>Camera Observations.....</i>	<i>22</i>
ENVIRONMENTAL VARIABLES	23
STATISTICAL ANALYSES.....	23
<i>Assessment of effects on flower visit frequency.....</i>	<i>24</i>
RESULTS.....	25
FACTORS EXPLAINING VARIATION IN VISIT FREQUENCY IN STUDY 1	26
FACTORS EXPLAINING VARIATION IN VISIT FREQUENCY IN STUDY 2	28
EFFECT OF DISTANCE FROM FOREST (OBJECTIVE 1 A).....	30
EFFECT OF DISTANCE FROM OIL PALM (OBJECTIVE 1 B)	31
DIFFERENCES IN VISIT FREQUENCY AMONG FORESTS (OBJECTIVE 1 C)	31
DIFFERENCES IN VISIT FREQUENCY BETWEEN PLANT SPECIES (OBJECTIVE 1 D)	31
ENVIRONMENTAL VARIABLES AFFECTING VISIT FREQUENCY (OBJECTIVE 1 E).....	32
EFFECT OF CAMERAS (OBJECTIVE 2).....	33
DISCUSSION	35
DISTANCE FROM FOREST.....	36
DISTANCE FROM OIL PALM	37
DIFFERENCES AMONG FORESTS	37
WEATHER VARIABLES.....	38
DIFFERENCES WITH CAMERA USE.....	39
DIFFERENCES AMONG PLANT SPECIES.....	40
IS THE SYSTEM POLLINATOR LIMITED?	40
CAN A MIXED FOREST AND OIL PALM LANDSCAPE MAINTAIN POLLINATORS AND POLLINATION SERVICES?	41
RECOMMENDATIONS FOR FUTURE WORK.....	42
REFERENCES.....	44
APPENDICES.....	48

APPENDIX A: POTENTIAL COVARIATES	49
APPENDIX B: A SAMPLE OF ALTERNATE GLMMs CONSIDERED IN MODEL SELECTION	52
<i>Study 1</i>	52
<i>Study 2</i>	53
APPENDIX C: CORRELATION PLOTS OF A SELECTION OF VARIABLES.....	54
<i>Study 1</i>	54
<i>Study 2</i>	55
APPENDIX D: FINAL MODELS	56
APPENDIX E: IMPUTATION OF MISSING TEMPERATURE VALUES.....	57
APPENDIX F: CORRELATIONS BETWEEN TEMPERATURE, HUMIDITY, AND TIME	58

Introduction

Tropical Forests

Tropical forests are essential for maintaining much of the world's biodiversity, as well as for maintaining ecological and global stability. They play a critical role in cycles which regulate global climate including water transpiration, cloud formation, atmospheric circulation and carbon storage (Devaraju et al. 2015; Lawrence & Vandecar 2015; Vira et al. 2015). Southeast Asia, and particularly the rainforests in Borneo, have been identified as a biodiversity hotspot which hosts many of the world's endemic species and is important in global carbon storage. Despite the global importance of Borneo forests, they are being increasingly threatened by forest fragmentation and degradation.

Forest Fragmentation and Degradation

Equatorial areas, including Borneo, are developing at a rapid pace, with agricultural ecosystems becoming the dominant landscape in many areas of the tropics (Sodhi et al. 2004; Foster et al. 2011; Meijaard et al. 2018). Large scale deforestation started in the 1800s in Southeast Asia mostly as a result of agricultural expansion, particularly an increase in local and global demand for rice (*Oryza sativa*) as well as perennial export crops including rubber (*Hevea brasiliensis*), coconut (*Cocos nucifera*), and oil palm (*Elaeis guineensis*) (Flint 1994). Along with mining operations and commercial logging, these disturbances are still causing massive land cover changes in Borneo today (World Wildlife Fund 2018).

Palm oil Industry

African oil palm (*Elaeis guineensis*) is of immense global importance as it is one of the world's most rapidly expanding equatorial crops (Koh & Wilcove 2008) and has been a major force in economic development in the tropics (Basiron 2007; Feintrenie et al. 2010). Oil produced from the fruits of these trees is used in many products worldwide including popular food items, detergents, and biofuels (Basiron 2007; Carter et al. 2007; Obidzinski et al. 2012). Oil palm has a high yield and low production costs, producing about 35% of all vegetable oil on less than 10% of oil crop land (Meijaard et al. 2018). With human populations as well as per capita consumption projected to rise, the demand for palm oil is showing no signs of stopping (Corley 2009, Meijaard et al. 2018). As of 2017, oil palm covered over 18.7 million hectares across the world (Foster et al. 2011; Meijaard et al. 2018).

Indonesia is one of the largest producers of oil palm, accounting for 32% of the total planted area of oil palm (Sheil et al. 2009; Meijaard et al. 2018). From 1997 to 2002 the central Indonesian government reclaimed over 20,000km² of former timber concessions in West Kalimantan to establish oil palm plantations (Curran et al. 2004). As a result, more than 52% of West Kalimantan's oil palm plantations were previously timber concessions (Curran et al. 2004), while many of the other plantations were formerly naturally forested areas (Gibbs et al. 2010; Vijay et al. 2016). As palm oil plantations are dominated by a monoculture of an exotic plant species, there are significant ecological effects of such widespread cultivated land. With growing worldwide demand for palm oil, widespread environmental effects are becoming evident and gaining more international attention (Meijaard et al. 2018).

With much focus on the environmental effects of oil palm, including widespread anti palm oil campaigns, companies are under pressure to mitigate the negative environmental effects of the industry (Meijaard et al. 2016; Yahya et al. 2017). Thus, improving biodiversity in oil palm landscapes has become a key management policy for oil palm stakeholders and various steps are being taken to achieve these goals (Meijaard et al. 2016; Yahya et al. 2017). Management actions such as developing oil palm on already degraded land along with landscape level planning and management, such as protecting remnant forests, are becoming more common in the industry (Edwards et al. 2011; Roundtable on Sustainable Palm Oil 2013; Yahya et al. 2017). These remnant forests increase the heterogeneity of the agricultural landscape and likely have a positive effect on many forest-dwelling taxa, including pollinators.

Pollinator Importance and Threats

Ecosystem services maintain global biodiversity and the production of ecosystem goods (Daily et al. 1997). Pollination is one of these essential services as it is largely responsible for the reproductive success of many native and cultivated plants, with estimates of 94% of all species being animal-pollinated in the tropics (Ollerton et al. 2011). Many crop species require animal facilitated pollination to achieve optimum fruit set and quality (Patrício-Roberto & Campos 2014). This has been seen in many common crop plants including watermelon (Bomfim et al. 2015), tomatoes (Neto et al. 2013; Deprá et al. 2014) and chillies (Landaverde et al. 2017). As with other ecosystem services, pollination is threatened worldwide due to many factors including habitat destruction and fragmentation and climate change (Daily et al. 1997; Jules & Shahani 2003; Collinge 2009; Patrício-Roberto & Campos 2014).

Food Security

Supporting a diverse community of pollinators and maintaining native species will be beneficial to the pollination of wild native plants, including edible and ornamental plants, as well as to crop species many people rely on. There is increasing demand on resources to provide the amount of food required to sustain a growing human population. Although modern agricultural practices have increased productivity when compared to the past, there is growing evidence that they are not reducing world hunger or aiding with maintaining world nutrition (FAO 2013). Rather, these conventional agricultural practices are having negative and far reaching ecological consequences (FAO 2013). As a result, global food security has become a topic of increasing interest and importance for many countries worldwide (Vira et al. 2015).

Pollinators in a Fragmented Landscape

The drastic changes the landscape undergoes as it is converted to modern agricultural land can disrupt pollination services. This is suggested by the reproductive success of crops having an inverse relationship with distance to remnant forest (Klein et al. 2003). Although pollinators are mobile they can be greatly affected by habitat fragmentation since they often require different habitats for nesting and foraging (Jules & Shahani 2003; Patrício-Roberto & Campos 2014).

Changes in the landscape as well as changes within the remnant fragmented areas may cause loss of genetic variability and population stability and may even cause the disappearance of a species in that area altogether (Sodhi et al. 2004; Patrício-Roberto & Campos 2014).

Declines in individual abundances, species richness and population density have been observed in a wide range of taxa in Southeast Asia due to increasing forest disturbance. For example, the abundance of pollinators such as bees, butterflies, and moths have been found to be significantly

higher in large primary forests when compared to smaller, degraded forest fragments and planted oil palm (Liow et al. 2001; Beck et al. 2002; Koh & Sodhi 2004; Lucey et al. 2014). Larger and less disturbed habitats are shown to be the most valuable for preserving the native pollinator species and are often suggested to be given the highest conservation priority (Koh & Sodhi 2004).

As it is not always feasible to protect large tracts of primary forests, smaller fragments may also provide benefits to the pollinator community. Protecting native forests or incorporating forest patches into agricultural land provides increased habitats for a variety of pollinators, as well as other wildlife and beneficial insects, such as predators of possible pests. Gray et al. (2015), for example, found that strips of riparian reserves supported ant populations and scavenging services within an oil palm plantation. Also, alteration of the surrounding matrix habitat can affect the availability of pollinators in the fragments as some habitats are more permeable than others (Jules & Shahani 2003). This has been observed in particular for butterflies (Roland et al. 2000; Ricketts 2001) and damselflies (Pither & Taylor 1998) and it is likely that bees and other pollinators would similarly be affected. Thus, steps may be taken for fragmented agricultural systems to support more pollinators.

This study was conducted in an oil palm plantation that has protected forests on both peat and mineral soils within the concession. While there have been studies of pollination ecology in oil palm plantations, with considerable attention on the African weevils *Elaeidobius kamerunicus* that substantially increase the fruit set of oil palm (Tandon et al. 2001; Prasetyo et al. 2014; Teo 2015; Yue et al. 2015), and various taxa such as ants (Bickel et al. 2006; Lucey et al. 2014), birds

and bats (Bickel et al. 2006; Lucey et al. 2014; Denmead et al. 2017), little attention has been given to bees. In one study, Liow et al. (2001) assessed the abundance and distribution of bees within an oil palm landscape in Malaysia.

Objectives

Because of the global importance of pollination and the threats to tropical forests, there is a need to understand the impact of habitat degradation and fragmentation on pollinator communities.

Understanding this effect can contribute to planning and management of productive landscapes to maintain local pollinators. Though Liow et al. (2001) studied bees in a similar landscape, my study, to the best of my knowledge, is the first to assess flower visit frequency within an oil palm landscape.

This study assesses the ability of a mixed forest and oil palm landscape, with both peat and mineral soil, to maintain pollinators and their services. I aim to do this by observing pollinator visits, at gradients from forest edge and planted oil palm, on six plant species within an oil palm plantation in West Kalimantan, Indonesia. As bees are the dominant pollen vector in tropical forests (Liow et al. 2001), I focus only on bee visits.

The main objectives of this study are as follows:

1. To assess the variables affecting flower visitation frequency in the study system; in particular:
 - a. Distance from forest
 - b. Distance from oil palm
 - c. Size of the nearest forest
 - d. Plant species
 - e. Environmental conditions
2. To assess the feasibility of using cameras to observe pollinator visits

Methods

Study area

This study was conducted from June to November 2017 within the oil palm concession of PT Kayung Agro Lestari in Kabupaten Ketapang in the province of West Kalimantan, Borneo, Indonesia (1°26'S and 110°13'E).

Description of general area

West Kalimantan, Borneo

The study was located in the “Borneo Lowland Rain Forest” ecoregion, which is within the “Tropical and Subtropical Moist Broadleaf Forests” biome (World Wildlife Fund 2018). Based on the Köppen climate system, the Borneo Lowland Rain Forest ecoregion falls in the “Tropical Wet” climate zone (World Wildlife Fund 2018). The study region is naturally biodiverse. There is a 54,000 ha peat swamp forest (Sungai Putri) to the south and a 90,000 ha National Park (Gunung Palung) to the North (Meijaard et al. 2016).

Gunung Palung National Park

Gunung Palung National Park (GPNP) is located in and around the Gunung Palung and Gunung Pantii mountains (The Gunung Palung Orangutan Project n.d.) and supports a diverse flora, including peat and freshwater swamp forests, along with a range of rare and endangered animals including ~17% of Borneo's orangutans (*Pongo pygmaeus*) (Curran et al. 2004; The Gunung Palung Orangutan Project n.d.). GPNP is the only national park in Indonesian Borneo with relatively intact lowland dipterocarp forest (Curran et al. 1999; Johnson et al. 2004). With deforestation within GPNP as well as in its surrounding 10km buffer, of which >70% is comprised of concessions and plantations like PT Kayung Agro Lestari (Curran et al. 2004), conservation outside of the park is increasingly important.

