The effect of pollination boxes and anthesising inflorescences on relative density of *Elaeidobius kamerunicus* in an oil palm plantation in West Kalimantan

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This project was a collaboration between the Center for Ecological and Evolutionary Synthesis (CEES) at the University of Oslo, the Norwegian University of Life Sciences, Tanjungpura University in Pontianak, PT Austindo Nusantara Jaya Agri and the Center for International Forest Research in Bogor.

Abstract

Palm oil is the most consumed vegetable oil globally and demand is expected to increase. This demand can be met through expansion and/or intensification (increase production per unit area) of oil palm plantations. Recent decreases in palm oil yields and the yield gap between the actual and potential palm oil yields, has spurred research into the underlying mechanisms influencing fruit set and palm oil yields. As fruit set in the oil palm (*Elaeis guineensis*) is strongly dependent on its main pollinator, the weevil *Elaeidobius kameruncis*, questions have been asked about whether the current population levels of these weevils suffice to support good fruit set and thus ensure productivity.

The plantation in this study, PT Kayung Agro Lestari (KAL), has taken action to increase their weevil population levels by introducing a form of assisted pollination, what they call "pollination boxes". The boxes contain post-anthesised male inflorescences, as this is where the eggs and larvae of *E. kamerunicus* develop. The inflorescences are sprayed with viable pollen daily until the weevils start hatching. The purpose of the pollination boxes is to increase the local weevil population and increase the chances of newly hatched weevils pollinating anthesising female inflorescences. These boxes have been placed throughout the plantation, distanced roughly 300 – 800m apart in the area where this study was performed.

During the preliminary phase of the study, several traps were designed and tested to capture weevils. As these traps did not provide satisfactory results, they were omitted from the study. An alternative approach to assess the local weevil density was to collect spikelets from anthesising male inflorescences and counting all weevils present. The effect of the pollination boxes on relative weevil densities was examined by sampling spikelets along transects up to ~400 m from the pollination boxes. The number of anthesising male and female inflorescences at each sampling location (5x5 palms) within the transects was also examined to assess to what degree the natural variation of anthesising inflorescences influences the relative weevil densities.

During the preliminary phase of the study, several traps were designed and tested to capture weevils. As these traps did not provide satisfactory results, they were omitted from the study. An alternative approach to assess the local weevil density was to collect spikelets from anthesising male inflorescences and counting all weevils present. During 12 sampling days, a

total 9467 weevils were collected in 37 sampling locations, registering 387 anthesising inflorescences. A generalised linear mixed model with a negative binomial distribution was used to model the relationship between weevil counts and explanatory variables.

At the scale of this study, no relationship was observed between distance to pollination boxes and the number of weevils found per spikelet. There was a weak negative correlation between the combined number of anthesising male and female inflorescences on the palms surrounding the focal palm and weevil density. This suggest that the weevils are distributed evenly throughout the plantation and that a dilution effect decrease the number of weevils found per spikelet where there are many other spikelets available. The strongest relationships found occurred between variables related to qualities of the male inflorescences and weevil density. The percentage development of flowers on the spikelets showed that the number of weevils increased until approximately 60% of the spikelets were covered by flowers and decreased thereafter. The available habitat per spikelet, measured as cm flower development per spikelet, was incorporated as both an offset variable and an explanatory variable and affected the relative weevil density negatively.

These results question the effectiveness of pollination boxes and suggest that they may not provide the benefit hoped for. Careful consideration should therefore be put into their continued use.

An alternative approach to pollination boxes might be to store and hatch weevils in a confined system in a storage warehouse, spray the weevils with viable pollen, and releasing them into high density areas of anthesising female inflorescences. This approach could have three possible benefits: (i) protect the weevils against predation, (ii) require less labour effort by eliminating daily maintenance of pollination boxes in the field, and (iii) increase the chances of weevils first visiting an anthesising female inflorescence. More research would be required to confirm these statements.

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1 Introduction

Palm oil produced from the African oil palm (*Elaeis guineensis*) is the most consumed vegetable oil, accounting for approximately 35% of the global output of vegetable oils (Meijaard et al. 2018) and can be found in a large variety of everyday products due to its versatile capacities. Among these products are shampoos, soaps and detergents, chocolate, ice cream and cosmetics and biofuel (WWF 2020). Indonesia and Malaysia are the leading producers of palm oil, together contributing 85% of the global supply (Carter et al. 2007, Meijaard et al. 2018). These countries occupy 32% and 60%, respectively, of the total planted area of industrial scale oil palm plantations, which were estimated to cover 18.7 million hectares (Mha) in 2017 (Meijaard et al. 2018). Indonesia is the largest oil palm producer and provided 42.5 Mt of the global production of 72.7 Mt in 2019/2020 (Statista 2020), with an average production of 4 tons per hectare (Meijaard et al. 2018).

As the human global population is growing and the living standards are rising in the developing world, the per capita consumption of palm oil is increasing and the demand for biofuel might exceed that of edible oil (Corley 2009). Corley (2009) calculated a future demand of 240 Mt palm oil in 2050, if population levels reach 9.2 billion people, requiring an additional area of 12–19 Mha of land for oil palm plantations (Corley 2009). The United Nations Development Programme (UNDP) has since upregulated the projected world population in 2050 to 9.7 billion people, if population levels grow at a slow pace (UNDP 2019). Afriyanti et al. (2016) expect an even higher demand of 264–477 Mt/year. They also explored different scenarios for Indonesia's capacity to meet future crude palm oil (CPO) demands without further deforestation and expansion into peatland. Their study concluded that Indonesia has the capacity to expand oil palm plantations up to 17 Mha and produce between 130 Mt and 176 Mt by 2050, depending on chosen scenario. This will require a higher production than the average 3.6–4.0 t/ha palm oil currently produced (Afriyanti et al. 2016, Meijaard et al. 2018). Increase in future oil palm production could be obtained through expansion and/or intensification (Meijaard et al. 2018).

Approximately 40% of the areas planted with oil palm in Indonesia are managed by smallholders (Jelsma et al. 2017). Smallholders produce substantially lower yields per hectare compared to industrial scale plantations (Glenday and Paoli 2015). The Indonesian government promotes cultivation of oil palm as a way of alleviating poverty, a policy that has

transformed rural communities and remote forested landscapes (Santika et al. 2019). Santika et al. (2019) examined how different aspects of well-being were affected in villages in Kalimantan, Indonesia, where oil palm plantations were developed. The study compared villages where oil palm constituted the primary land use between 2000 and 2014, but not five years prior to this period, to villages where oil palm was not the primary land use during the same period. They reported that the association between oil palm and well-being was affected by the village community livelihoods before the study period. While village communities that had relied on subsistence-based livelihoods prior to the establishment of oil palm plantations experienced an overall decrease in basic, physical, and financial well-being, the association between oil palm and these well-being aspects was overall positive in villages that had previously already relied on market-oriented livelihoods (Santika et al. 2019). These findings indicate that an abrupt change from subsistence-based livelihoods to a market economy may actually promote poverty rather than alleviate it (Santika et al. 2019). Between 2000 and 2015, two-thirds of newly established oil palm plantations in Kalimantan were developed in villages mainly relying on subsistence-based livelihoods (Santika et al. 2019).

Borneo is part of Sundaland, one of 25 biodiversity hotspots in the world, and harbours many endemic species (Myers et al. 2000). The total area of Borneo is 743 000 km^2. In 1973, 558 000 km^2 (75.1%) of the island was covered with natural and near natural forest. By 2015, 371 000 km^2 of forest had been degraded or lost, leaving 49.9% of natural or near natural forest (Gaveau et al. 2016, McAlpine et al. 2018). Important drivers of deforestation are industrial and smallholder oil palm plantations, and forest fires caused by both natural causes and anthropogenic practices (Carlson et al. 2012, Wooster et al. 2012, Gaveau et al. 2016). Expansion of oil palm plantations can contribute to deforestation in several, and often overlapping ways. Intact forests can be cleared or forests that previously have been degraded by logging or fire can be replaced by oil palm plantations. Areas can be deforested for other reasons and subsequently be planted with oil palm, or increasing accessibility to previously inaccessible forests can indirectly ease establishment of oil palm plantations (Fitzherbert et al. 2008). The Indonesian part of Borneo experienced large-scale forest loss and degradation due to extraction of timber and burning, which allowed early establishment of oil palm plantations on land that had already been cleared and degraded (Meijaard et al. 2018). After 2005, however, there has been a steep increase in rapid conversion of remaining forests to industrial plantations (Gaveau et al. 2016), more so in the Malaysian part of Borneo than in the Indonesian part (Meijaard et al. 2018).

Land use intensification and increased palm oil yields does not necessarily prevent deforestation or conversion of land into oil palm plantations. Higher yields of oil palm may cause the global price of oil palm to drop, outcompeting other vegetable oils like rapeseed and soy grown in temperate regions. This would increase pressure on tropical regions. Higher yields of oil palm may also function as an incentive to grow more palm oil. Both factors may lead to higher rates of deforestation in tropical regions and threaten the biodiversity they contain (Carrasco et al. 2014).

These cases highlight the importance of having global and national policies in place to support sustainable palm oil production (Byerlee et al. 2014, Meijaard et al. 2018). One initiative with this aim is the Roundtable on Sustainable Palm Oil (RSPO) who certify oil palm companies that meet a set of set of environmental and social criteria. The RSPO currently has more than 4000 members globally that have committed to produce, source, and/or use sustainable palm oil certified by the RSPO (RSPO 2020). Another global initiative is the Convention on Biological Diversity (CBD), of which 196 countries are members (Meijaard et al. 2018). They aim to conserve biological diversity and to a sustainable use of the components of biological diversity, as well as fair sharing of the benefits from utilising genetic resources (CBD 2020). Indonesia's Forest Licensing Moratorium is a national initiative that regulates land allocation in oil palm production, prohibiting allocation of new oil palm leases in primary forest and peatland areas (Meijaard et al. 2018). The success of such initiatives depends on the enforcement of their policies.

Several studies have reported declining yields of palm oil (Donough et al. 1996, Nurul Fatihah et al. 2019) and a stagnation in oil palm produced per hectare (Woittiez et al. 2017). Many factors may contribute to these trends (Woittiez et al. 2017), but one of the biotic factors that has been pointed out as a possible contributor is insufficient pollination of the oil palm (Li et al. 2019). In oil palm, pollination is mainly performed by the West African weevil *Elaeidobius kamerunicus* (Wahid and Kamarudin 1997). Plantations in South East Asia initially experienced increases in fruit set and oil yields after introduction of the weevil in the early 1980s, but declines have been reported since the late 1980s (Nurul Fatihah et al. 2019).

Poor pollination may lead to low fruit set, oil to bunch (O/B) ratio (Donough et al. 1996), and bunch failure (Corley and Tinker 2016), although poorly pollinated bunches may experience a compensation effect where individual fruit grow larger because there are less fruit in the bunch that compete for space (Li et al. 2019). Poor pollination can presumably be caused by

insufficient numbers of *E. kamerunicus* (Prasetyo et al. 2014), low availability of anthesising male inflorescences per hectare (Dhileepan 1994, Nurul Fatihah et al. 2019), and low viability of pollen (Donough et al. 1996, Yun-Yun and Shuang-Quan 2009, Nurul Fatihah et al. 2019). Dhileepan (1994) indicated that pollen loads carried by weevils may be more important to fruit set than the weevil population per inflorescence, and also showed that fruit set can become worse at very high weevil population levels (Dhileepan 1992).