PT Kayung Agro Lestari

The study area, PT Kayung Agro Lestari (KAL), is owned and managed by PT Austindo Nusantara Jaya (ANJ), which is a member of the Roundtable on Sustainable Palm Oil (RSPO). (PT Austindo Nusantara Jaya Tbk 2016). KAL was established in 2004 and was acquired by ANJ in December 2005 (PT Austindo Nusantara Jaya Tbk 2016). KAL has a total of 16,620 hectares of land (PT Austindo Nusantara Jaya Tbk 2016), and is a matrix of planted oil palm, mills, residential and office areas, roads, and remnant protected forests. From 1990 to 2000 the area was part of a logging concession (PT Marsela Wana Sekawan) and before being converted to oil-palm, it was primarily logged-over natural forest (about 8,000 hectares) with the remainder being degraded land including localized grasslands (Meijaard et al. 2016). Land clearing started in 2010 with the first seedlings being planted that same year (Meijaard et al. 2016; PT Austindo

Nusantara Jaya Tbk 2016). As of 2016, a total of 9,871 hectares had been planted (PT Austindo Nusantara Jaya Tbk 2016).

The majority of the plantation is on peat soil, with a substantial portion of mineral soil and some small sandy patches. As peat soil, which has major implications with carbon storage (Jaenicke et al. 2008; Tonks et al. 2017), is saturated with water, and the terrain is flat, drainage ditches are located along the planted palm to aid with water mitigation. The majority of the oil palm was planted in 2011 and 2012, with small sections being planted in 2010 and 2013. The landscape is highly managed with little understory growing among the planted palms (Figure 1). The ground cover among the palms ranges from bare soil to low grasses and some other small herbaceous plants. The palms are planted about 9m apart resulting in a mostly closed canopy.

21% (3884 hectares) of the concession has been identified as having High Conservation Value (HCV) and is protected by the company (Meijaard et al. 2016). In general, designation of HCV areas are based on a variety of values including if the area provides important ecosystem services or if it has exceptional value for biodiversity (Edwards et al. 2011). The HCV area in this concession includes 16 forested areas, ranging from 20-2,3330 hectares. KAL employs a permanent staff to monitor the HCVs for fires, illegal logging, and poaching (Meijaard et al. 2016). The specific study sites were chosen based on these conservation areas within the plantation as well as forested areas adjacent to, but outside of, the plantation boundary.



Figure 1: Representative oil palm, *Elaeis guineensis*, and understory present throughout the plantation. Some variation is found in different areas involving the height of the oil palm, soil type, and % ground cover.

The mean temperature at the nearest meteorological observation station in Ketapang, approximately 50 km from the study area, was 27.7°C (range: 20.7°C to 35.3°C) from June 1- November 1 in 2017 (Raspisaniye Pogodi Ltd. 2018). At that site, the mean average temperature for 2017 was 24.7°C, which was lower than the mean temperature of the ten year period between January 1 2008 and January 1 2018 (27.6°C) (Raspisaniye Pogodi Ltd. 2018).

Study Species

Six angiosperm species from four different plant families were selected for the study (Table 1). Four of these (*Citrullus lanatus* (Thunb.) Matsum. & Nakai (watermelon), *Capsicum frutescens* L. (chili), *Solanum lycopersicum* L. (tomato), and *Solanum melongena* L. (eggplant)) were selected because of their use as crops in the study region. The other two species (*Melastoma malabathricum* L. and *Turnera subulata* (Smith)) were chosen because of their wide distribution within the study area. All are non-native except *M. malabathricum*, which is a common colonizing plant often found along degraded forested areas (Australian Tropical Rainforest Plants 2010) and occurs in cleared, degraded areas near forest edges within the plantation.

Turnera subulata is an introduced and potentially invasive plant in Indonesia (Institute of Pacific Islands Forestry 2006). It was planted within KAL along roadsides to aid with biological pest control as it serves as a food source and host plant for a carnivorous bug, *Sycanus* sp., which is believed to predate on fire caterpillars, the most common pest to oil palm (Sawit Indonesia 2014). The fire caterpillar, including *Setora nitens*, *Darna trima*, *Ploneta diducta*, and *Setothosea asigna*, can cause significant damage and reduce production (Sawit Indonesia 2014; Asian Agri 2017). By increasing *T. subulata*, the company hopes to increase the *Sycanus* sp. population and reduce the pest caterpillar (Sawit Indonesia 2014; Asian Agri 2017). With large showy yellow flowers, the plants are a common sight within the concession.

Table 1: Description of each of the six observed plant species: plant family; common crop plant: yes (Y), no (N); monoecious (M) or hermaphroditic (H); petal colour: yellow (Y), white (W), purple (P); main pollination vector: insect (I), wind (W), insect & wind (IW); reward: nectar (N), pollen (P), nectar & pollen (NP). *C. lanatus*, *C. frutescens*, *S. lycopersicum*, & *S. melongena* were grown in individual poly bags and brought to the study area. *M. malabathricum* was found growing naturally in the study area. *T. subulata* was planted by ANJ.

Species	Common Name	Family	Crop Plant (Y/N)	Monoecious/ Hermaphroditic	Petal Colour (Y/W/P)	Main Pollination (I/W/IW)	Reward (N/P/NP)
<i>Citrullus lanatus</i>	Watermelon	Cucurbitaceae	Y	M	Y	I	NP
<i>Capsicum frutescens</i>	Chilli	Solanaceae	Y	H	W	IW	NP
<i>Solanum lycopersicum</i>	Tomato	Solanaceae	Y	H	Y	IW	P
<i>Solanum melongena</i>	Eggplant	Solanaceae	Y	H	P	IW	P
<i>Melastoma malabathricum</i>	Malabar melastome	Melastomataceae	N	H	P	I	P
<i>Turnera subulata</i>	White Alder	Passifloraceae	N	H	Y	I	NP

Study design

I conducted two studies. The first was a systematic planned grid-based study (Study 1) with observations conducted at a maximum distance of 208m from natural forest and 144m from oil palm. The second was a large-scale transect study (Study 2) with observations conducted at a maximum distance of 2130m from natural forest.

Study 1

In Study 1 observations were conducted on all the study plant species. The plants were organized as a grid with 12 different plots situated in a cleared area. The three columns go from a forest (Forest 4) while the four rows follow a gradient from edge of planted oil palm (Figure 2A).

The plants in Study 1 were observed between July 22 and September 5, 2017. A prior agreement was made with a local village leader Yohanes Terang to plant and raise the crop plants. The plants were grown in individual poly bags so they could be easily moved. There was a total of 397 plants; 134 *C. lanatus*, 108 *S. melongena*, 105 *S. lycopersicum*, and 50 *C. frutescens* plants. The crops were placed throughout the cleared area that already had scattered individuals of naturally growing *M. malabathricum* and planted *T. subulata*. With at least one plant of either species growing close to each plot, observations were conducted on *T. subulata* and *M. malabathricum* flowers alongside the crop observations.

The crop plants were organized into 12 different plots, each with about six columns of plants and about six rows. The plants were allocated at random so at least one of each species was placed in

each plot though the numbers of individuals varied. The exact placing of plants within the plots was organized randomly.

The methods for Study 1 initially included collecting data on fruit set as well as on mature fruits. Similar to the methods in other studies (Stanghellini et al. 1998), I planned to isolate a selection of the flowers (by using mesh to prevent any pollinator visits) to compare the fruit set and quality of the insect pollinated flowers to the self-pollinated flowers. These methods were not completed as many of the crop plants had already produced flowers and fruits before being transported to the study area. Also, periods of extremely dry, hot weather and a lack of an agricultural watering and shading system in place, the condition of the plants deteriorated which made the fruit data either impossible or unreliable to collect.

Table 2: Description of the four forested areas in both studies. Approximate size and continuity determined using Google Earth Pro and information provided from ANJ, forest use provided by ANJ.

Forest	Approx. Size (ha)	Continuous (Y/N)	Hill/Flat	Condition/Type
1	381	Y	F	Secondary, Community Forest outside of concession
2	4574	Y	F	Secondary, enclave + HCV Kawasan Lindung + forest outside of concession
3	203	N	H	Secondary, enclave Bukit Bujang
4	53.9	N	H	Secondary, HCV Bukit Kasai

Study 2

Observations for Study 2 were conducted between October 15-29, 2017. These transects were located along roadsides where *T. subulata* had been planted as close to the forest edge as possible and continued for at least 300m into the plantation. I established two transects for each forest area to assess visitation in relation to each forest and among the different forests.

In Study 2 I sampled along six different transects which each started at a forest edge and went along a gradient into planted oil palm (Figure 2B). The transects were located near three forested areas, with two transects at each forest, which differ in size and condition (Table 2). Forest 1 is a large, continuous forest that extends beyond the plantation boundary; Forest 2 is partially a conserved area within the plantation but extends beyond the boundary; and Forest 3 is an isolated hill surrounded by oil palm. The transects varied in length and distance from forest because of the available suitable land (Study 1) and the locations of the observed plants (Study 2) (Table 3).

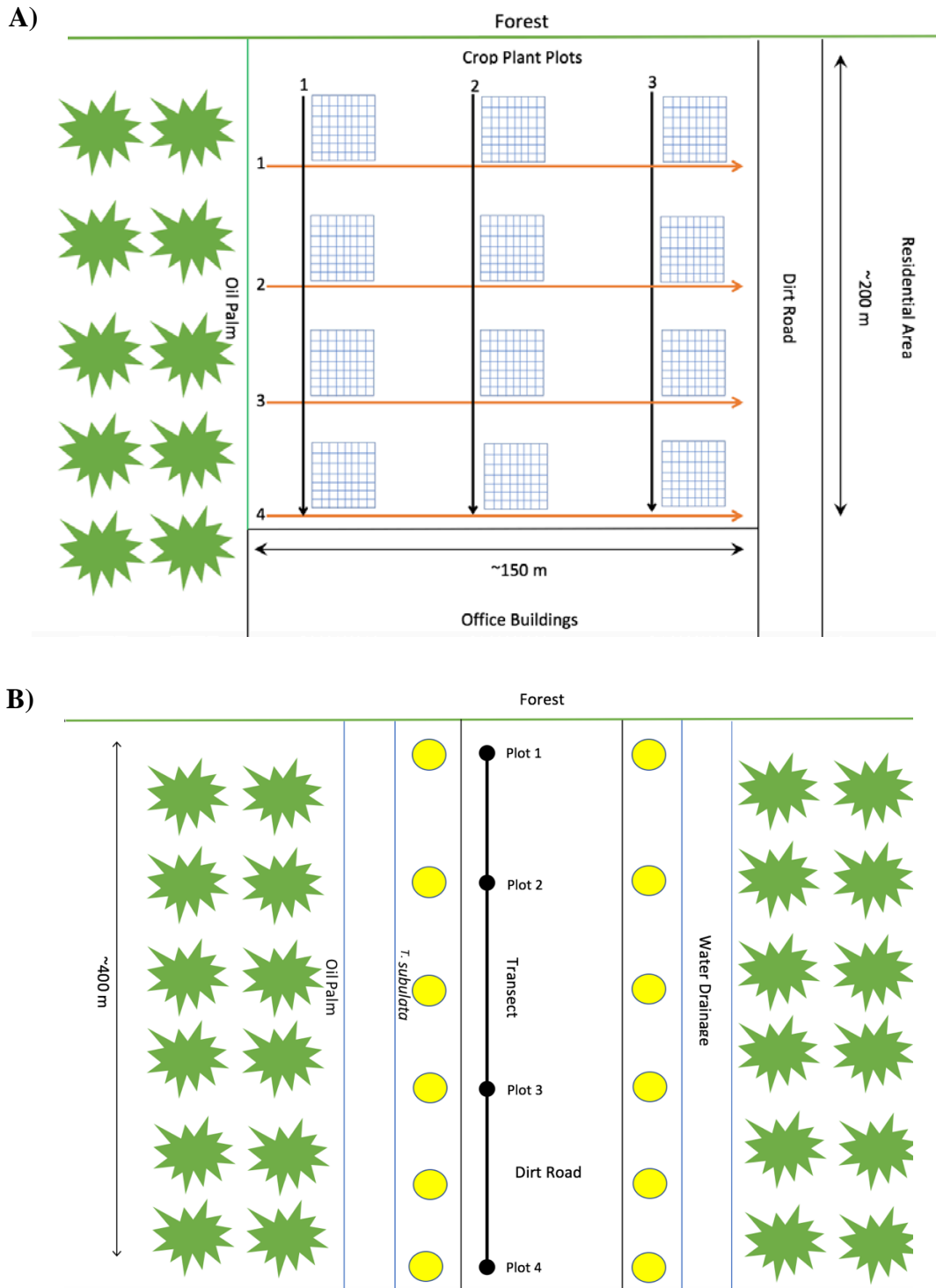


Figure 2: Schematics (not to scale) of the two studies. **A)** Grid layout of the crop plant plots for Study 1. The observed plants were the crop species (*C. lanatus*, *S. melongena*, *C. frutescens*, *S. lycopersicum*), as well as some *M. malabathricum* and *T. subulata*. Columns 1-3 represent transects with gradient from forest while rows 1-4 represent transects with gradient from oil palm. **B)** Transect layout for Transects A, B, C, D, E, & F in Study 2. Figure shows one representative transect. *T. subulata* was the only observed plant species.

For each transect I designated plot 1 at “0m” from the forest though there was often some grass or shrubs growing between the taller trees and this first plot. In some places the plot was up to 50 m away from tall forest but with other natural vegetation in between. I recorded the location on a Garmin eTrex H handheld GPS unit and then walked along the road away from the forest until I was 100m from the first plot. I looked for the nearest *T. subulata* bush and marked that location on the GPS unit as plot 2 at “100m”. I repeated this process for plot 3 at “200m” and plot 4 at “300m”. If no suitable bush occurred at the location 100m away from the last, I would continue walking away from the forest until I located the nearest one. Therefore, plots 1-4 represent a gradient away from forest but were not exactly spaced. To assess pollinator activity further within the plantation, I located and selected four control points where *T. subulata* occurred over 800m from forest (with a range from 824-2130m).

Distance from forest

I selected observation points using the location given by the GPS unit but the “distance from forest” measure used in the analyses takes into account all surrounding forests and not just the edge the transect started at. To determine the distance from forest, I used the measuring tool on Google Earth Pro to measure to nearest forest edge.

Table 3: Description of transects and control points: Forest ID = the forest they are closest to (1-4); the maximum distance from forest (in metres) (measured using Google Earth Pro); number of ten minute observation periods at that location throughout the study; soil type (P=peat; M=mineral; S=sandy); planted year of adjacent oil palm (2010, 2011, 2012); plant species observed at each location (1= *Turnera subulata*, 2= *Citrullus lanatus*, 3= *Melastoma malabathricum*, 4= *Solanum melongena*, 5= *Solanum lycopersicum*, 6= *Capsicum frutescens*); and study (1 or 2).

Transect	Forest ID	Max. Distance from Forest (m)	# of Obs. Periods	Soil Type	Palm Planted Year	Plant Species Observed	Study
1	4	180	144	M	2011	2,3,4,5,6	1
2	4	169	442	M	2011	1,2,3,4,5,6	1
3	4	208	137	M	2011	2,3,4,5,6	1
A	1	308	37	P/M	2012	1	2
B	1	423	59	M	2012	1	2
C	2	438	62	M	2012	1	2
D	2	210	63	M	2012	1	2
E	3	280	44	P	2012	1	2
F	3	280	36	P/M/S	2010/11/12	1	2
Control 1	1	824	5	P	2012	1	2
Control 2	1	1080	8	P	2012	1	2
Control 3	3	1023	5	P	2011	1	2
Control 4	2	2130	4	P	2010/11	1	2

Data Collection

Observations

To estimate flower visitation frequencies, I observed visits on the plant species described above. The sequence and starting point in which the transects were observed was chosen at random. At the selected location, I chose a number of flowers that could be observed without missing any visits. The number depended on how many flowers were open on the plant and their location and ranged from 1-36 with a mean of 4.6.

Initial observations showed a diversity of insect visitors, of which bees were the most common to all the observed plant species. Because of the diversity and challenging taxonomy of bees and other insect groups found in this landscape, I focus my study only on visits by bees and consider them as a single group. Each observation period was 10 minutes long and I used a timer to notify when the observation period ended. During each period I recorded every visit to the preselected flowers. I defined a visit as a bee coming into contact with the reproductive parts of the flower. To keep observation periods as similar as possible I selected the most prominent and healthy flowers. During the observations I stood as far away as possible from the observed flowers, remained still for a few minutes before starting the observation, and made minimal movements during the observation period. The observations were performed regardless of weather condition, except during rain.

Visit observations were repeated at each flowering plant in each plot in Study 1 and at each plot in each transect in Study 2, as many times as time would allow. The number of observation

periods per plant species varied depending on flowering period, plant condition, weather conditions, time constraints, and other unforeseeable circumstances (Table 4).

The mean time of observation was around 9:30 am, with the earliest observation being at 5:30 am and the latest being around 6:00 pm. Observations were focused in morning hours because this appeared to be when pollinator activity was the highest and because all the flower species were open at this time.

Table 4: Overview of sampling effort for each plant species. Include total number of ten-minute observation periods, total number of flowers observed, total number of observation days, and range of observation days throughout the study.

Species	# of Obs. Periods	# of Flowers	# of Obs. Days	Date of First Obs.	Date of Last Obs.	Study
<i>C. lanatus</i>	186	343	25	07/24	09/05	1
<i>C. frutescens</i>	280	748	24	07/28	09/05	1
<i>S. lycopersicum</i>	56	326	21	07/30	09/05	1
<i>S. melongena</i>	94	192	19	07/28	09/05	1
<i>M. malabathricum</i>	32	163	13	07/25	09/05	1
<i>T. subulata</i>	398	3059	20	07/22	10/29	1,2

Camera Observations

I used Brinno BCC200 Pro cameras (Chen & Chou 2011) to obtain additional data while I did other observations or was not in the field. I set up the cameras using a T1 Clamp tripod attached to a wooden pole that would stand vertically when placed into the ground (Figure 3A). The

cameras were housed in a waterproof casing and A)

the focus was adjusted manually during each setup. Due to the height of the plants, the camera was sometimes at the same height of the flowers and recorded perpendicularly but when possible, the camera was positioned facing downwards to

better view the flower. Care was taken not to block access to pollinators. A frame rate of 1 picture per second was chosen (resolution 1280 x

720) for all observation periods (Figure 3B). The recordings were longer than ten minutes long, but to keep the observations comparable to the direct

observations, I treated every ten minutes as a separate observation. The videos were saved to SD cards which were labelled and stored until

they could be viewed on a computer using Brinno Video Player. Automatic detection could not be used because of too much movement in the pictures, so I viewed them frame by frame.



B)

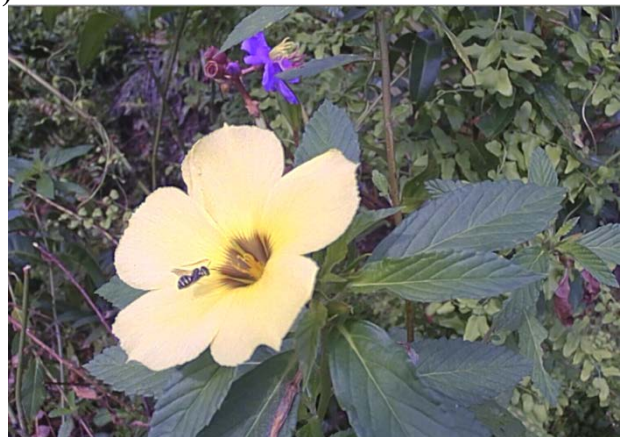


Figure 3: A) Setup of a Brinno BCC200 Pro camera using a T1 Clamp tripod attached to a wooden pole, to observe planted *T. subulata* adjacent to oil palm. **B)** Picture of bee visiting *T. subulata* taken with camera.

Environmental variables

For each observation period I recorded the date, time of day, and temperature and relative humidity (recorded with a Suncare thermo-hydrometer (model 303C)), wind (categorical scale of how often the observed plant moved during the ten-minute observation; never, some, or often), wetness of the vegetation (categorical scale of dry, damp, or wet) and direct sun (yes: direct sun for 100% of the observation, some: direct sun for some of the observation, or no: no direct sun).

I also obtained additional data from other sources to describe the ambient conditions during the observation periods. ANJ provided rainfall data from a rain-station at the plantation which gives a value for daily rainfall. A weather logger was used to record the light intensity and temperature at three-hour intervals at one location on the plantation. I obtained additional data from a weather station in Ketapang, a city about 50km away from the concession (these weather variables included temperature and humidity), as well as a weather station in Pontianak, a city about 188 km away (these weather variables included maximum temperature, minimum temperature, daily rainfall, wind speed, wind direction, gust speed, cloud cover, humidity, air pressure, weather classification of the day, and the weather classification for the time nearest the observation (3 hour intervals)).

Statistical Analyses

The protocol of Zuur et al. (2010) was followed in the data exploration phase. I checked the covariates for outliers, trends, and correlations. Data analyses were performed using R (version 3.4.3 with macOS version 10.13.5) (R Core Team 2017) and R Studio Version 1.1.453 (R Studio Team 2016). All models were generated using the “glmer” function in the R package “lme4”

version 1.1-15 (Bates et al. 2015). Figures 3.2 and 3.3 were generated using “ggplot” function in the R package “ggplot2” version 2.2.1 (Wickham 2009).

Assessment of effects on flower visit frequency

As bee visits are counts I used a generalized mixed model (GLMM) with a Poisson error distribution. I used number of visits as a response variable and the number of flowers as an offset variable, following Reitan & Nielsen (2016). Using a GLMM allowed me to evaluate both random and fixed effects. A description of all potential covariates can be found in Appendix A.

I used an information-theoretic approach to identify the most parsimonious model using the Bayesian information criterion (BIC). I first developed a series of alternative GLMMs that included different combinations of the explanatory variables of interest related to bee visits. I ranked these by their BIC values (a model with a low BIC is more parsimonious than a model with a high BIC). A summary of some of the alternative models considered can be found in Appendix B.

Many studies have shown that bee activity is affected by ambient weather. So, along with forest ID and distance from forest and oil palm, I also included: temperature, humidity, air pressure, presence of direct sun, amount of rainfall from the day before the observation, time of day. I included both linear and quadratic relationships due to the potential for non-linear responses to humidity, temperature, and time of day. I also included several random effects including: observation ID (a unique ID for each observation period to account for over dispersion); transect (to account for unsystematic spatial variation); and observation day (to account for temporal variation). Correlation matrices for a selection of the covariates can be found in Appendix C.

Results

The fieldwork for Study 1, where visit observations were conducted on six plant species in a grid layout, included 32 observation days and resulted in a total of 355 bee visits in 723 10-minute observation periods. The mean temperature during the observations was 28.8°C (range: 23.8°C-34.0°C) when measured at the nearest weather station and 31.8°C (range: 24°C-45.2°C) when measured with the handheld recorder. The mean humidity during the observations was 72.4% (range: 50%-96%) when measured at the nearest weather station and 69.7% (range: 36%-95%) when measured with the handheld recorder.

The field work for Study 2, where visit observations were conducted on *T. subulata* along transects throughout the planted palm, took place during 15 observation days and resulted in a total of 894 bees visits in 323 observation periods. The mean temperature during the observations was 28.5°C (25°C-32.4°C) when measured at the nearest weather station or 33.9°C (26.9°C-41.1°C) when measured with the handheld recorder. The mean humidity during the observations was 79.4% (60%-94%) when measured at the nearest weather station or 66.2% (44%-90%) when measured with the handheld recorder.

The maximum bee visits per flower for a ten-minute observation period was seven (to *C. lanatus* flowers), while 69% of the observations had no visits. The overall mean was 0.22 visits per flower per ten-minute observation for all plant species (Table 5). As I recorded no visits to *S. lycopersicum* flowers, and thus had found no variation to explain, observations on this species (n=56) were excluded from further analyses. The two studies were analysed separately. For a description of the full models, see Appendix D.

Table 5: Summary of bee visits in both studies during 1046 observation periods between July 22 and October 29 2017. # of visits observed = total number of bee visits in all 10-minute observation periods combined. Study 1 was a small scale grid based study and Study 2 was a large scale transect study.

Species	# of Visits Observed	# of Observation Periods	% of Observation Periods with Zero Visits	Max Visits / Flower/ 10 min	Mean Visits / Flower/ 10 min	Study
<i>C. lanatus</i>	184	186	64.5	7	0.62	1
<i>T. subulata</i>	89	75	53.3	1.4	0.30	1
<i>M. malabathricum</i>	30	32	78.1	2.5	0.19	1
<i>S. melongena</i>	42	94	85.1	3.5	0.18	1
<i>C. frutescens</i>	10	280	98.6	1.5	0.01	1
<i>S. lycopersicum</i>	0	56	100	0	0	1
<i>T. subulata</i>	894	323	39.0	6.3	0.32	2

Factors explaining variation in visit frequency in Study 1

The best model (Model 1) to explain the variation in visit frequency to flowers in Study 1 included distance from forest, plant species, sun, time of day, and camera as fixed effects (Table 6). Observation ID as a random effect was also included, comprising 34.5% of the variation in visitation frequency (Table 7).