Declines in weevil populations may be caused by predation and parasitism. Among the species that prey on *E. kamerunicus* are rats, spiders and ants (Hakim et al. 2018). High rainfall can reduce the viability of pollen (Donough et al. 1996) and the weevils' pollen load (Dhileepan 1994). Several attempts have been made to quantify the necessary weevil population to ensure good fruit set. Donough et al. (1996) reported that in oil palm plantations in Sabah, Malaysia, between 20,000–80,000 weevils per hectare were necessary to ensure adequate pollination for obtaining fruit set of 55%. This number is an order of magnitude higher than the approximately 7000 weevils per hectare reported needed for a fruit set of 60% in Kerala, India (Dhileepan 1994). The probability of weevils visiting receptive female inflorescences increases the larger the weevil population becomes (Dhileepan 1992, Donough et al. 1996), but does not necessarily increase fruit set. Efficient pollination is important for fruit set, and according to Dhileepan (1992), this is affected by the weevil's pollen carrying capacity, how much pollen remains on the weevil's body as it enters a receptive female inflorescence, and the transfer rate of pollen to the receptive stigmas. Dhileepan (1992) found that the pollen carrying capacity of weevils was inversely proportional to the number of weevils per spikelet, likely due to increased intraspecific competition, causing weevils to carry and transfer less pollen to receptive female inflorescences and resulting in a lower fruit set (fruit set of 72.1% when the number of weevils per spikelet reached 99.2 weevils compared to 84.9% fruit set when he found an average of 18.7 weevils per spikelet).

Manual pollination has been tested to make up for decreases in fruit set and oil yields (Donough et al. 1996, Prasetyo et al. 2014, Meléndez and Ponce 2016). Manually assisted pollination is labour intensive and has led to a search for more efficient techniques. Prasetyo et al. (2014) tested the "hatch and carry" method, which uses *E. kamerunicus* as a vector for pollinating female inflorescences, rather than manual assisted pollination by humans. Post-anthesis male inflorescences were collected from fields with abundant male inflorescences and stored in hatch and carry boxes. Emerging weevils were sprayed with pollen before they

were released. Their study reported an increase in both weevil populations and fruit set (Prasetyo et al. 2014) when this method was used.

As an increasing demand for palm oil threatens the existence of tropical forests and the biodiversity they contain (Sheil et al. 2009), it has become increasingly important to understand the ecological processes of the pollination service provided by *E. kamerunicus* and how this service can contribute to increasing oil yields in existing plantations.

This study was carried out in the oil palm plantation PT Kayung Agro Lestari (KAL) in Ketapang, West Kalimantan, Indonesia. In May 2017 the plantation started using pollination boxes, a form of assisted pollination similar to that of the hatch and carry technique. Six post-anthesis male inflorescences containing developing weevils are stored for six days in pollination boxes located throughout the plantation. These inflorescences are sprayed daily with viable pollen to increase the chances of newly emerged weevils pollinating anthesising female inflorescences. The effect of the pollination boxes on the relative density of weevil populations had not yet been tested when this study started in June 2017.

OBJECTIVE I: EFFECT OF POLLINATION BOXES

The main aim of this study was to investigate whether the management measures initiated to increase local population density of *E. kamerunicus* generated the intended effect. In this part of the study, the relative weevil density was assessed by establishing transects starting at pollination boxes and extending up to ~400m into the plantation. Several traps were designed and tested to assess weevil visits to male and female inflorescences. As these traps did not provide significant results, an alternative approach was used instead by collecting spikelets with weevils from anthesising male inflorescences. In particular I tested the following hypothesis:

H1: The relative population density of *Elaeidobius kamerunicus* decreases at increasing distance to pollination boxes.

OBJECTIVE II: EFFECT OF SPATIAL VARIATION OF ANTHESISING INFLORESCENCES ON SURROUNDING TREES

The weevils are strongly attracted to the anis-scented volatile compound produced by both anthesising male and female inflorescences (Syed 1979, Lajis et al. 1985). Areas with high

density of anthesising inflorescences release large amounts of volatile compounds, possibly attracting more weevils to the area. This might lead to an increase in the number of weevils per spikelet, if the attractiveness of the area is high enough, or to a reduction in the number of weevils per spikelet through an dilution effect see (Dauber et al. 2010, Hegland 2014) for a general discussion on this. The aim of this part of the study was to examine how spatial variation in number of anthesising inflorescences affected relative weevil density in sampling locations of 5x5 palms. This was performed by counting all anthesising inflorescences in those 25 palms. In particular I tested the following hypothesis:

H2: The relative population density of *Elaeidobius kamerunicus* is affected by the number of inflorescences at anthesis in neighbouring palms.

2 Methods

2.1 Study area

2.1.1 West Kalimantan, Borneo

Borneo is the third largest island in the world and is divided between three countries: Indonesia (Kalimantan), Malaysia, and Brunei. Borneo is found in the tropical and subtropical moist broadleaf forest biome, and the island is divided into nine ecoregions. West Kalimantan is part of the Borneo lowland rain forest ecoregion (Loucks 2020). The Köppen Climate Classification System classifies West Kalimantan's climate as tropical rain forest climate (Af.), and the island is situated in the tropical wet climate zone, i.e. average monthly precipitation of ≥60mm (Climate-Data 2020). The area lacks a marked seasonality.

2.1.2 PT Austindo Nusantara Jaya (ANJ)

PT Austindo Nusantara Jaya (ANJ) is a holding company that in 2017 owned four functional plantations in Indonesia, two in North Sumatra, one in Belitung Island, and one in West Kalimantan, with the latter being my study area (ANJ 2017). As a member of the Roundtable of Sustainable Palm Oil (RSPO), ANJ is dedicated to fulfil the set of environmental and social criteria required to produce Certified Sustainable Palm Oil (CSPO) (ANJ 2017, RSPO 2020). In 2017, ANJ had received RSPO certification for the plantations in North Sumatra and Belitung Island, while, at the time of this study (2017), the certification for the West Kalimantan plantation was still being processed (ANJ 2017). By the end of 2019, the West Kalimantan plantation had also received its RSPO certification (ANJ 2019). Certifications are only granted when new plantings have not replaced primary forest or High Conservation Value (HCV) areas existing before 2005, and re-certification is required every fifth year (Meijaard et al. 2018).

2.1.3 Oil palm plantation - PT Kayung Agro Lestari (KAL)

The study was conducted June – October 2017 in the oil palm plantation managed by ANJ's subsidiary PT Kayung Agro Lestari (KAL). The plantation is located in Ketapang Regency, West Kalimantan, Indonesia (1°26'S 110°13'E).

PT KAL was established in 2004, and the first palm seedlings were planted in 2010 after the land was cleared (ANJ 2017). Between 1990 and 2000 the area of PT KAL was part of a logging concession managed by PT Marsela Wana Sekawan. Before PT KAL developed the area to an oil palm plantation, the primary land cover consisted of about 8000 ha of logged-over natural forest and some degraded land with frequently burned grasslands (Meijaard et al. 2016). In 2013, KAL hired a team of experts led by Dr. Nyoto Santoso, a RSPO approved HCV assessor, to conduct a HCV assessment of the plantation area (KAL 2014). The HCV Resource Network defines HCV as "*a biological, ecological, social or cultural value of outstanding significance or critical importance"* (HCV 2018). The goal of this assessment is to identify and protect environmental and social features that are of high conservation value, to prevent them from being damaged or destroyed (HCV 2018). The HCV assessment concluded that 3884 ha (21%) of the concession constituted a HCV area, which was set aside and protected for the orangutan population that inhabited the area (Meijaard et al. 2016). The HCV assessment further concluded there was no primary forest in the area of PT KAL, and that the remaining fragments of forest were composed of young secondary forest and underbrush (KAL 2014). In 2017, PT KAL had a land bank of 17998 hectares (ANJ 2017).

The plantation is divided into blocks of varying sizes of ~10-70 ha. The largest blocks are found in the middle of the plantation, while blocks bordering concession forest or the surrounding area are smaller. The oil palm trees (*E. guineensis*) of the varieties Socfindo and Sriwijaya were planted between 2010 and 2013. Most of the plantation is on peat soil, but the hills and slopes are mineral soil. Discrete blocks contain palms belonging to the same variety that were planted in the same year and on the same soil type. Palm trees are planted in an equilateral triangular configuration, distanced roughly 9 m apart, resulting in a planting density of ~143 palms per hectare, following the industry standard (Corley and Tinker 2016, Bonneau et al. 2018). Drainage ditches within and along the blocks help lower the water table (Corley and Tinker 2016).

The understory vegetation among the palms is mainly made up of small herbaceous species and low grasses, varying both within and between blocks. The vegetation helps protect the soil surface from erosion, reduces runoff, and maintains soil fertility (Corley and Tinker 2016). The vegetation is highly managed by the plantation and herbicides are used with regular intervals to prevent competition with the palm trees.

2.2 Study species

2.2.1 Elaeis guineensis Jacq.

Elaeis guineensis Jacq., also known as the African oil palm (figure 1), is a long-lived perennial in the Arecaceae family, order Arecales. The species originates from West Africa (Ruiz-Samblas et al. 2013) but is currently distributed and cultivated throughout the tropics (Corley and Tinker 2016).

Figure 1: *Elaeis guineensis*, the African oil palm.

Plantation workers are looking for detached fruit. Picture by Lynn Jørgensen

E. guineensis is an entomophilous species primarily pollinated by the weevil *Elaeidobius kamerunicus* (Meléndez and Ponce 2016). Several other species in the genus *Elaeidobius,* some bees, *Thrips sp*., and numerous other insect species are also known to visit *E. guineensis* flowers (Syed 1979, Hala et al. 2012), although their effectiveness as pollinators is variable.

The palms may also rely on wind pollination to some degree, depending on local climatic conditions (Syed 1979).

Generally, unisexual inflorescences are produced in alternating cycles on the monoecious palms (Williams and Thomas 1970). Young palms usually start inflorescence production in the male phase (Corley and Tinker 2016), but the frequency and time spent in subsequent sex cycles is strongly influenced by environmental factors. Male inflorescence production is promoted by water deficit and shading, either due to climatic conditions such as drought or interpalm competition (Williams and Thomas 1970, Adam et al. 2011). Plantation managers therefore have the potential to affect the sex ratio of inflorescences, by management practices such as pruning of leaves (Li et al. 2019). Genetic factors also affect the sex ratio and it is increasingly common to plant high yielding oil palms that are shifted towards a higher expression of the female phase at the expense of male inflorescence production (Prasetyo et al. 2014).