Table 6: The output for the GLMM (Model 1) that best explains the variation in bee visit frequency to flowers in Study 1, based on 667 observation periods. **Forest Distance** = Distance (m) from nearest forest, using Google Earth Pro. **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*, *C. frutescens*). **Time of day** = Minute of the day observation was conducted. SE = standard error. 95% confidence limits were calculated as estimate $\pm 1.96 * SE$. The random effect is “observation ID” (n=667).

Fixed Effect	Estimate	SE	95% Confidence Limits	
			Lower	Upper
Intercept	-3.66	0.882	-5.38	-1.93
Forest Distance	-0.00617	0.00285	-0.0118	-0.000580
Camera (yes)	0.669	0.300	0.0820	1.26
Species (<i>C. lanatus</i>)	3.57	0.462	2.67	4.48
Species (<i>M. malabathricum</i>)	2.27	0.647	1.00	3.54
Species (<i>S. melongena</i>)	2.88	0.514	1.87	3.88
Species (<i>T. subulata</i>)	2.65	0.502	1.67	3.64
Time of day	-0.00286	0.00124	-0.00528	-0.000435
Sun (some)	0.713	0.288	0.148	1.28
Sun (yes)	1.13	0.360	0.4278	1.84

Table 7: The relative contribution of explained variation, assuming all variables are independent, in bee visit frequency to flowers in Study 1, based on Model 1. **Forest Distance** = Distance (m) from any forest, measured using Google Earth Pro. **Species** = Plant species observed (factor, 5 levels: *C. lanatus*, *T. subulata*, *M. malabathricum*, *S. melongena*, *C. frutescens*). **Time of day** = Minute of the day observation was conducted. **Camera** = Whether observation was observed directly or via camera (factor, 2 levels: yes, no). **Unexplained variation** = unique ID for each observation period. Fixed effect variance = var (Model 2 estimate * variable). Random effect variance = Model 2 estimate.

	Covariate	Variance contribution (%)
Fixed Effects	Species	58.2
	Sun	2.81
	Time of day	2.07
	Camera	1.38
	Forest distance	1.07
Random	Unexplained variation	34.5

Factors explaining variation in visit frequency in Study 2

The best model (Model 2) for visit frequency to flowers in Study 2 included distance from forest, forest ID, sun, temperature, time of day, and camera as fixed effects (Table 8). Observation ID was included as a random effect, accounting for 24.8% of the variation in flower visit frequency (Table 9).

Table 8: The output for the GLMM (Model 2) that best explains the variation in bee visit frequency on *T. subulata* in Study 2 based on 323 observation periods. **Forest Distance** = Distance (m) from nearest forest, measured using Google Earth Pro. **Forest** = The closest forested area (factor, 3 levels: 1,2,3). **Sun** = Presence of direct sunlight on observed flowers (factor, 3 levels: yes, some, no). **Temperature** = The temperature (°C) obtained from handheld recorder with missing values estimated from a linear regression. **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). SE = Standard error. 95% confidence limits were calculated as estimate $\pm 1.96 * SE$. Random effect is "observation ID" (n = 323).

Fixed Effect	Estimate	SE	95% Confidence Limits	
			Lower	Upper
Intercept	-3.53	1.14	-5.76	-1.30
Forest Distance	-0.00129	0.000282	-0.00184	-0.000737
Forest 2	0.157	0.161	-0.159	0.473
Forest 3	-1.10	0.208	-1.51	-0.692
Sun (some)	1.12	0.316	0.501	1.74
Sun (yes)	1.66	0.335	1.00	2.32
Temperature	0.198	0.0677	0.0653	0.331
Time of Day	-0.00967	0.00275	-0.0151	-0.00428
Camera (yes)	-1.58	0.154	-1.88	-1.28

Table 9: The relative contribution of explained variation, assuming all variables are independent, in bee visit frequency on *T. subulata* in Study 2, based on Model 2. **Forest Distance** = Distance (m) from any forest, measured using Google Earth Pro. **Forest** = The closest forested area (factor, 3 levels: 1,2,3). **Sun** = Presence of direct sunlight on observed flowers (factor, 3 levels: yes, some, no). **Temperature** = The temperature (°C) obtained from handheld recorder. Missing values were estimated using a linear regression. **Time of day** = Minute of the day the observation was started. **Camera** = Whether observation was observed in field or via camera (factor, 2 levels: yes, no). **Unexplained variation** = unique ID for each observation period. Fixed effect variance = var (Model 1 estimate * variable). Random effect variance = Model 1 estimate.

	Covariate	Variance contribution (%)
Fixed Effects	Sun	21.7
	Camera	18.9
	Time of day	13.4
	Temperature	9.30
	Forest	7.32
	Forest distance	4.48
	Random Effects	Unexplained variation

Effect of distance from forest (Objective 1 a)

The best models from both studies found a significant decrease in visitation frequency included distance from forest. Model 1 distance from forest explained 1.1% of the variation (Table 7) and in Model 2 distance from forest explained 4.5% of the variation in visit frequency (Table 9).

Both showed a decrease in visitation frequency with greater distance from forest (Figure 4A;5A).

For Study 1, the expected visitation frequency decreases by ~72%* at the maximum distance of 208m from forest, and for Study 2 the expected visitation frequency decreases by ~94%† at the maximum distance from forest of 2130m.

* $\exp^{(-0.00617) * 208} = 0.2768$, $1-0.276874=0.723 * 100 = 72.3\%$

† $\exp^{(-0.00129) * 2130} = 0.06387$, $1-0.0639*100=93.6\%$

Effect of distance from oil palm (Objective 1 b)

Visitation data from Study 1 was used to assess differences in visit frequency in relation to distance from nearest planted oil palm. The distance from oil palm did not appear in the best model and there does not appear to be a significant effect of this distance. The best model including distance from oil palm was 7 BIC units larger than the best model without.

Differences in visit frequency among forests (Objective 1 c)

The best model for Study 2 included forest ID, accounting for 7.3% of the variation in visit frequency (Table 9). The larger forests (Forest 1 and 2) had similar and higher visitation frequencies compared to the smaller forest (Forest 3) (Figure 5B). Based on the model estimates, the expected visit frequency for Forest 3 at any distance is 66.7%[‡] lower than for Forest 1.

Differences in visit frequency between plant species (Objective 1 d)

Data from Study 1 was used to assess the difference in bee visit frequency between the six observed plant species. There was a difference among plant species, though they were not all significantly different from each other. Species identity explained the most variation in Study 1 (58.16%) (Table 7). *C. lanatus* had the highest visit frequency, followed by *T. subulata*, *S. melongena*, *M. malabathricum*, and *C. frutescens* (Figure 4B). *C. frutescens* was the only species

[‡] $\exp^{-1.10} = 0.3325$, $(1-0.3325)*100 = 66.7\%$

with a significantly lower visitation frequency, with the other plant species having from 9-35%[§] increased expected visitation frequency.

Environmental variables affecting visit frequency (Objective 1 e)

Several environmental variables were associated with bee visitation frequency. Direct sunlight was positively associated with visit frequency in both datasets (Figure 4D; 5D). Sunlight explained 2.8% of the variation in Model 1 (Table 7) and 21.7% of the variation in Model 2 (Table 9). In direct sunlight, based on the model estimates, expected visit frequency is ~3%^{**} higher in Study 1 and ~5%^{††} higher in Study 2 when compared to visits to flowers with no direct sunlight during the observation.

Temperature was included in Model 2, explaining 9.3% of the variation in visitation frequency (Table 9). The temperature that explained the variation the best was that measured with a handheld recorder ($\Delta\text{BIC} = -9.4$ when compared to the temperature values recorded at the nearest weather station) with missing values estimated using a linear regression based on the observation day, time of day, and other weather sources (Appendix E). Model 2 shows an increase in visit frequency with temperature (Figure 5E). Temperature was not included in Model 1.

Time of day was present in both of the models, explaining 2.1% and 13.4% of the variation in Models 1 and 2 respectively (Table 7;9). The model with the lowest BIC ($\Delta\text{BIC} = -0.9$ units less than Model 2) for Study 2 included a quadratic relationship with time. I selected Model 2 as the

[§] example for comparison with *C. lanatus*, $\exp^{(3.57)}=35\%$

^{**} $\exp^{(1.13)}=3.1\%$

^{††} $\exp^{(1.66)}=5.3\%$

final model because it was the most parsimonious, and the small change (<2 units) in BIC values suggest a negligible difference in the abilities of the models to explain the variation of the study. Model 1 and 2 both show a negative linear relationship between visit frequency and time of day (Figure 4C; 5C).

Effect of cameras (Objective 2)

420 of the 1046 observation periods were recorded using cameras, with a total of 70 recorded hours. The best model for Study 2 included camera as a fixed effect (explaining 18.9% of the variation) (Table 9). When the camera is used, the expected visitation frequency is lower than if the observation was done directly (Figure 5F). Camera was not initially in the best model for Study 2 as removing it gave a slight improvement of $\Delta\text{BIC} = -0.5$. But, because the change in BIC was <2 units, I included it to better address Objective 2 (effect of camera use). Camera accounted for only 1.4% of the variation for Study 1 (Table 7). In Model 1 the observations with camera gave a slightly higher expected visit frequency (Figure 4E), which was opposite of the relationship shown in Model 2.

Figure 4: The relationship of expected visit frequency per flower per 10-minute observation period to flowers in Study 1 with each of the most significant variables (with all other variables remaining constant): **A)** Distance from forest (m), **B)** Plant species, **C)** Time of day, **D)** Sun presence, and **E)** Camera method. Graphs based on estimates from Model 1, error bars represent upper and lower estimates.

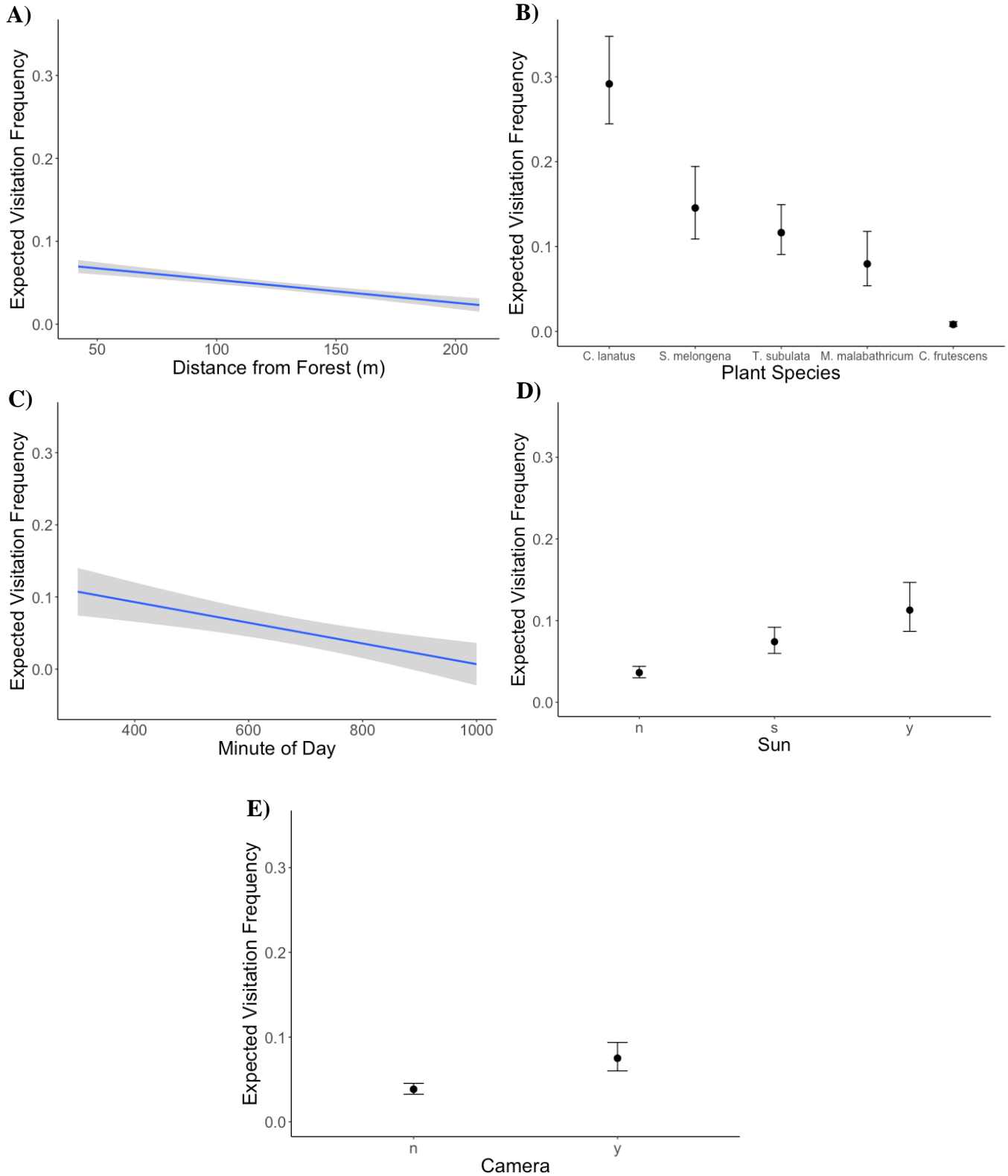
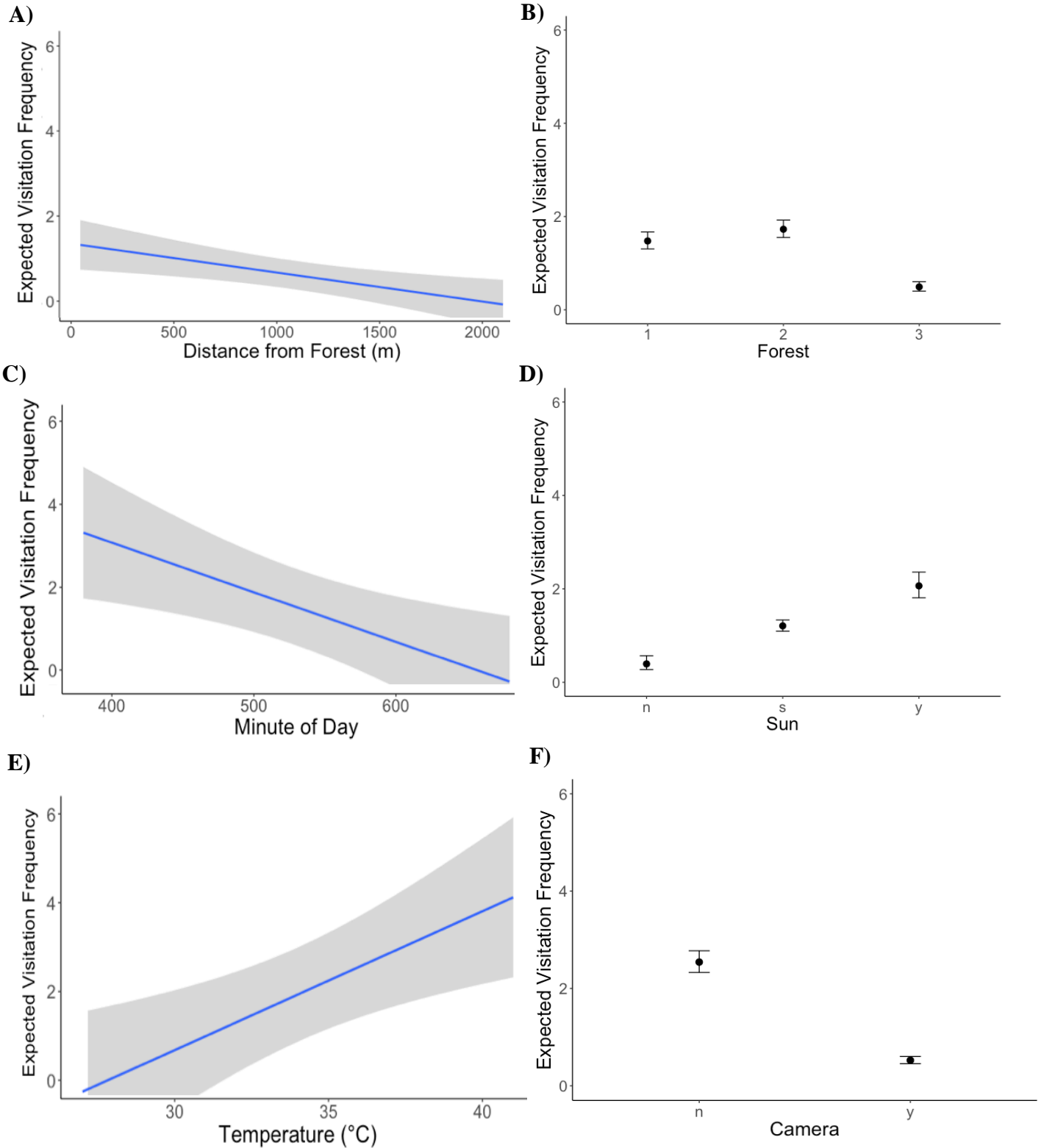


Figure 5: The relationship of expected visit frequency per flower per 10-minute observation period to flowers in Study 2 with each of the most significant factors (with all other variables remaining constant): **A)** Distance from forest (m), **B)** Forest ID, **C)** Time of day, **D)** Sun presence, **E)** Temperature, and **F)** Camera method. Graphs based on estimates from Model 2, error bars represent upper and lower estimates.



Discussion

Bees were the most common flower visitor which is typical in Southeast Asia (Corlett 1990; Nagamitsu & Inoue 1997; Momose et al. 1998; Liow et al. 2001). Visitation frequency varied among plant species, the nature of the nearest forest, distance to forest, as well as time of day, camera method, and weather variables (temperature and direct sunlight). Similar patterns were observed in visit frequencies in Study 1, the small scale grid based study and in Study 2, the large-scale transect study, despite having different layout and focal plant species.

Distance from forest

In both studies bee visit frequency decreased with increasing distance from forest. Similar patterns have been found elsewhere, for example, with flowers having higher visitation frequency near native forests on a coffee plantation in Costa Rica (Ricketts 2004); an increase in bees near natural grasslands (Steffan-Dewenter & Tscharntke 1999), and better pollination service near natural habitats on watermelon farms (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 do not reside among the oil palm itself. This implies the natural forests possess more foraging and nesting resources for bees than the oil palm.

Observations were conducted at a maximum distance from forest of 208m in Study 1 and 2130m in Study 2. The small amount of variation explained by distance from forest in Study 1 (1.07%) could possibly be explained by the short distance sampled. The distances sampled in Study 2, however, are similar to those used elsewhere: Ricketts (2001) observed bee visits up to a

maximum of 1600m from forest, with sites “far from forest” being at least 800m away and Steffan-Dewenter and Tsharntke (1999) observed bee visits up to 1000m from natural grasslands. Although flight distances of 2km have been recorded in bees, few species exceed 400m during usual foraging (Richards 2001) and flight distances are correlated with body size (Steffan-Dewenter & Tsharntke 1999). So, while the distance may be too far for many bees to fly, large bees which were common in the plantation, could fly the distance from the nearest forest to the control points furthest into the plantation.

Distance from Oil Palm

Distance from oil palm was assessed in Study 1 as the four rows of plots go along a gradient from oil palm edge with a maximum distance of 144m. I did not observe an effect on visitation with distance from oil palm which implies that palm oil does not support bees as the natural forests do. Although oil palm is a closed canopy forest, it is highly managed with very little incorporated biodiversity.

Differences among forests

There was a significant difference in visit frequency in Study 2 with transects near Forests 1 and 2 having high and similar visit frequencies while transects closest to Forest 3 had significantly lower visitation frequencies. Similar results have been found in other studies, i.e. higher visitation frequencies observed on plants near larger forests compared to smaller forests (Ricketts 2004; Benedick S. et al. 2006). My results suggest larger forests are more effective for conserving bees and their implied pollination services, but even small patches have a more

positive effect than the planted oil palm. Although Edwards et al. (2011) suggested high conservation value areas should be at least 1,000 hectares, my results indicate that even forests as small as 54 hectares within an agricultural monoculture can boost bee visit frequency.

Weather variables

During data exploration I found temperature, humidity, and time of day were highly correlated (with correlations between 0.709-0.905) (Appendix F). These high correlations make the size of the variance contributions for each individual variable highly uncertain and thus it makes sense to combine their variance contributions. Combined temperature, time of day, and humidity contribute 2.1% of variation in Model 1 and 22.7% of the variation of visit frequency in Model 2. While visitation frequency has a positive relationship with temperature, it has a negative relationship with both time of day and humidity.

With global temperatures expected to increase, it is essential to understand the effects of rising temperatures on pollinators. In my study, flower visit frequency increased within the temperature range during the observation periods. My results suggest these bees can tolerate some increase in temperatures. However, this is not a reliable assumption as I do not know the expected response beyond the observed range. It is also important to note that potential climate change effects include changes in weather patterns which may have unexpected and cascading ecological effects.

As honeybees have been shown to have a unimodal relationship with temperature in regards to maximum visit frequency (Nielsen et al. 2017), my observations likely did not illustrate the

complete temperature relationship. As one of the alternative models (with a quadratic temperature term) in my model selection process had a slightly lower BIC than the final model, it suggests the unimodal relationship is present in the study system but the pattern is not clear in my data.

When the observed flowers were in direct sunlight for the entire observation the visit frequency was highest and was lowest when observed flowers were not in direct sunlight during any of the observation. This effect is highly relevant when using different shading techniques which is common in the region. Although shading may help protect plants from drying out, I have shown that flowers in shade receive lower visitation frequencies that might negatively affect yields.

Differences with camera use

I used cameras in 40.2% of all the observation periods. In Study 2, where only *T. subulata* flowers were observed, the expected visit frequency was much lower for the flowers observed with the camera. The effect of the cameras was opposite for Study 1, as higher visitation frequencies are expected with the camera compared to without. The negative effect of camera in Study 2 is likely due to the selection of observed flowers. During direct observations I chose the most open and healthy flowers located at the top of the *T. subulata* bushes, but this was not always possible when using the cameras. The differences in results between the two studies suggest it is feasible to use cameras to record visitation frequency but the results are highly dependent on how the cameras are set up and how the observed flowers are selected.

Differences Among Plant Species

C. lanatus had the highest expected visit frequency, followed by *S. melongena*, *T. subulata*, *M. malabathricum*, with the lowest, and only significantly different species being *C. frutescens*, followed by *S. lycopersicum* with no observed visits. The difference in visit frequency among plant species is likely due to the observed plants having very different floristic characteristics and thus different potential pollinators. The low visitation frequencies for some species could therefore suggest a lack of some essential pollinators in this system. This conclusion is supported by findings in other studies which found bee species having varying responses to forest fragmentation, likely because of their nesting requirements (Brosi et al. 2008).

Is the system pollinator limited?

Many crop plants, including *C. lanatus*, have been shown to depend on animal pollination for optimum yields (Stanghellini et al. 1998). *C. lanatus* flowers have been estimated to require at least 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 suggests a visit frequency of at least 0.11 visits per flower per 10 minutes would be required during the one day the flower is open, which is lower than the average visit frequency to *C. lanatus* in this study (0.62). Based on this comparison, it would seem the pollinator system in this study area is adequate for optimum fruit set and quality for *C. lanatus* and possibly *S. melongena*. *C. frutescens* and *S. lycopersicum*, on the other hand, likely did not receive enough visits to have optimum yields. These are highly speculative estimates since pollinators have different pollinating abilities and the species of the visiting bees in this study have not been recorded.

Can a mixed forest and oil palm landscape maintain pollinators and pollination services?

Palm oil stakeholders are under pressure now more than ever to improve their environmental performance and this study adds to the ongoing discussion. Oil palm expansion changes land cover, which often results in reduced abundance of biodiversity including bees and the pollination services they provide. However, my results show maintaining native forests within the agricultural landscape can increase pollinator availability which would likely support the reproduction in both wild plants and entomophilous crops.

More pollinators could be supported within the planted oil palm if the agricultural field was more similar to natural forests in providing nesting locations and foraging resources. Based on my results and results from other studies (Liow et al. 2001), oil palm plantations support fewer pollinators than natural forests. However, as Meijaard et al. (2016) discusses, the effect of oil palm needs to be considered in context of what the area could have been if it had not been converted to oil palm. Surely oil palm, as a forest, albeit of a monoculture of managed, exotic trees, has potential to support more biodiversity than, for example, a deforested or mined area. Liow et al., for instance, found that an oil palm plantation in Johor had more bee individuals than a nature reserve in Singapore (Liow et al. 2001). The significant effect of all study forests, including Forest 4 which was only 54 hectares, implies bees show some resilience to land use but are still dependent on natural forests. Similar findings of small forest fragments positively affecting pollinators has been observed in other highly fragmented systems (Brosi et al. 2008). It is important to note the remnant forests in my study system were not pristine primary forests and

all have some degree of human disturbance. This implies, though large primary forests are important to conserve, protecting other forests is also beneficial to bees and likely other taxa.