Inflorescences develop from buds in the axils of leaves, one inflorescence per leaf. Since the male inflorescence serves as the breeding site for *E. kamerunicus*, a lower production of male inflorescences may cause declines in both weevil populations and pollen production (Dhileepan 1994), and ultimately decreased oil yields

While the female and male inflorescence are quite distinct, they both consist of spikelets arranged in a spiral fashion around a central peduncle (Corley and Tinker 2016). The sex of the inflorescence is determined approximately two years before the inflorescence emerges and becomes visible in the leaf axil (Adam et al. 2005, Corley and Tinker 2016). At the point of emergence, the inflorescence is enclosed by two fibrous peduncular bracts, which start to rupture and slowly disintegrate approximately six weeks before the inflorescence reaches anthesis, revealing the sex of the inflorescence (Adam et al. 2005, Forero et al. 2012).

The peduncle of the male inflorescence is longer than that of the female inflorescence. The length of male spikelets are typically 10-20 cm, and individual spikelets bear 400-1500 yellow coloured, staminate flowers (figure 2). The staminate flower contains two whorls of three stamens (Adam et al. 2005, Corley and Tinker 2016). The male inflorescence becomes larger in size as the oil palm ages, regarding both the length of individual spikelets and the amount of spikelets per inflorescence (Corley and Tinker 2016). When the male inflorescence reaches maturity, anthesis progresses acropetally from the base to the top of the spikelets

(Tandon et al. 2001) over a period of 4-5 days (Dhileepan 1994). The staminate flowers produce a volatile compound that has an anise-like odour (Lajis et al. 1985), which serves to attract *E. kamerunicus* (Syed 1979, Beaudoin-Ollivier et al. 2017). During anthesis, 20-100 gram pollen is produced and released by each inflorescence (Dhileepan 1994, Corley and Tinker 2016).

Figure 2: Male inflorescences of oil palm (*E. guineensis*).

The inflorescence in the left picture has recently ruptured through the peduncular bract and has not yet entered anthesis. The inflorescence on the right is likely in the next last day of anthesis. Flower development has progressed towards the top of the spikelets. The pollinator *E. kamerunicus* is visible on the spikelets in the right picture. Picture by Lynn Jørgensen

The spikelets of the female inflorescence bear 4-30 trimerous flowers (Tandon et al. 2001, Adam et al. 2005), depending on palm age (Corley and Tinker 2016). Each trimerous flower contains one pistillate flower and two nonfunctional staminate flowers (Adam et al. 2005). Similar as in the male inflorescence, anthesis occurs acropetally (Tandon et al. 2001). Anthesis in female inflorescences lasts for a total of 36-48 hours (Corley and Tinker 2016). When the female flower is receptive, an exudate is visible on the three-lobed stigmatic surface

(Tandon et al. 2001, Corley and Tinker 2016). Successful pollination is signalled to pollinators when the colour of the stigmatic lobes changes from cream-coloured to pink or violet and finally dark purplish (figure 3) (Adam et al. 2005, Forero et al. 2012).

Figure 3: Female inflorescences of *E. guineensis* at anthesis.

The cream-coloured flowers in the inflorescences to the left have just recently started opening, and some of the flowers are still closed. The flowers turn from cream-coloured to bright pink (picture to the right). At this point, the inflorescence is still receptive. Anthesis lasts 36-48 hours, and the flowers of the inflorescence turn into a dark purple-blackish colour after anthesis is completed. Picture by Lynn Jørgensen

Depending on the efficiency of pollination, normally 30-60% of the flowers in an inflorescence are fertilized. The fertilized flowers develop into fruit bunches, and each bunch may carry 500-4000 fruits (Forero et al. 2012, Corley and Tinker 2016). The bunch may also contain parthenocarpic, or unfertilized, seedless fruit (Corley and Tinker 2016) as a result of poor pollination (Vardi et al. 2008). It takes approximately 180 days after pollination for the fruit, a sessile drupe, to reach maturity (Tandon et al. 2001). The fruit's pericarp is composed of exocarp, mesocarp, and endocarp surrounding a kernel. Crude palm oil is extracted from

the mature, fleshy mesocarp, while kernel palm oil is obtained from crushed kernels (Barcelos et al. 2015).

Oil palms reach maturity and start yielding around 2.5-3 years after planting (Corley and Tinker 2016) and the life cycle of a plantation is approximately 25 years. At this point yields are declining, and increasing palm height complicates harvesting (Corley and Tinker 2016).

2.2.2 Elaeidobius kamerunicus

The African oil palm weevil, *Elaeidobius kamerunicus* Faust (Coleoptera, Curulionidae) is the most efficient pollinator of oil palm (*E. guineensis*) (Meléndez and Ponce 2016). It was introduced from West Africa to oil palm plantations in Malaysia in 1981, and from Malaysia to Indonesia in 1983 (Prasetyo et al. 2014) to increase fruit set in the oil palm plantations.

E. kamerunicus (figure 4) is strongly attracted to the anis-like scent emitted by both the male and female flowers during anthesis (Syed 1979, Lajis et al. 1985). The adult weevils are phytophagous and feed on the anther filaments of male flowers, becoming covered with pollen in the process (Henderson 1988, Dhileepan 1994, Moore 2001, Adaigbe et al. 2011, Meléndez and Ponce 2016). The male inflorescence of *E. guineensis* also serves as the breeding site for *E. kamerunicus*, who use anthesizing male flowers as their only site for oviposition (Adaigbe et al. 2011) The weevils are holometabolous, undergoing complete metamorphosis inside the staminate flowers (Siswanto and Soetopo 2020). The larvae that hatch from the deposited eggs, feed on rotting plant material from the male flowers. The larvae go through a pupae stage before the fully developed imagos (adults) emerge (Kevan 1986). The sexually mature adults visit both male and female inflorescences in their search for food, potential mates, or sites for oviposition (Kevan 1986, Dhileepan 1994). The female inflorescence emits an odour that mimics that of the male inflorescence (Moore 2001). If the weevils are covered in pollen upon their arrival to a female inflorescence, the pollen may be transferred to the stigmas as the weevils search for food (Dhileepan 1994, Tandon et al. 2001, Adaigbe et al. 2011). As the female inflorescence does not provide any nectar or oviposition sites, the weevils merely stay for a short while before flying off in the search for resources (Kevan 1986, Tandon et al. 2001).

E. kamerunicus is an efficient pollinator of oil palm due to their high pollen-carrying capacity (Meléndez and Ponce 2016). Male weevils carry more pollen compared to female weevils due

to their larger body size and the presence of setae on their elytra (Dhileepan 1992, Moore 2001, Permana et al. 2017). *E. kamerunicus* is dependent on the male inflorescence of oil palm to complete their life cycle. A consequence of this obligate relationship is a high transfer rate of conspecific, viable pollen (Meléndez and Ponce 2016).

Figure 4: Female weevil of *E. kamerunicus*.

The females lack setae on their elytra and are therefore easily distinguished from male weevils. Picture by Lynn Jørgensen

2.3 Pollination boxes

In May 2017, PT Kayung Agro Lestari (KAL) started testing a new concept called "pollination boxes" (figure 5). The pollination boxes are placed under a roof for protection against rain and direct sunlight. Male inflorescences that have entered post anthesis are stored inside these boxes to increase local densities of *E. kamerunicus*. The boxes are raised on legs, and the lids are covered with mesh to prevent predators, mainly ants and rats, from entering the boxes to prey on the eggs, larvae, pupae and imagos (Prasetyo et al. 2014).

To utilize the pollination boxes the plantation workers first localise high-density areas of anthesizing male inflorescences. Once a male inflorescence enters post anthesis, the workers cut down the inflorescences to examine if they hold eggs and larvae of *E. kamerunicus*. Male inflorescences containing eggs and larvae are then moved to the pollination boxes. According to PT KAL, most of their male flower bunches hold approximately 1000-3000 weevil eggs and larvae. Depending on availability of male inflorescences in the plantation, four to six male inflorescences are transferred to each pollination box, potentially bringing 4000-18000 weevils to the area if all weevils emerge.

Figure 5: Wooden pollination box under roof.

Four to six male inflorescences of *E. guineensis* that have entered the post anthesis stage are stored inside the boxes for a period of six days. During this period, the inflorescences are sprayed daily with viable pollen to increase the chance that weevils pollinate a receptive female inflorescence. On the 7th day, the inflorescences are removed from the box and stored underneath it (visible in the picture), to make room for new inflorescences inside the box. Picture by Lynn Jørgensen

The inflorescences are then stored inside the boxes for six days. During this period, the plantation workers open the lid of the box, allowing emerging weevils to leave each morning.

The workers spray viable pollen on the stored inflorescences to increase the chances that newly emerged imagos become covered in pollen while exiting the flowers of the inflorescence, and thereby increasing the probability of pollinating female flowers that are subsequently visited. The pollen used to spray the inflorescences is collected by plantation workers and dried in a heating cabinet for 12 hours at 30°C, followed by 14 hours at 40°C. The pollen is subsequently mixed with talc powder in a 1:5 ratio. After the six-day period, most weevils have emerged, and the inflorescences are replaced by new inflorescences. The old inflorescences are stored on the ground underneath the pollination boxes for the next six days in case not all weevils have emerged yet. Every evening, plantation workers close the lids of the pollination boxes to protect the inflorescences against predators.

The purpose of the pollination boxes is to increase local densities of *E. kamerunicus*, and thereby enhancing pollination efficiency, with the ultimate goal of increasing oil yields.

2.4 Study design

2.4.1 Trap design

Several traps were designed to capture weevils and examine the relative density of weevil populations visiting anthesising male inflorescences and female inflorescences and additionally examine whether the weevils were present on native palms in forest surrounding PT KAL. Two main trap designs were tested: funnel traps and sticky traps with fly glue. Pollen was used as bait on all traps. Description of traps in appendix A.

2.4.2 Transects – distance to pollination boxes

To examine if pollination boxes and local availability of male and female inflorescences at anthesis affected the relative density of *E. kamerunicus* populations, transects were established within four blocks (E50, F50, F45, and E46; figure 6) of the plantation. Each block contained one pollination box. I also geolocated all other active pollination boxes throughout the plantation. The palm trees within all the study blocks were planted in 2011, on peat soil. While three of the blocks contained pollination boxes that were actively in use, the pollination box in the last block (E46) had been inactive since the 14th of July 2017 and was therefore used as a control.

Each transect comprised a minimum of four sampling locations located 0-400 m from the pollination box, with sampling locations preferably within 0-50 m, 50-100 m, 100-200 m and 300-400 m, but the exact sampled distances were based on the availability of male inflorescences at anthesis. The palm trees to be sampled were identified by walking along rows of palm trees within each block. Palm trees that contained a minimum of one male inflorescence, in the chosen stage of anthesis, were geolocated and their GPS coordinates were used to measure the distance between the palm tree and the pollination box.

At an unknown time during the study, the plantation started reusing the pollination box in block E46, initially included as a control transect. During sampling of the last transect in E46, it was evident that the pollination box was being used and data from this transect has been included in the analysis the same way as for the other transects. Due to uncertainty about whether the pollination box was in use during sampling of the first transect, these data have been excluded from the analysis.