Management practices such as maintaining a mixed understory, including natural flowers, grasses, and shrubs, while still allowing easy access for harvesting, along with polyculture farming, can increase many taxa within various agricultural landscapes (Ricketts 2001, 2004; Kremen 2015; Ghazali et al. 2016; Yahya et al. 2017). My results suggest the same can be said for oil palm landscapes. I conclude that creating a more heterogenous agricultural matrix can help sustain bees in an oil palm plantation. Results from this study can be used to aid palm oil stakeholders, policy makers and certification bodies (such as the Roundtable on Sustainable Palm Oil) to promote oil palm landscapes which improve local and regional biodiversity.

Recommendations for future work

In this study I quantified flower visits, which only partially explains the pollination system as visits does not necessarily equal successful pollination of flowers. To better understand the plant-pollinator system it would be ideal to take into account fruit set as well as quality of mature fruits.

Visitation in my study was dominated by bees, which I treated as one functional pollinator group. However, there are many types of bees of a wide range of sizes, behaviours, and pollinating abilities. It has been shown in other studies that bee species are affected disproportionately by distance to native vegetation (Kremen et al. 2002). It has also been observed that species richness may increase with disturbed areas while individuals decrease

(Liow et al. 2001). Because of these known differences between bee species, identification to species or morpho species of the visitors would be recommended in future studies.

To better understand the plant- pollinator system it would be beneficial to study the relationships within the remnant forest. I did not find any focal plant within the forested areas, likely due to scattered distribution, the majority of the flowers located in the canopy, and general flowering expected in lowland dipterocarp forests (Sakai et al. 1999). It would also be useful to better describe the forests, for example, tree size, spacing, height, and species, to further understand the differences between the forests and their effects on visit frequency. In future studies, I would suggest increasing the distance from palm oil to better assess its effect on bees. I also would take into account ground cover in the observations and analyses.

Finally, this study was based in one plantation in a limited number of locations over several weeks, thus my results only explain the variation in bee frequency within this system. To better understand the plant-pollinator system on a larger landscape scale would involve sampling over broader spatial and temporal scales.

References

- Adlerz WC. 1966. Honey bee visit numbers and watermelon pollination. *Journal of Economic Entomology* **59**:28-30.
- Asian Agri. 2017. The benefits of *Turnera subulata*, Available from <http://www.asianagri.com/en/medias/media/articles/the-benefits-of-turnera-subulata> (accessed March 2018).
- Australian Tropical Rainforest Plants. 2010. Available from http://keys.trin.org.au:8080/key-server/data/0e0f0504-0103-430d-8004-060d07080d04/media/Html/taxon/Melastoma_malabathricum_subsp._malabathricum.htm (accessed March 2018).
- Basiron Y. 2007. Palm oil production through sustainable plantations. *European Journal of Lipid Science and Technology* **109**:289-295.
- Bates D, Machler M, Bolker B, Walker S. 2015. Fitting Linear Mixed-Effects Models Using (lme4). *Journal of Statistical Software* **67**:1-48.
- 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.
- Benedick S., Hill J. K., Mustaffa N., Chey V. K., Maryati M., Searle J. B., Schilthuizen M., C. HK. 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.
- Bickel TO, Bruhl CA, Gadau JR, Holldobler B, Linsenmair K. 2006. Influence of habitat fragmentation on the genetic variability in leaf litter ant populations in tropical rainforests of Sabah, Borneo. *Biodiversity and Conservation* **15**:157-175.
- Bomfim IGA, Freitas BM, Aragão FASd, Walters A. 2016. Pollination in Cucurbit Crops in Pessarakli M, editor. *Handbook of Cucurbits: Growth, Cultural Practices, and Physiology* CRC Press.
- Bomfim IGA, Melo Bezerra ADD, Nunes AC, Freitas BM, Aragão FASd. 2015. Pollination requirements of seeded and seedless mini watermelon varieties cultivated under protected environment. *Pesquisa Agropecuária Brasileira* **50**.
- Brosi BJ, Daily GC, Shih TM, Oviedo F, Durán G. 2008. The effects of forest fragmentation on bee communities in tropical countryside. *Journal of Applied Ecology* **45**:773-783.
- Carter C, Finley W, Fry J, Jackson D, Willis L. 2007. Palm oil markets and future supply. *European Journal of Lipid Science and Technology* **109**.
- Chen M-S, Chou Y-C. 2011. Time lapse camera. Brinno Inc.
- Collinge SK 2009. *Ecology of Fragmented Landscapes*. The John Hopkins University Press, Baltimore, Maryland.
- Corlett RT. 1990. Flora and reproductive phenology of the rain forest at Bukit Timah, Singapore. *Journal of Tropical Ecology*:55-63.
- Corley RHV. 2009. How much palm oil do we need? *Environmental Science and Policy* **12**:134-139.
- Curran LM, Caniago II, Paoli GD, Astianti D, Kusneti M, Leighton M, Nirarita CE, Haeruman H. 1999. Impact of El Nino and logging on canopy tree recruitment in borneo. *Science* **286**:2184-2188.

- Curran LM, Trigg SN, McDonald AK, Astiani D, Hardiono YM, Siregar P, Caniago I, Kasischke E. 2004. Lowland forest loss in protected areas of Indonesian Borneo. *Science* **303**:1000-1003.
- Daily GC, et al. 1997. Ecosystems Services: Benefits Supplied to Human Societies by Natural Ecosystems. *Issues in Ecology* **2**.
- Denmead LH, Darras K, Clough Y, Diaz P, Grass I, Hoffmann MP, Nurdiansyah F, Fardiansah R, Tschardt T. 2017. The role of ants, birds and bats for ecosystem functions and yield in oil palm plantations. *Ecology* **98**:1945-1956.
- Deprá MS, Delaqua GCG, Freitas L, Gaglianone MC. 2014. Pollination Deficit In Open-Field Tomato Crops (*Solanum Lycopersicum* L., Solanaceae) In Rio De Janeiro State, Southeast Brazil. *Journal of Pollination Ecology* **12**:1-8.
- Devaraju N, Bala G, Modak A. 2015. Effects of large-scale deforestation on precipitation in the monsoon regions: Remote versus local effects. *Proceedings of the National Academy of Sciences of the United States of America* **112**:3257-3262.
- Edwards DP, Fisher B, Wilcove DS. 2011. High Conservation Value or high confusion value? Sustainable agriculture and biodiversity conservation in the tropics. *Conservation Letters* **5**.
- FAO 2013. *Climate-Smart Agriculture Sourcebook*. Food and Agriculture Organization of the United Nations, Rome.
- Feintrenie L, Chong WK, Levang P. 2010. Why do Farmers Prefer Oil Palm? Lessons Learnt from Bungo District, Indonesia. *Small Scale Forestry* **9**.
- Flint EP. 1994. Changes in land use in South and Southeast Asia from 1880 to 1980: a data base prepared as part of a coordinated research program on carbon fluxes in the tropics. *Chemosphere* **29**:1015-1062.
- Foster WA, et al. 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.
- Ghazali A, Asmah S, Syafiq M, Yahya MS, Aziz N, Peng TL, Norhisham AR, Puan CL, Turner EC, Azhar B. 2016. Effects of monoculture and polyculture farming in oil palm smallholdings on terrestrial arthropod diversity *Journal of Asia-Pacific Entomology* **19**:415-421.
- Gibbs HK, Ruesch AS, Achard F, Clayton MK, Holmgren P, Ramankutty N, Foley JA. 2010. Tropical forests were the primary sources of new agricultural land in the 1980s and 1990s. *Proceedings of the National Academy of Sciences of the United States of America* **107**:16732-16737.
- Gray CL, Lewis OT, Chung AYC, Fayle TM. 2015. Riparian reserves within oil palm plantations conserve logged forest leaf litter ant communities and maintain associated scavenging rates. *Journal of Applied Ecology* **52**:31-40.
- Institute of Pacific Islands Forestry. 2006. *Turnera subulata*, Available from http://www.hear.org/pier/species/turnera_subulata.htm (accessed March 2018).
- Jaenicke J, Rieley JO, Mott C, Kimman P, Siegert F. 2008. Determination of the amount of carbon stored in Indonesian peatlands. *Geoderma* **147**:151-158.
- Johnson AE, Knott CD, Pamungkas B, Pasaribu M, Marshall AJ. 2004. A survey of the orangutan (*Pongo pygmaeus wurmbii*) population in and around Gunung Palung National Park, West Kalimantan, Indonesia based on nest counts. *Biological Conservation* **121**:495-507.

- Jules E, Shahani P. 2003. A broader ecological context to habitat fragmentation: Why matrix habitat is more important than we thought. *Journal of Vegetation Science* **14**:459-464.
- Klein AM, Steffan-Dewenter I, Tschardt T. 2003. Pollination of *Coffea canephora* in relation to local and regional agroforestry management. *Journal of Applied Ecology* **40**:837-845.
- Koh LP, Sodhi NS. 2004. Importance of reserves, fragments, and parks for butterfly conservation in a tropical urban landscape. *Ecological Applications* **14**:1695-1708.
- Koh LP, Wilcove DS. 2008. Is oil palm agriculture really destroying tropical biodiversity? *Conservation Letters* **1**:60-64.
- Kremen C. 2015. Reframing the land-sparing/land-sharing debate for biodiversity conservation. *Annals of the New York Academy of Sciences* **1355**.
- Kremen C, Williams NM, Thorp RW. 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.
- Landaverde P, Quezada-Euan JJG, 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.
- Lawrence D, Vandecar K. 2015. Effects of tropical deforestation on climate and agriculture. *Nature Climate Change* **5**:27-36.
- Liow LH, Sodhi NS, Elmquist T. 2001. Bee diversity along a disturbance gradient in tropical lowland forests of south-east Asia. *Journal of Applied Ecology* **38**:180-192.
- Lucey JM, Tawatao N, Senior MJM, Vun Khen C, Benedick S, Hamer KC, Woodcock P, Newton RJ, Bottrell SH, Hill JK. 2014. Tropical forest fragments contribute to species richness in adjacent oil palm plantations. *Biological Conservation* **169**:268-276.
- Meijaard E, Garcia-Ulloa J, Sheil D, Wich SA, Carlson KM, Juffe-Bignoli D, Brooks TM. 2018. Oil palm and biodiversity. A situation analysis by the IUCN Oil Palm Task Force. IUCN Oil Palm Task Force Gland, Switzerland:IUCN. xiii + 116pp.
- Meijaard E, Nardiyono, Rahman H, Husson S, Sanchez KL, Campbell-Smith G. 2016. Exploring Conservation Management in an Oil-palm Concession. *International Journal of Nature Resource Ecology and Management* **1**:179-187.
- Momose K, Yumoto T, Nagamitsu T, Kato M, Nagamasu H, Sakai S, Harrison RD, Itioka T, Hamid AA, Inoue T. 1998. Pollination Biology In A Lowland Dipterocarp Forest In Sarawak, Malaysia. I. Characteristics Of The Plant-Pollinator Community In A Lowland Dipterocarp Forest. *American Journal of Botany* **85**:1477-1501.
- Nagamitsu T, Inoue T. 1997. Aggressive foraging of social bees as a mechanism of floral resource partitioning in an Asian tropical rainforest. *Oecologia* **110**:432-439.
- Neto CdMeS, Lima FG, Gonçalves BB, Bergamini LL, Bergamini BAR, Elias MAdS, Franceschinelli EV. 2013. Native Bees Pollinate Tomato Flowers And Increase Fruit Production. *Journal of Pollination Ecology* **11**:41-45.
- Nielsen A, Reitan T, Rinvoll AW, Brysting AK. 2017. Effects of competition and climate on a crop pollinator community. *Agriculture, Ecosystems & Environment* **246**.
- Obidzinski K, Andriani R, Komarudin H, Andrianto A. 2012. Environmental and Social Impacts of Oil Palm Plantations and their Implications for Biofuel Production in Indonesia. *Ecology and Society* **17**.

- Ollerton J, Winfree R, Tarrant S. 2011. How many flowering plants are pollinated by animals? . *Oikos* **120**.
- Patrício-Roberto G, Campos M. 2014. Aspects of Landscape and Pollinators—What is Important to Bee Conservation? *Diversity* **6**:158.
- Pither J, Taylor PD. 1998. An Experimental Assessment of Landscape Connectivity. *Oikos* **83**:166-174.
- Prasetyo AE, Purba WO, Susanto A. 2014. Elaeidobius kamerunicus: Application Of Hatch And Carry Technique For Increasing Oil Palm Fruit Set. *Journal of Oil Palm Research* **26**:195-202.
- PT Austindo Nusantara Jaya Tbk. 2016. About us: Location map, Available from <https://anj-group.com/en/location-map> (accessed March 2018).
- R Core Team. 2017. R: A language and environment for statistical computing. . R Foundation for Statistical Computing Vienna, Austria.
- R Studio Team 2016. RStudio: Integrated Development Environment for R. RStudio, Inc., Boston, MA.
- Raspisaniye Pogodi Ltd. 2018. Weather archive in Ketapang (airport), Available from [http://rp5.md/Weather_archive_in_Ketapang_\(airport\)](http://rp5.md/Weather_archive_in_Ketapang_(airport)) (accessed March 2018).
- Reitan T, Nielsen A. 2016. Do not divide count data with count data; a story from pollination ecology with implications beyond. *PLoS ONE* **11**.
- Richards AJ. 2001. Does Low Biodiversity Resulting from Modern Agricultural Practice A. *Annals of Botany* **88**:165-172.
- Ricketts TH. 2001. The matrix matters: effective isolation in fragmented landscapes. *The American Naturalist* **158**:87-99.
- Ricketts TH. 2004. Tropical Forest Fragments Enhance Pollinator Activity in Nearby Coffee Crops. *Conservation Biology* **18**:1262-1271.
- Roland J, Keyghobadi N, Fownes S. 2000. Alpine Parnassius Butterfly Dispersal: Effects of Landscape and Population Size. *Ecology* **81**:1642-1653.
- Roundtable on Sustainable Palm Oil. 2013. Principles and criteria for the production of sustainable palm oil.
- Sakai S, Momose K, Yumoto T, Kato M, Inoue T. 1999. Beetle pollination of *Shorea parvifolia* (section *Mutica*, Dipterocarpaceae) in a general flowering period in Sarawak, Malaysia. *American Journal of Botany* **86**:62-69.
- Sawit Indonesia. 2014. Pengendalian Hama Ulat Api: Bunga Pukul Delapan, Cantik Nan Bermanfaat, Available from <https://sawitindonesia.com/rubrikasi-majalah/hama-penyakit/pengendalian-hama-ulat-api-bunga-pukul-delapan-cantik-nan-bermanfaat/> (accessed March 2018).
- Schloerke B, Crowley J, Cook D, Briatte F, Marbach M, Thoen E, Elberg A, Larmarange J 2018. GGally: Extension to 'ggplot2'.
- Sheil D, Meijaard E, Van Noordwijk M, Kanninen M. 2009. The Impacts and Opportunities of Oil Palm in Southeast Asia: What do We Know and What do We Need to Know. Center for International Forestry Research, Bogor, Indonesia.
- Sodhi NS, Koh LP, Brook BW, Ng PKL. 2004. Southeast Asian biodiversity: an impending disaster. *Trends in Ecology and Evolution* **19**:654-660.
- Stanghellini MS, Ambrose JT, Schultheis JR. 1998. Seed production in watermelon: A comparison between two commercially available pollinators. *HortScience* **33**:28-30.

- Steffan-Dewenter I, Tschardt T. 1999. Effects of habitat isolation on pollinator communities and seed set. *Oecologia* **121**:432-440.
- Tandon R, Manohara TN, Nijalingappa BHM, Shivanna KR. 2001. Pollination and Pollen-pistil Interaction in Oil Palm, *Elaeis guineensis*. *Annals of Botany* **87**:831-838.
- Teo TM. 2015. Effectiveness of the oil palm pollinating weevil, *Elaeidobius kamerunicus*, in Malaysia. *UTAR Agriculture Science Journal*.
- The Gunung Palung Orangutan Project. n.d. . The Gunung Palung Orangutan Project: About G.P., Available from <http://people.bu.edu/orang/about.html> (accessed March 2018).
- Tonks AJ, Aplin P, Beriro DJ, Cooper H, Evers S, Vane CH, Sjögersten S. 2017. Impacts of conversion of tropical peat swamp forest to oil palm plantation on peat organic chemistry, physical properties and carbon stocks. *Geoderma* **289**:36-45.
- Vijay V, Pimm SL, Jenkins CN, Smith SJ. 2016. The impacts of oil palm on recent deforestation and biodiversity loss. *PLoS ONE*.
- Vira B, Wildburger C, Mansourian S 2015. Forests, Trees and Landscapes for Food Security and Nutrition: A Global Assessment Report. International Union of Forest Research Organizations Vienna.
- Wickham H 2009. *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag New York.
- World Wildlife Fund. 2018. Southeastern Asia: Indonesia and Malaysia, Available from <https://www.worldwildlife.org/ecoregions/im0102> (accessed March 2018).
- Yahya MS, 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.
- Yue J, Yan Z, Bai C, Chen Z, Lin W, Jiao F. 2015. Pollination Activity of *Elaeidobius kamerunicus* (Coleoptera: Curculionidae) on Oil Palm on Hainan Island. *Florida Entomologist* **98**:499-505.
- Zuur AF, Ieno EN, Elphick CS. 2010. A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution* **1**:3-14.

Appendices

- A. Potential covariates
- B. A sample of alternate GLMMs considered in model selection
- C. Correlation plots of a selection of variables Correlations between temperature, humidity, and time
- D. Final models
- E. Imputation of missing temperature values
- F. Correlations between Temperature, Humidity, and Time

Appendix A: Potential covariates

	Covariate	Description
Weather variables	Weather	Factor variable, 9 levels, describing weather from Pontianak weather station at time closest to observation: cloudy, light drizzle, light rain showers, moderate to heavy rain showers, partly cloudy, patchy light rain with thunder, patchy rain, sunny, torrential rain shower
	Temperature	<p>Max: Maximum temperature as measured at Pontianak weather station (29-38 degrees Celsius)</p> <p>Min: Minimum temperature as measured at Pontianak weather station (24-29 degrees Celsius)</p> <p>Pontianak temperature: Temperature as measured at Pontianak weather station (24-37 degrees Celsius)</p> <p>Ketapang temperature: Temperature as measured at Ketapang weather station (25-32.4 degrees Celsius)</p> <p>Logger temperature: Temperature on plantation in shade (18.9-37.8 degrees Celsius)</p> <p>Temperature measured with thermohydrometer: 24-45.2 degrees Celsius</p>
	Rain	<p>Pontianak rain: Daily rainfall as measured by Pontianak weather station (0-35.5mm)</p> <p>Rain: Daily rainfall on plantation (0-127mm)</p> <p>Yesterdayrain: Amount of rainfall on plantation the day before observation (0-127mm)</p>

		Last rain: Days since last rainfall (0-17)
	Wind	<p>Wind direction: factor variable, 11 levels, measured at Pontianak weather station (E, ENE, ESE, NNE, S, SE, SSE, SSW, SW, W, WSW)</p> <p>Pontianak wind, factor variable, 6 levels: Wind speed measured at Pontianak weather station (1-6)</p> <p>Gust, factor variable, 7 levels: Gust speed measured at Pontianak weather station (1-7)</p> <p>Wind, factor variable, 3 levels, describing how often the observed flower(s) moved during the observation period: often, some, never</p>
	Cloud	<p>% Cloud cover measured at Pontianak weather station (0-100%)</p> <p>Light: Measured by logger in shaded area (0-23422lux)</p> <p>Sun, factor variable, 3 levels, describing time observed flower(s) were in direct sun for the observation period: yes, some, no</p>
	Humidity	<p>% Humidity measured at Pontianak weather station: 41-98%</p> <p>% Humidity measured at Ketapang weather station: 50-96%</p> <p>% Humidity measured by thermohydrometer at observation location: 36-95%</p>
	Pressure	Air pressure measured at Pontianak weather station (1006-1013)
Temporal variables	Day	<p>Observation day, factor variable, 47 levels: 1-100</p> <p>Day of year (203-302)</p>

		Month (7-10)
	Time	Minute of the day (330-1067)
Spatial variables	Forest	Forest patch, factor variable, 4 levels: 1-4
	Size	Size of forest patch: 53.9, 203, 381, 4574m ²
	Continuous Forest	Factor variable, 2 levels: yes, no
	Soil	Factor variable, 3 levels: mineral, peat, sand
	Planted year	Factor variable 3 levels, year the adjacent oil palm was planted: 2010, 2011, 2012
	Distance to forest	Distance to nearest forest edge: 42-2130m
	Distance to oil palm	Distance to nearest oil palm edge:39-144m
	Transect	Factor variable, 9 levels: A, B, C, D, E, F, G, H, I, Control
Plant variables	Species	Factor variable, 6 levels: <i>C. lanatus</i> , <i>T. subulata</i> , <i>M. malabathricum</i> , <i>S. melongena</i> , <i>C. frutescens</i> , <i>S. lycopersicum</i>
	Flowers	Number of flowers observed per observation: 1-36
	Wetness	Factor variable, 3 levels, describing how wet vegetation was during observation period: wet, moist, dry
Method	Camera	Factor variable, 2 levels: yes, no

Appendix B: A sample of alternate GLMMs considered in model selection

Study 1

Fixed									Random			
Distance from forest	Distance from oil palm	Temperature	Temperature ν^2	Time of day	Time of day ν^2	Species	Sun	Camera	Observation ID	Observation Day	BIC	Δ BIC from Model 1
x					x	x	x	x	x		992	-0.9
x				x		x	x		x		992.4	-0.5
x				x		x	x	x	x		992.9	0
	x				x	x	x	x	x		996.5	3.6
	x			x		x	x	x	x		996.9	4
x		x				x	x	x	x		997.2	4.3
	x	x				x	x	x	x		1000.5	7.6
x			x			x	x	x	x		1002.3	9.4
x				x		x	x			x	1203.8	210.9

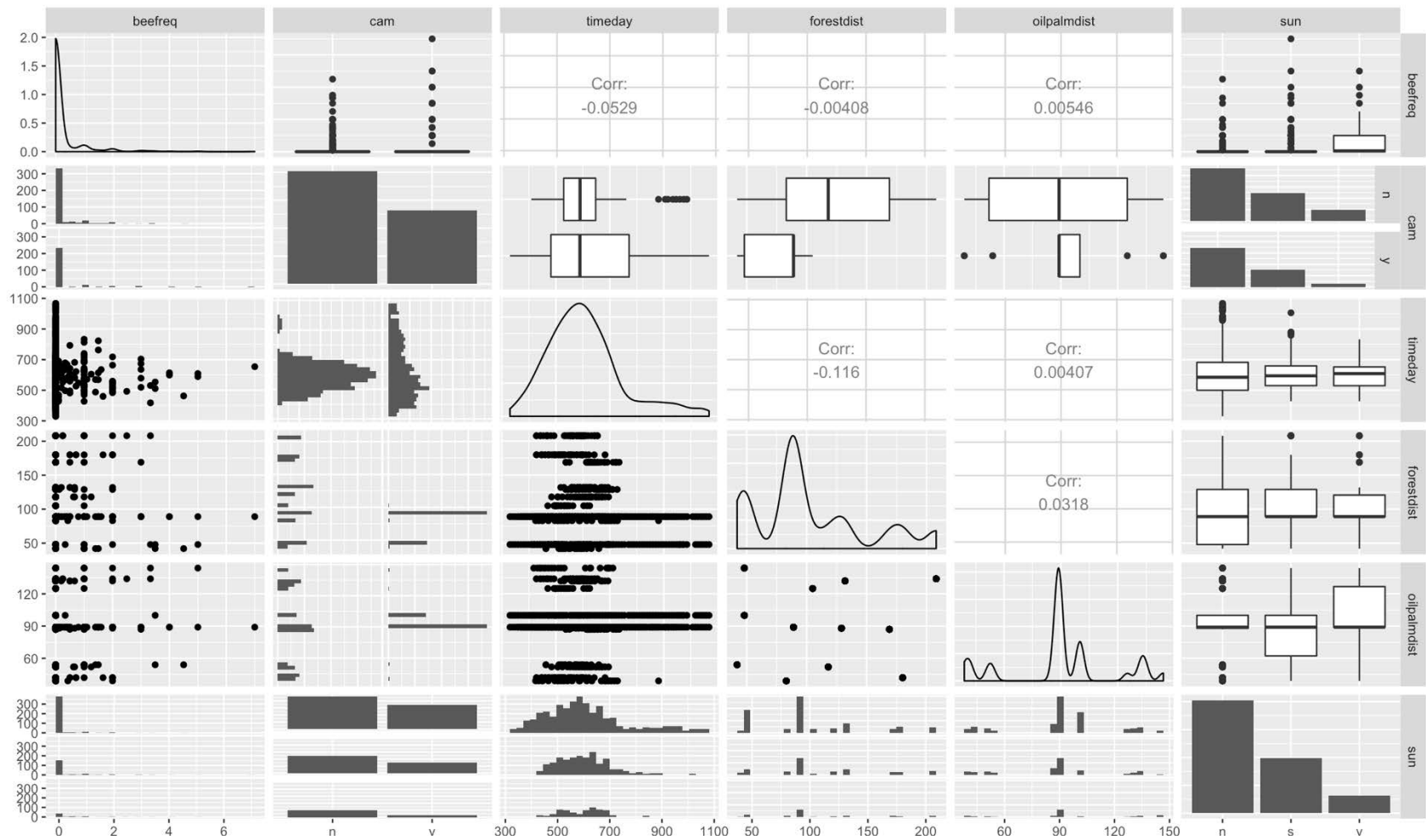
Study 2

Fixed												Random			
Distance from forest	Temperature	Temperature $\wedge 2$	Humidity	Humidity $\wedge 2$	Time of day	Time of day $\wedge 2$	Forest ID	Sun	Cam	Soil	Palm Planted year	Observation ID	Observation Day	BIC	Δ BIC from Model 2
x	x				x		x	x	x			x		1272.3	0
x		x			x		x	x	x			x		1275.9	3.6
x					x		x	x	x			x		1275.9	3.6
x	x		x		x		x	x	x			x		1277.2	4.9
x	x					x	x	x	x			x		1277.7	5.4
x	x						x	x	x			x		1279.8	7.5
x	x			x	x		x	x	x			x		1281.4	9.1
x	x				x		x	x	x	x		x		1282.4	10.1
x		x					x	x	x			x		1283.1	10.8
x	x						x	x	x		x	x		1283.7	11.4
x	x				x		x		x			x		1288.1	12.2
	x				x		x	x	x			x		1290.8	14.9
x	x				x		x	x				x		1377.4	101.5
x	x				x		x	x	x				x	1528.1	252.2