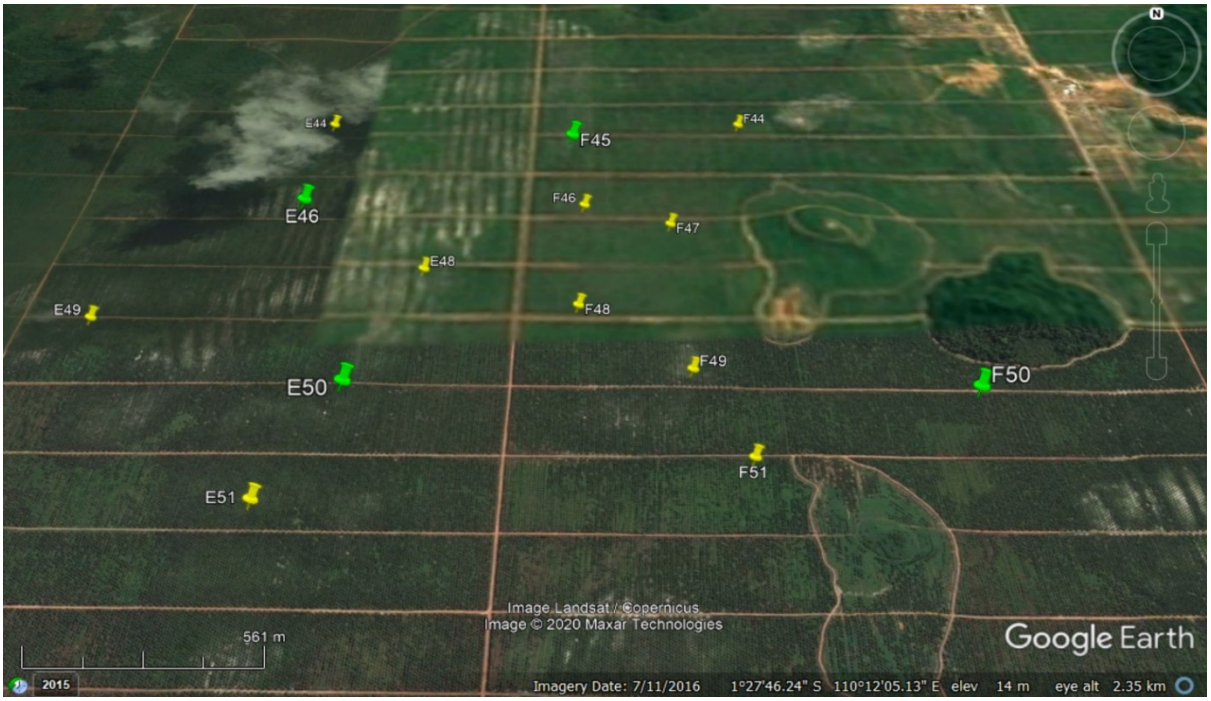

Figure 4: Google Earth map of pollination boxes.

Overview of the blocks in my study area. The green marks display pollination boxes included in my study; E46, E50, F45, and F50 (K29 is not visible on the map). The yellow marks represent surrounding pollination boxes.

To obtain data on relative weevil densities unaffected by pollination boxes a new control transect, K29, was established a few days prior to the end of the study. Unfortunately, the

nearest location where no active pollination boxes could be confirmed was located ~10 km away from the other pollination boxes and the conditions in this block were substantially different; the palm trees were planted in 2012 and were much smaller compared to the palms in the other blocks, making direct comparisons difficult. The location and activity status of pollination boxes in the blocks surrounding K29 is not known. Two transects were sampled in block F50, E50 and E46. One transect was sampled in block F45 and K29, respectively.

2.4.3 Spikelets from male inflorescences – flower visitation

To assess the relative density of weevils on spikelets at different distances from pollination boxes, six spikelets were collected per sampled inflorescence from the focal palm tree (palm 13 in figure 7) within each sampling location. A minimum of four inflorescences were sampled along each transect. At some occasions, extra male inflorescences at anthesis were sampled.

2.4.4 Male and female inflorescences at anthesis surrounding the focal palm trees

To assess the effect of the availability of inflorescences at anthesis on the relative density of the weevil population at each sampling location, the number of male and female inflorescences at anthesis in 25 palm trees surrounding the focal tree were counted. As the palms are planted in the configuration of an equilateral triangle, with the palms distanced roughly 9 m apart, the area of the 25 palms corresponded to a patch of ~36 m x 31.2 m = 1123.2 m^2. The palm tree in the middle, palm number 13, was the palm tree sampled for weevils (figure 7).

The average number of anthesising male and female inflorescences per sampling location was extrapolated to the hectare, based on data from 61 observations of inflorescences in 37 unique sampling locations. Since each sampling location is ~1123 m^2, the average number of anthesising inflorescences was multiplied by 8.9 to obtain the average number of anthesising inflorescences per hectare

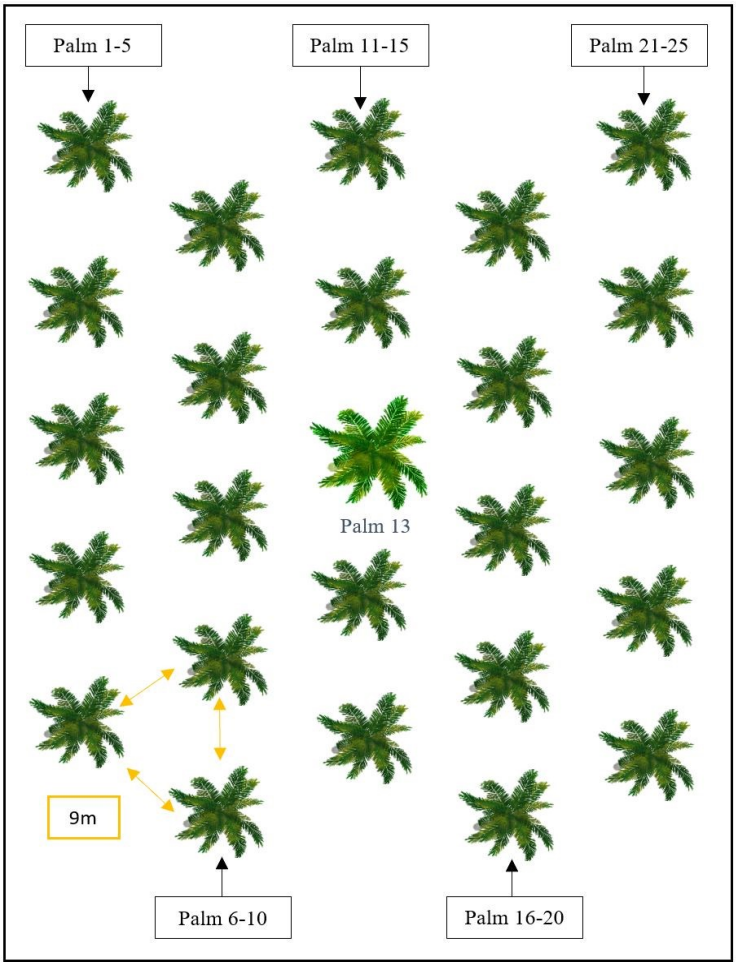

Figure 5: Planting configuration of palm trees.

Palm trees of *E. guineensis* planted in an equilateral triangular configuration, palms distanced 9 m apart and 7.8 m between palm rows. Weevils were collected from spikelets on palm 13, and all male and female inflorescences at anthesis were counted in 25 palms in each sampling location. Each transect had a minimum of four sampling locations.

2.5 Data collection

2.5.1 Testing traps

In the preliminary testing phase during the 5th to the 14th of September (2017), two sets of traps were tested simultaneously in palm trees with and without an anthesising male inflorescence. Traps were positioned around the anthesising male inflorescence and matched in a similar fashion in the palm tree without an anthesising male inflorescence.

Choice of palms to test the traps was regulated by the availability of anthesising male inflorescences. The traps were tested on two palms with anthesising male inflorescences, in sequential order. During this period, a third palm was used as a control because it did not contain any anthesising male inflorescences.

The traps were left out for 130-385 minutes between 07:00 a.m. and 2:30 p.m. At the end of each sampling day, the traps were emptied. Pollen and sheets with sticky glue were replaced at the start of each new sampling day.

2.5.2 Transects

Spikelets were collected along the length of transects during 14 sampling days between the 09th and 28th of October 2017. Each transect was sampled over two consecutive days, and the sampling locations within each transect were sampled in a random order determined by the randomising function in R (R Core Team 2017).

If the sampled inflorescence had entered the post-anthesis stage on the second day of sampling a transect, an alternative inflorescence at anthesis was located nearby and sampled instead. Some extra inflorescences were sampled when encountered.

2.5.3 Spikelets from male inflorescences – flower visitation data

Spikelets with weevils were collected from all sampling locations within each transect to assess the relative density of weevil populations at each location. Spikelets were collected in a stratified matter from each inflorescence; two random spikelets from the base, middle, and top of the inflorescence. Less spikelets were sampled from some inflorescences, and extra inflorescences were sampled in other cases (table 1). The aim was to collect a minimum 24 spikelets per transect. The inflorescences in transect D were very small, and less spikelets were gathered in this transect. On sampling day 1 in transect F, only 21 spikelets were gathered due to human error. The spikelets that lack from transect H are due to an abrupt end of the study and could not be examined after collection. To collect weevils, individual spikelets were covered with a plastic bag before being cut at the base with a pair of scissors. The date and time of collection of individual spikelets, in addition to their position on the inflorescence, was noted on a piece of paper and bagged together with the spikelets. Sampling of spikelets was performed between 09:00 am and 5:00 pm regardless of weather.

Table 1: *Number of spikelets collected per transect. Transect A and E were located in block F50, transect C and E in block E50, transect D in block F45, transect E in block E46, and transect H (control transect) was located in block K29.*

			Transects				
Spikelets:	A	C	D	E	F	G	H
Day 1	35	24	21	30	21	30	23
Day 2	24	24	21	36	29	29	19

Bags with weevils were stored in a freezer compartment in a refrigerator at <-10°C. Weevils on each spikelet were counted under a stereo microscope to enable me to distinguish between male and female weevils.

The length of each spikelet was measured in centimetres, as was the part of the spikelet with developed flowers, corresponding to the available weevil habitat (= flower development in the following). From these numbers, the percentage flower development of each spikelet was calculated as flower development/spikelet length x 100 (figure 8).

Since spikelets flower acropetally (Tandon et al. 2001), the flower development (in cm) increases until the end of anthesis and pollen production, and varies between individual spikelets within an inflorescence.

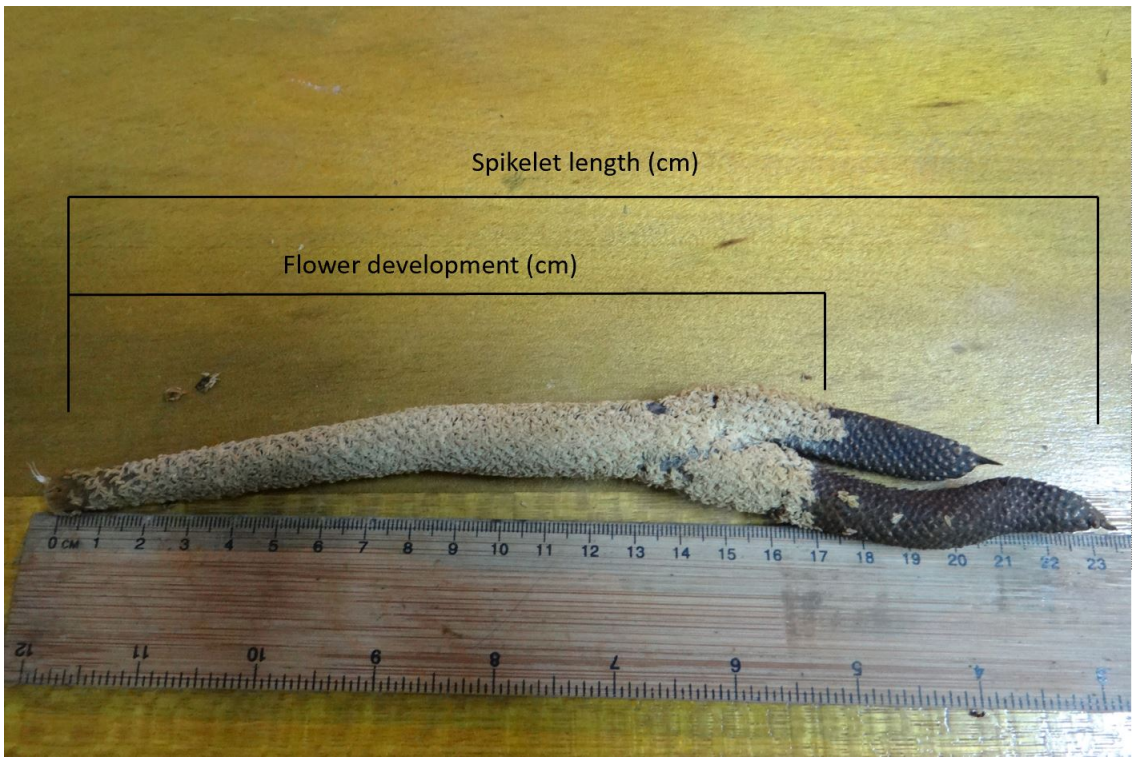

Figure 8: Spikelet measures.

The length of the spikelet and the part of the spikelet with developed flowers (= flower development) was measured with a ruler (in cm). These measures were subsequently used to calculate percentage flower development per spikelet. The spikelet in the picture is unusual in that it possesses two tips, while the large majority of spikelets only have one tip.

2.5.4 Male and female inflorescences at anthesis surrounding the focal palm trees

The number of inflorescences in the 25 palm trees in each sampling location were counted by walking around the palm tree both clockwise and anti-clockwise. Inflorescences were recorded into the categories “Male” or “Female” (figure 2 and 3), and further into “Pre-anthesis”, “Anthesis”, “Post-anthesis” or “Wallet fruit” (inflorescence covered by a peduncular bract). Only anthesising male and female inflorescences were included in the statistical analysis. Male inflorescences that recently entered the post-anthesis stage, potentially hold large numbers of eggs and larvae of *E. kamerunicus* (Tuo et al. 2011, Prasetyo et al. 2014). Unfortunately, although attempted it was impossible to determine when the inflorescences had entered the post-anthesis stage. The potential contribution of post-anthesised male inflorescences to the relative weevil population was therefore not considered in the statistical analysis.

2.6 Plantation data

Plantation data for 2018 was gathered by plantation workers. The data is mainly from Division 14, an area in the plantation consisting of nine blocks. Two of the blocks from this study, F50 and E50 are found within this division. Block F45 from Division 13 is also included. Data from block E46 and K29 has not been made available. Overview of data in appendix B.

Data was gathered by entering every 20th palm row (row 3, 23, 43 etc.) within blocks, a total of six rows per block. Data was gathered from one block once a year, in such a manner that the entire Division would be sampled throughout the year. The number of anthesising male inflorescences were counted in every 20th row. The total number of anthesising male inflorescences was subsequently divided by the number of sampled palms within the relevant rows and multiplied by the number of palms within a hectare to obtain the number of male inflorescences at anthesis per hectare. Male inflorescences that completed anthesis approximately seven days prior to data collection were harvested. Nine spikelets were removed from the inflorescence, three from the base, middle, and top, respectively. The spikelets were stored in plastic pipes in a storehouse for one week. The emerging adult weevils were killed and counted. The average number of weevils per spikelet was calculated by taking the sum of all the weevils that emerged from the spikelets and dividing this number by nine.

One post-anthesised male inflorescence within each sampled row was also cut down, the number of spikelets were counted, and the average number of spikelets per inflorescence was calculated from these numbers. One mature fruit bunch from each sampled row was harvested when at least five fruit had detached and fallen to the ground. The fruit was chopped into pieces, and the fertilised fruit, parthenocarps and unfertilised fruit were counted.

The approximate weevil population per hectare was calculated by multiplying the number of male inflorescences per hectare by the average number of spikelets per inflorescence and the average number of weevils per spikelet.

2.7 Statistical analyses

The data was initially explored following the protocol of Zuur et al. (2010) to check for outliers, homoscedasticity, linearity and overdispersion. Data from the traps were excluded from analyses due to insignificant results during data collection.

The number of weevils per spikelet/cm flower development per spikelet was used as a relative measure of the local population density of weevils. A generalised linear mixed model (GLMM) approach was used to model the relationship between weevil counts and explanatory variables related to distance to pollination boxes and abundance of male and female inflorescences in the vicinity of the focal palms. As the resulting models showed an overdispersed error distribution, a negative binomial error distribution was used and models were generated with the "glmer.nb" function in the R package "lme4". To account for variation in developed flowers available in each spikelet, flower development (in cm) per spikelet was included as an offset variable in both models (Reitan and Nielsen 2016).

A forward selection procedure was used to identify the best model explaining the variation in number of weevils per spikelet per cm flower development. The Akaike information criteria corrected for small sample sizes (AICc) was used as the model selection criterion. The starting model had one random effect (palm ID), and variables were added successively until the best (lowest) AICc value was found.

A general additive model (GAM) revealed that the relationship between the number of weevils per spikelet/cm flower development per spikelet (available weevil habitat) and the percentage flower development per spikelet was non-linear. A quadratic term for the variable "percentage flower development" was therefore included as an explanatory variable in the analyses.

A total of 17 covariates, including fixed effects, a quadratic term, a statistical interaction, and random effects were tested during the forward selection procedure (appendix C). Several of the tested variables were expected to show some degree of correlation, as they were similar in nature. "Percentage development of flowers on spikelets" is, as mentioned above, descriptive of how far anthesis has progressed on individual spikelets, while "flower development per spikelet" is not per se indicative of how far anthesis has progressed but rather describes a measure of habitat available to weevils. "Total anthesis" incorporates both male and female

inflorescences at anthesis and might be correlated to anthesising male and/or female inflorescences. Correlation plots of the variables are shown in appendix D.

All statistical analyses were performed in R, version 3.6.1 for Windows, and RStudio version 1.3.959 (R Core Team 2017, RStudio 2020).

3 Results

3.1 Trap results

Four traps, trap A, B, F, and G, remained throughout the testing period that took place between the 5th and 14th of September 2017. The traps altogether were emptied 54 times over seven different days. A total of 27 weevils were captured, with a mean of 0.5 weevils per day per trap (range of zero to six weevils). In 39 of the observations, no weevils were caught. Overview of results given in appendix A.

3.2 General results

The relative population density of weevils was recorded along eight transects during 14 days of sampling. A total of 429 spikelets were collected from 43 palm trees, yielding 10702 weevils. Transect B from block E46 was excluded from further data analyses.

Separate models were created to explain the observed variation in the data that included and excluded the control transect (model 1 and model 2, respectively). The data that excluded the control transect was collected from six transects during ten days of sampling. The shortest distance from a sampling location to a pollination box was 4.82 m, while the furthest was 386.83 m. Spikelets were collected at 33 different distances within this range. Altogether 323 spikelets were gathered from 33 palm trees, providing a total of 7371 weevils. Between zero and 120 weevils (mean 22.8) were observed per spikelet (table 2). When the control transect was included, 37 palm trees, 365 pikelets, and 9467 weevils were sampled (table 2).

The sex ratio of the sampled weevils in the dataset that excluded the control transect was female biased (males = 2047, females = 5259), a trend also observed in the study of Yue et al. (2015). In some instances, the sex of the weevil was difficult to determine and these weevils were only included to the total number of weevils. The scatterplot in figure 9 shows a correlation between male and female weevils, and preliminary analyses on the sexes separately revealed similar best models. All analyses are therefore performed on the total number of weevils.

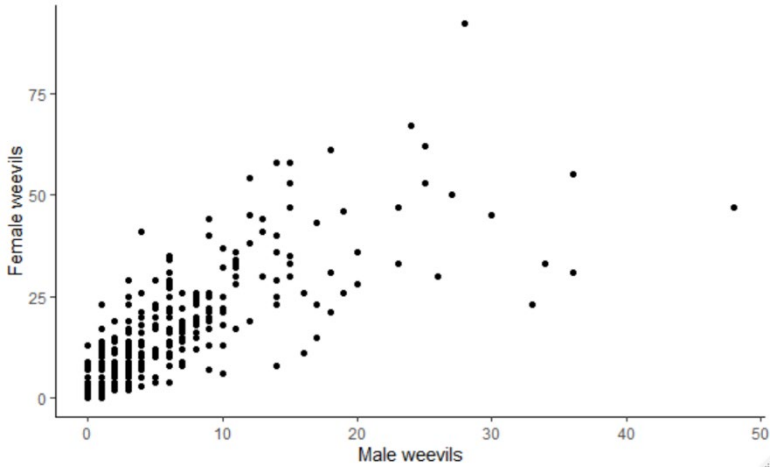

Figure 9: Scatterplot.

Scatterplot showing the correlation between male and female weevils. $R^2 = 0.6$.

The number male and female inflorescences at anthesis in the 25 palm trees surrounding each sampling point were counted. Excluding the control transect, 126 male and 211 female inflorescences were recorded at anthesis (including the control, 142 and 256), with many of the inflorescences as double entries, as the same transect was sampled in two consecutive days (33 and 37 unique sampling locations, excluding and including the control transect). Between one and six male (mean 2.4) and zero and eight female inflorescences (mean 3.9) at anthesis were recorded per sampling location (table 3). The combined range of male and female inflorescences at anthesis varied between two and twelve (table 2).

The correlation between “total anthesis” and “female anthesis” was R = 0.77, which is considered a strong correlation. “Total anthesis” and “male anthesis”, on the other hand, had a correlation of R = 0.5, considered weak to moderate. There was no correlation between male and female anthesis. Another strong correlation occurred between “percentage flower development per spikelet” and “cm flower development per spikelet” (R = 0.72). See appendix D. The other variables showed correlations $R \leq 0.5$ and are considered to weak or non-existing, depending on value.