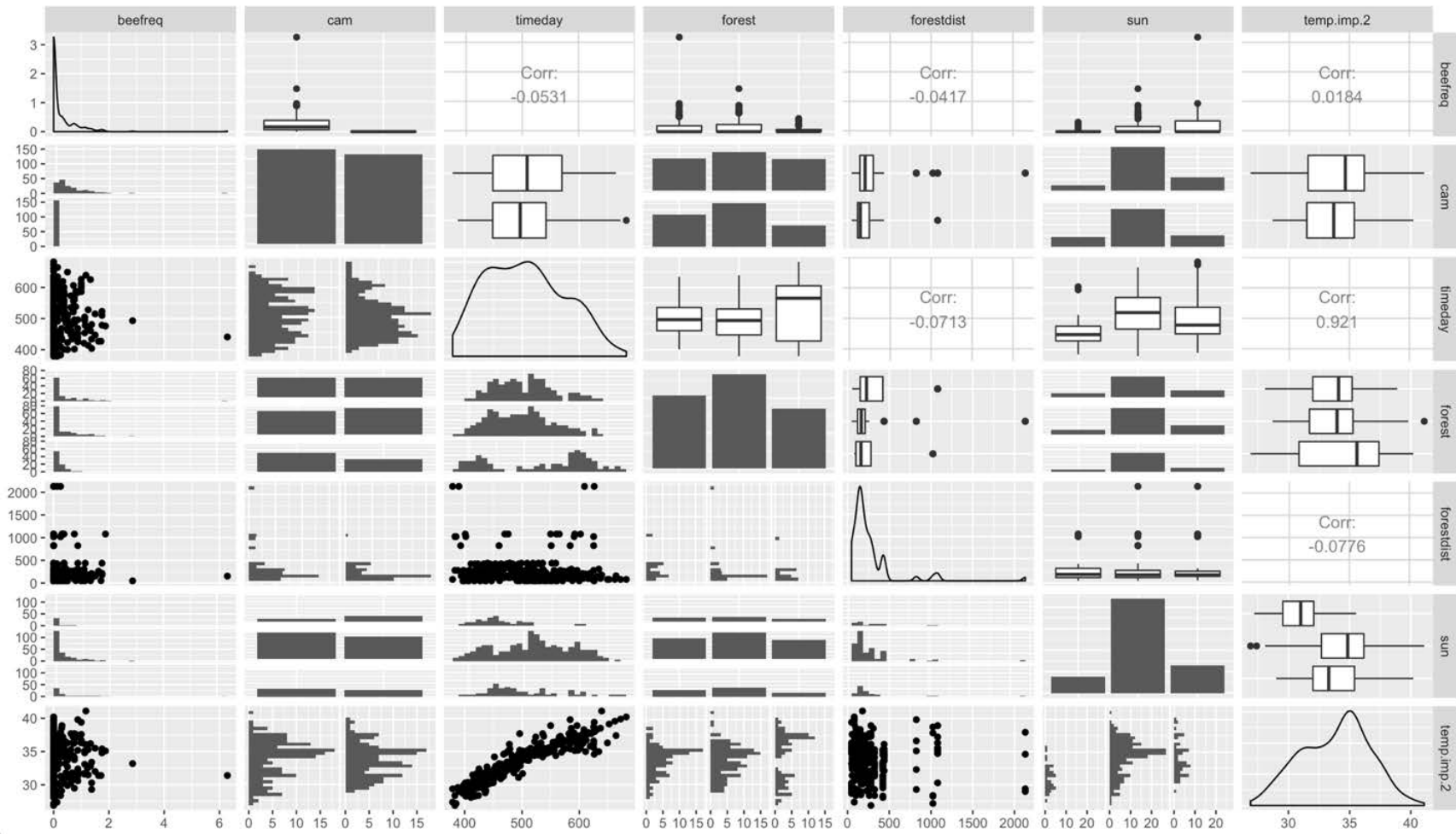
Appendix C: Correlation plots of a selection of variables

Correlation plots created using “ggpairs” extension in the package “GGally” (Schloerke et al. 2018).

Study 1



Study 2



Appendix D: Final models

Model 1:

Generalized linear mixed model fit by maximum likelihood (Laplace Approximation) ['glmerMod']

Family: poisson (log)

Formula: bee ~ timeday + cam + sun + forestdist + species + (1 | id)

Data: GHIfinal

Offset: log(flowers)

AIC	BIC	logLik	deviance	df.resid
943.4	992.9	-460.7	921.4	656

Model 2:

Generalized linear mixed model fit by maximum likelihood (Laplace Approximation) ['glmerMod']

Family: poisson (log)

Formula: bee ~ forestdist + forest + sun + temp.imp.2 + timeday + cam + (1 | id)

Data: AFketa

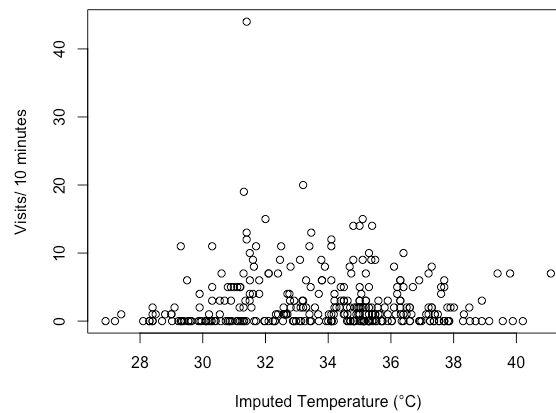
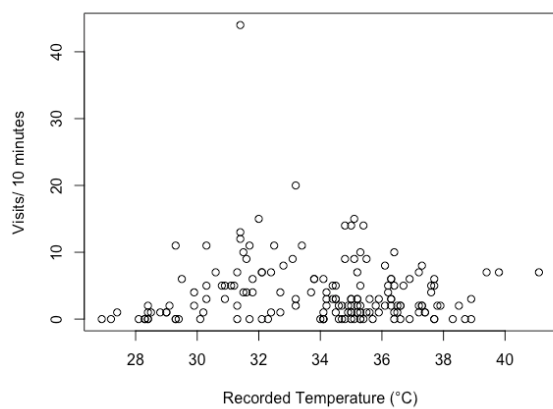
Offset: log(flowers)

AIC	BIC	logLik	deviance	df.resid
1234.6	1272.3	-607.3	1214.6	313

Appendix E: Imputation of missing temperature values

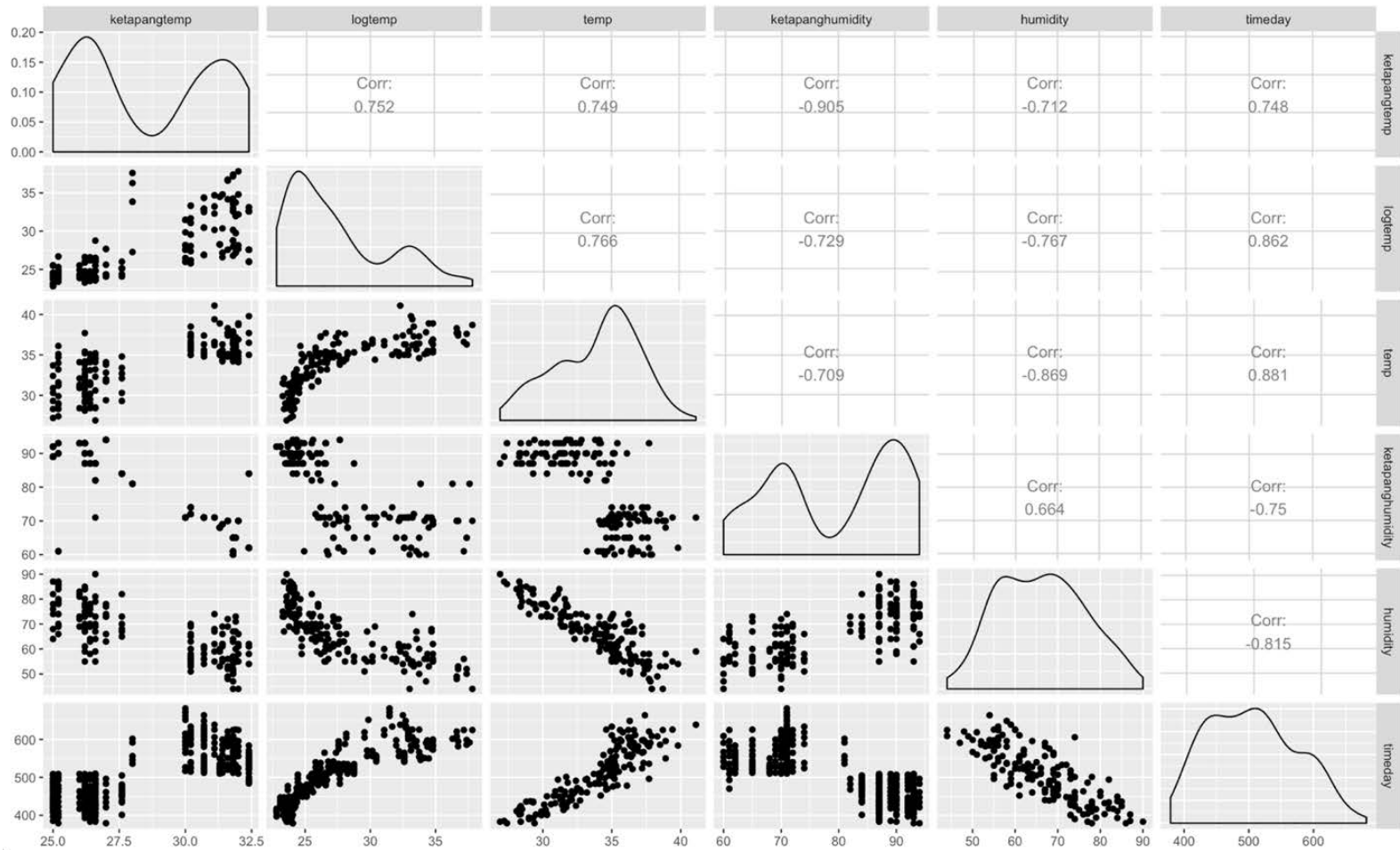
```
#linear regression using other temp. sources, sun, humidity, and observation day
lm.imp.2<-lm(temp~pontitemp+timeday+observationday+
             logtemp+sun+ketapangtemp+ketapanghumidity, data=AFketa)

pred.2<-predict(lm.imp.2,AFketa)
summary(pred.2)
impute<-function(a,a.impute){ifelse(is.na(a),a.impute,a)}
AFketa$temp.imp.2<-impute(AFketa$temp,pred.2) #fill in NA's in temperature with predictions from linear regression
```



Appendix F: Correlations between Temperature, Humidity, and Time

Correlation plots created using “ggpairs” extension in the package “GGally” (Schloerke et al. 2018).





Norges miljø- og biovitenskapelige universitet
Noregs miljø- og biovitenskapelige universitet
Norwegian University of Life Sciences

Postboks 5003
NO-1432 Ås
Norway