Table 2: *Overview of data gathered between the 10th and 28th of October, 2017.* ***Sampling days*** *= active sampling days.* ***Spikelets*** *= number of spikelets sampled.* ***Weevils*** *= total number of weevils collected.* ***Lowest and highest per spikelet*** *= minimum and maximum number of weevils observed on a single spikelet.* ***Palm trees =*** *number of palms from which spikelets were sampled.* ***Transects*** *= sampled transects.* ***Distance*** *= range of distances sampled.* ***Distance measured*** *= number of different distances sampled within the distance range.* ***Inflorescences at anthesis*** *= total number of inflorescences at anthesis per sampling location of 5 x 5 palms.* ***Male*** *and* ***female (sampling location)*** *= number of male and female inflorescences at anthesis per sampling location.* ***Total number of inflorescences*** *= total number of inflorescences at anthesis observed across all transects.* ***Male*** *and* ***female (transects)*** *= the number of male and female inflorescences at anthesis observed across all transects.*

DATA GATHERED	Without control transect K29	With control transect K29
Weevil data		
Sampling days	10	12
Spikelets	323	365
Weevils	7371	9467
Lowest per spikelet	0	0
Highest per spikelet	120	140
Palm trees	32	37
Transects	6	7
Distance	4.8 - 386.8 m	4.8 - 386.8 m
Distances measured	32	38
Availability of inflorescences		
Inflorescences at anthesis	2 - 12	2 - 12
Male (sampling location)	1 - 6	1 - 6
Female (sampling location)	0 - 8	0 - 9
Total number of inflorescences	315	387
Male (transects)	116	132
Female (transects)	199	255

Table 3: *Number of male and female inflorescences at anthesis observed within 50 m distance categories between 0 and 400 m from pollination boxes. Average number of inflorescences per sampling location calculated by summing all inflorescences observed and dividing by the number of sampled locations.*

Distance	Male anthesis	Female anthesis	Sampling locations	Mean male anthesis per sampling location	Mean female anthesis per sampling location
0 - 50m	29	61	13	2.2	4.7
51 - 100m	26	39	10	2.6	3.9
101 - 150m	16	24	6	2.7	4.0
151 - 200m	19	48	10	1.9	4.8
201 - 250m	18	20	6	3.0	3.3
251 - 300m	6	4	2	3.0	2.0
301 - 350m	12	26	6	2.0	4.3
351 - 400m	16	34	8	2.0	4.3
Total	142	256	61	2.4	3.9

Extrapolation of average number of anthesising male and female inflorescences per sampling location resulted in 21.4 and 34.7 anthesising male and female inflorescences per hectare, respectively.

Of the 323 spikelets sampled, 276 had a percentage flower development of >61% when the control transect was excluded, while 304 spikelets had a percentage flower development >61% when including the control transect.

3.3 Best model

The best model to explain number of weevils per spikelet in the data that excluded the control transect (model 1) is shown in table 4 and table 5. The best model for the data that included the control transect (model 2) is given in table 6 and table 7.

In model 1, the regression coefficient of the explanatory variable "flower development on spikelet" equalled -1.1, and the offset and explanatory largely cancel each other's effect. The regression coefficient for the explanatory variable "flower development on spikelet" in model 2 equalled – 0.5, which means that the number of weevils per spikelet is approximately inversely proportional to the square root of the length of flower development.

Table 4: The relative contribution of covariates in model 1 (without control transect). **Flower development (habitat)** = part of the spikelets covered in flower (in cm), corresponding to available weevil habitat. **Spikelet position** = position of spikelet within inflorescence (base, middle or top). **Percentage flower development** = percentage of spikelets covered in flowers, indicating how far anthesis has progressed. **Total anthesis** = total number of anthesising inflorescences per sampling location. **Palm ID** = random variable; palm from which spikelets were sampled.

Covariate	Variance contribution
Flower development (habitat)	28.9%
Spikelet position	1.1%
Percentage flower development	11.9%
Total anthesis	3.9%
Palm ID	54.1%

Table 5: Generalised linear mixed model output for model 1 (without control transect) for observed number of weevils per cm flower development (habitat) on spikelets from the 9th to 25th October, 2017. **Flower development =** amount (cm) of spikelets covered in flowers, corresponding to available weevil habitat. **Spikelet position** = spikelet position within inflorescence; factor variable with three levels (1 = bottom, 2 = middle, 3 = top). **Percentage development** = quadratic term, describing percentage flower development on spikelets. **Total anthesis** = the number of male and female inflorescences per sampling location (5 x 5 palms).

Fixed effect	Estimate	Std. Error	z value	Pr(>|<|)	
Intercept	-12.5	2.7	-4.7	2.73E-06	***
Flower development (habitat)	-1.1	0.3	-4.3	1.44E-05	***
Spikelet position 2	0.2	0.1	2.1	0.033	*
Spikelet position 3	0.0	0.1	-0.1	0.9056	
Percentage development	7.7	1.3	5.7	1.04E-08	***
(Percentage development)^2	-0.9	0.2	-5.6	2.19E-08	***
Total anthesis	-0.1	0.0	-2.0	4.33E-02	*

Table 6: The relative contribution of covariates in model 2 (without control transect). **Planting year** = factor variable with two levels (2011, 2012). **Flower development (habitat**) = part of spikelets covered in flowers (in cm), available weevil habitat. **Percentage flower development =** percentage of spikelets covered in flowers, indicating how far anthesis has progressed.

Covariate	**Variance contribution**
Planting year	22.4%
Flower development (habitat)	7.2%
Percentage flower development	7.9%
Palm ID	62.5%

Table 7: Generalised linear mixed model output for model 2 (with control transect) for observed number of weevils per cm flower development (habitat) on spikelets from the 9th to 27th October, 2017. Based on 365 observations. **Planting year** = factor, 2 levels (2011 and 2012). **Percentage development** = quadratic term, describes percentage development of flowers on spikelets. **Flower development =** amount of spikelet covered in flowers (cm), constituting available weevil habitat.

Fixed effect	Estimate	Std. Error	z value	Pr(>|<|)	
Intercept	-4.4	1.8	-2.5	1.41E-02	*
Planting year 2012	1.0	0.3	3.3	9.43E-04	***
Percentage development	3.6	0.9	3.9	1.08E-04	***
(Percentage development)^2	-0.5	0.1	-4.0	7.63E-05	***
Flower development	0.5	0.2	3.1	1.86E-03	**

3.3.1 H1: Distance to pollination box

Hypothesis 1 "The relative population density of Elaeidobius kamerunicus decreases at increasing distances to pollination boxes" was not supported by either model (table 4-5, table 6-7). Neither of the distance variables, "distance to pollination box" or "number of pollination boxes within a 500 m radius", was included in the best models. The variable "number of pollination boxes within a 500 m radius" was not analysed in the model that included the control transect K29 (model 2), since no information was available about potential pollination boxes surrounding block K29. The relationship between the distance to pollination boxes and the number of weevils per cm flower development is shown in figure 10.

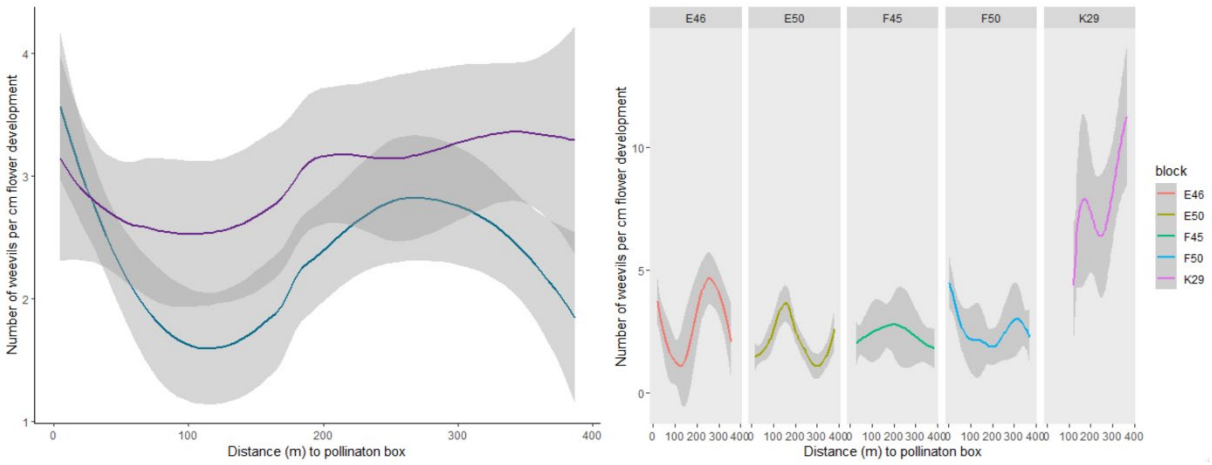

Figure 10: Distance to pollination box.

The relationship between distance to pollination box and the number of weevils per cm flower development (available weevil habitat). The left panel shows this relationship for all blocks combined. The blue line displays the data without the control transect, and the purple line shows the data that includes the control transect. The grey bands display the 95% confidence interval. The right panel gives an overview of the relationship between distance and weevils for each block separately. The palm trees in block E46, E50, F45, and F50 were planted in 2011, while the palm trees in control transect K29 were planted in 2012.

3.3.2 H2: Availability of male and female inflorescences at anthesis

Hypothesis 2 "The relative population density of Elaeidobius kamerunicus is affected by the number of inflorescences at anthesis in neighbouring palms" was supported by the model excluding the control transect (model 1). The variable "total number of male and female inflorescences at anthesis" was included in the best model (table 4-5) to explain the number of weevils found per cm flower development per spikelet, though contributing only 3.9% to the explained variation (table 4). The expected frequency of weevils decreased with increasing availability of male and female inflorescences at anthesis (figure 11). The addition of male or female inflorescences separately increased the AICc values of the tested models.

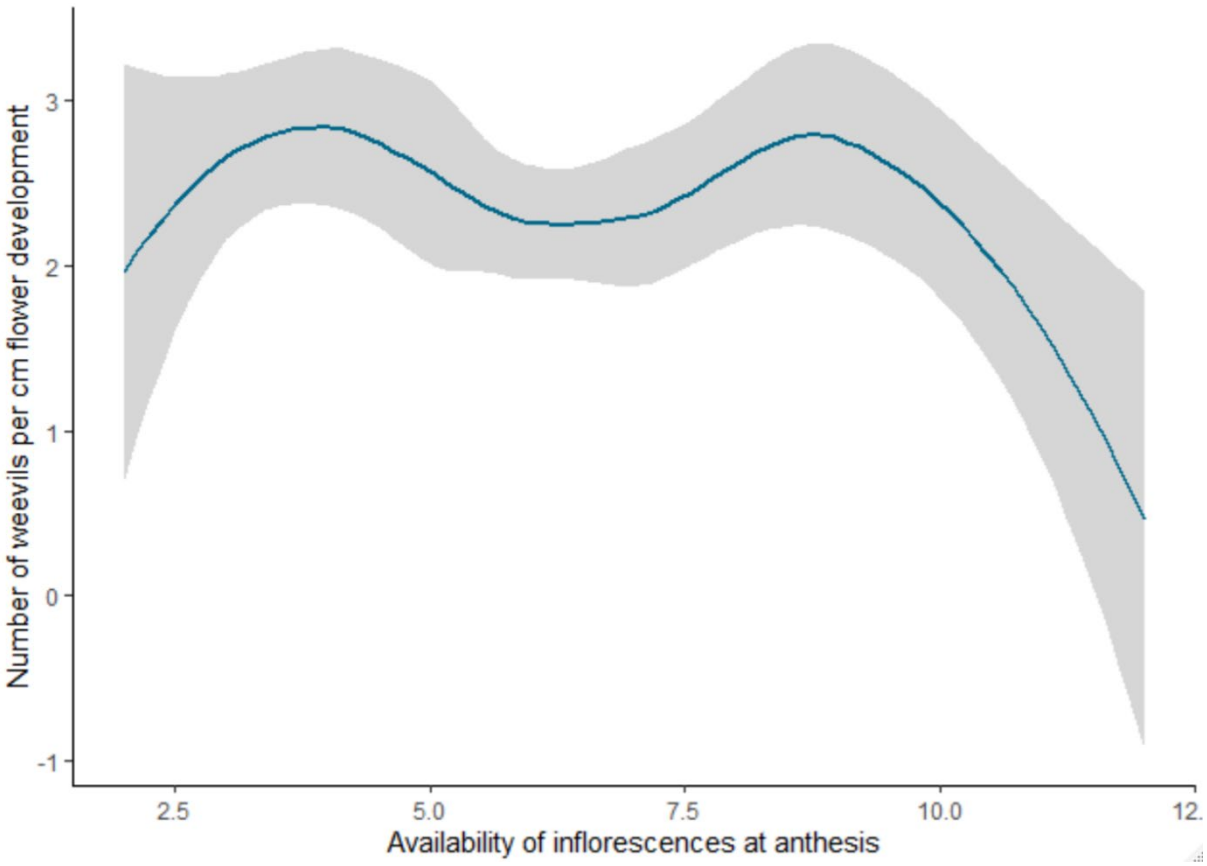

Figure 11: Availability of inflorescences.

Model relationship of availability of male and female inflorescences at anthesis on the number of weevils found per cm flower development on spikelets. The number of available inflorescences were counted within in an area of 5 x 5 palm trees, corresponding to ~1123m^2. The 95% confidence interval is shown as a grey band.

The expected frequency of weevils per cm flower development in relation to the total number of inflorescences at anthesis per sampling location is shown in figure 12. Spikelets located in the middle of inflorescences are expected to have a higher presence of weevils. The expected number of weevils are expected to decrease slightly as the number of inflorescences per sampling location increase in model 1.

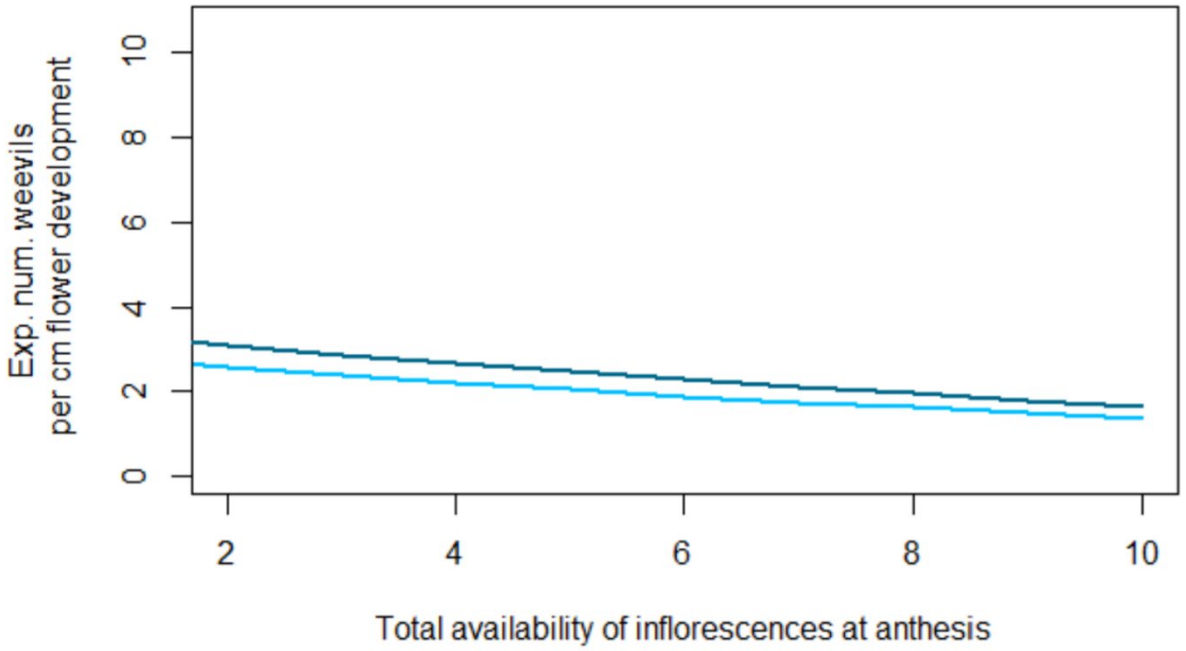

Figure 16: Inflorescence frequency plot.

Expected frequency of weevils per cm flower development in relation to number of anthesising inflorescences per sampling location. Colourised by spikelet position: spikelet position 1 and 3 (bottom and top spikelets) share the same value and are situated on top of each other (shown in light blue). Spikelet position 2 (middle) is shown in dark blue.

Model 2 (including the control transect) did not incorporate male, female, or a combination of both inflorescences to explain the observed variation. H2 was therefore not supported for model 2.

3.3.3 Other variables

Flower development in centimetres on individual spikelets, or the habitat available to weevils, was the major contributor, contributing 28.9% to the explained variance in model 1 (table 4). Except from the random variable palm ID, it was the only variable that contributed to >20%

of the variance in model 1. Flower development was significantly negatively correlated to the number of weevils per spikelet in model 2 and contributed 7.2% to the variation in the model. Flower development was negatively correlated to number of weevils per cm flower development on spikelets.

The percentage development of flowers on spikelets was included as a quadratic term and contributed 11.9% of the explained variation in model 1. Percentage development explained 7.9% of the variance in model 2. The number of weevils per spikelet/flower development reached a plateau at around 60% flower development on spikelets and decreased thereafter (figure 13). In both models, the linear term of percentage development of flowers on spikelets was positively correlated to weevils per cm flower development per spikelet, while the squared part of the term was negatively correlated to number of weevils per cm flower development per spikelet.

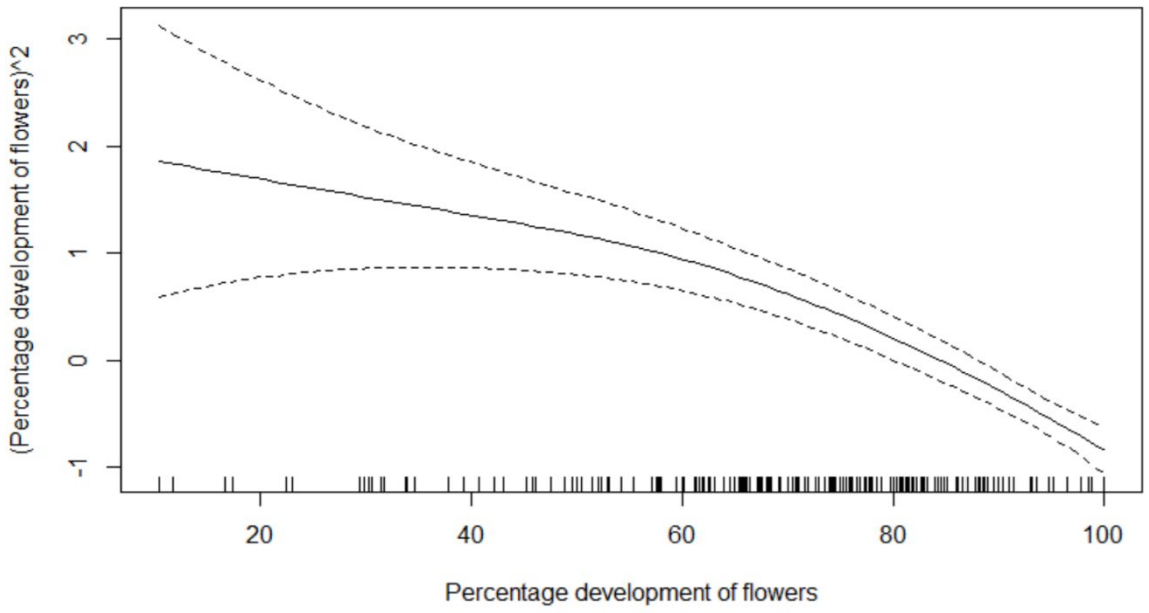

Figure 13: GAM analysis.

GAM analysis of the relationship between the number of weevils per cm flower development in relation to the percentage of spikelets covered in flowers shows a non-linear relationship. The variable “percentage development of flowers on spikelets” was therefore included as a quadratic term in model 1 and model 2. The dotted lines show the 95% confidence interval.

The expected frequency of number of weevils per cm flower development in relation to percentage development of flowers on spikelets also reached a plateau where ~60% of the spikelets were covered in flowers, and a slightly higher presence of weevils was expected for spikelets located in the middle of the inflorescence in model 1 (figure 14).

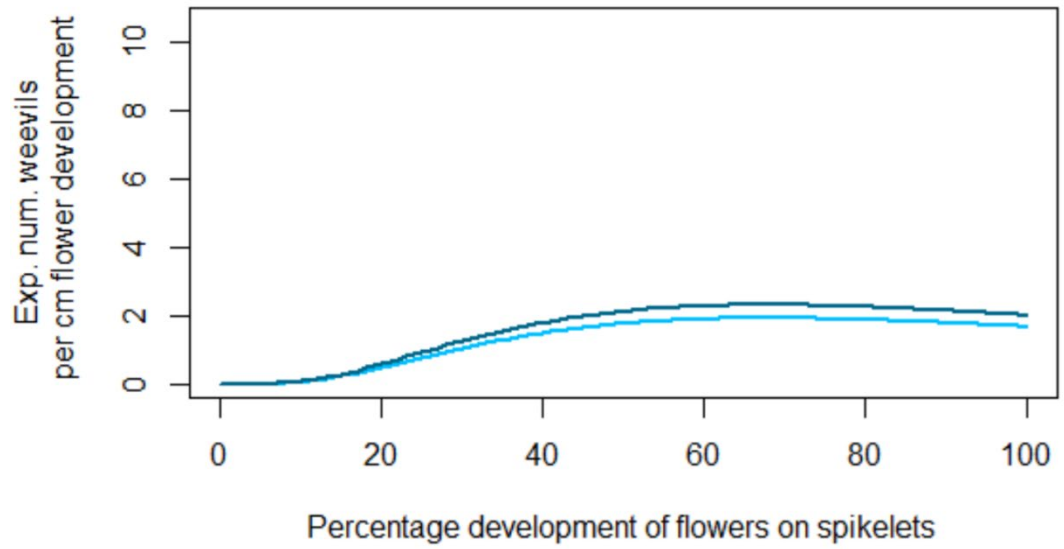

Figure 14: Percentage development frequency plot.

The relationship of expected weevils per cm flower development in relation to percentage development of flowers on spikelets. Colourised by spikelet position: The lines of spikelet position 1 and 3 (bottom and top position) are situated on top of one another and are shown in light blue. The middle spikelet is shown in dark blue. Data from model 1.

Spikelet position (figure 15) within the inflorescence was a factor variable with three levels (base, middle and top). This variable was included in the best model in model 1, but not in model 2. The spikelet position in the middle showed a weak positive correlation. The entire contribution from this variable to the explained variation in model 1 was only 1.1%.

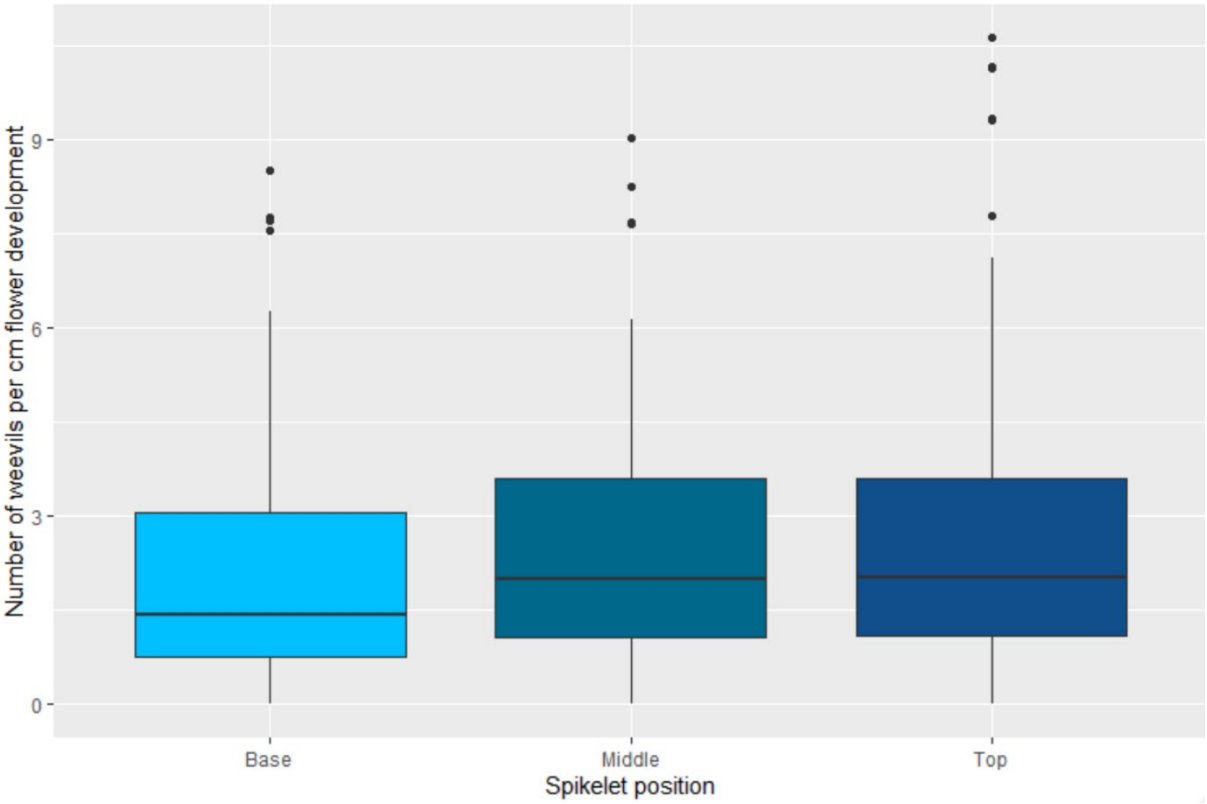

Figure 15: Spikelet position boxplot.

Boxplot showing the relationship between spikelet position within an inflorescence and the number of weevils found per cm flower development (habitat) for model 1.

The factorial variable “planting year” of the palm trees consisted of two levels; year 2011 and 2012. All palm trees included in this study were planted in 2011, except from the palms in the control transect which were planted in 2012. This variable explained 22.4% of the observed variation in model 2. The planting year 2012 showed a strong positive correlation, meaning that more weevils were observed per cm flower development on the spikelets in 2012 compared to palms planted in 2011 (figure 16).

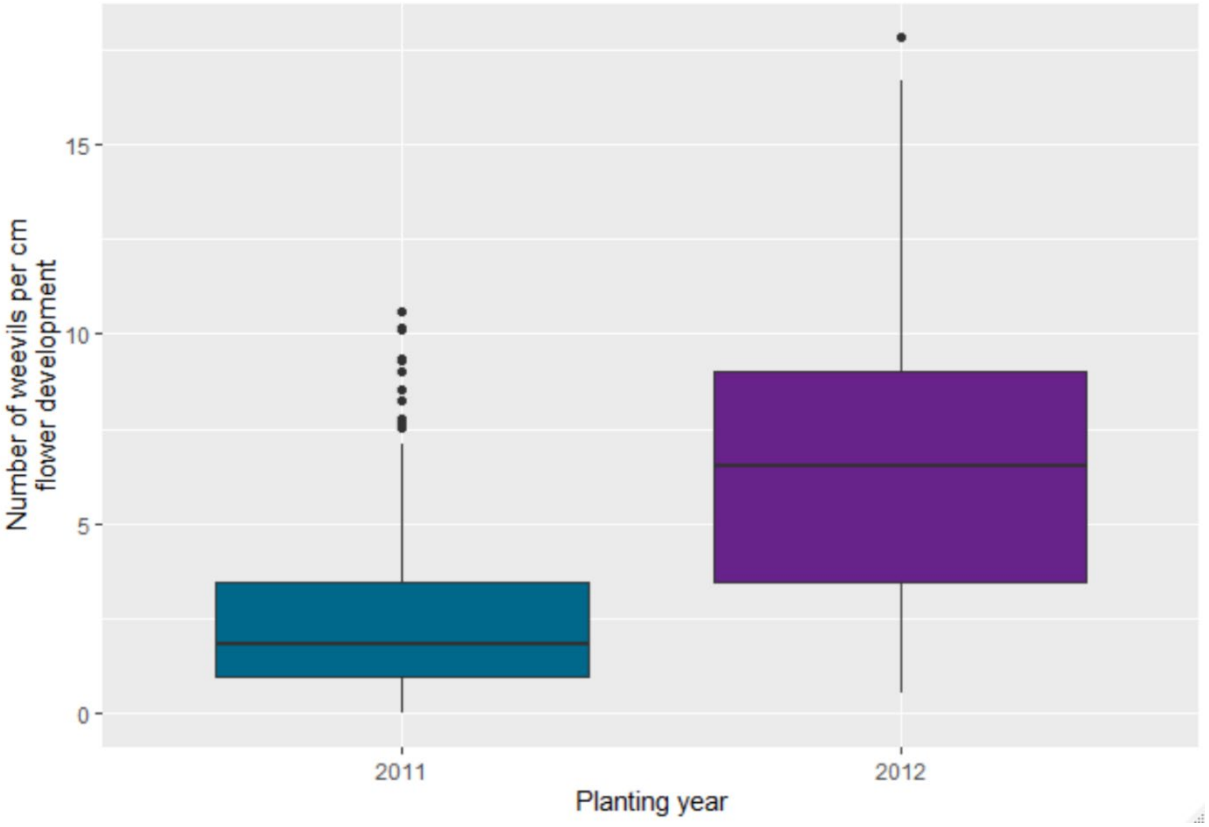

Figure 16: Planting year boxplot.

Boxplot showing how the number of weevils per cm flower development on spikelets is affected by planting year: 2011 (left) and 2012 (right).

Planting year 2012 gave a higher expected frequency of weevils per cm flower development (habitat) compared to planting year 2011 (figure 17).

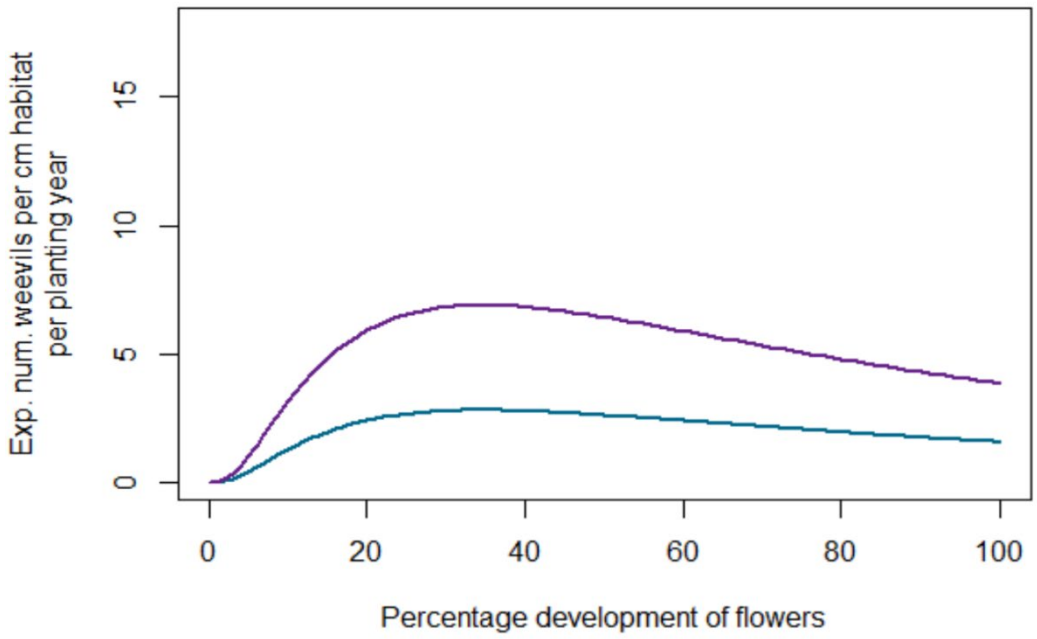

Figure 17: Percentage flower development per planting year.

Expected frequency of number of weevils per cm flower development (habitat) per planting year in model 2. Planting year 2011 is depicted as a blue line and year 2012 in purple.

The random variable palm ID was the major contributor in both models, contributing 54.1% and 62.5% to the variation in model 1 and 2, respectively.

3.4 Plantation data

The data gathered by plantation workers in PT KAL is displayed in appendix B, table 7 and figure 18 (unpublished data). Blocks were sampled in a rotating fashion throughout the year in such a manner that each block was sampled once.

In appendix B, the left panel in row 1 shows the average number of spikelets per inflorescence, the middle panel shows the average number of anthesising male inflorescences per hectare, and the right panel shows the average number of weevils emerged per spikelet,

calculated from 45 spikelets (nine spikelets from six separate male inflorescences). Row 2 shows the average number of weevils per hectare in the left panel, this data averages numbers of anthesising male inflorescences per hectare, number of spikelets, and weevils per spikelet. The right panel shows the average percentage fruit set. The data is shown per block, and the three blocks included in my study have been marked with an orange bar (E50), green bar (F45), and purple bar (F50).

Table 7: Plantation data from PT KAL 2018. The table shows the lowest and highest numbers obtained for all blocks combined and additionally the data for the blocks that were in my study (block E50, F45, and F50).

			Blocks		
	Lowest	Highest	E50	F45	F50
Spikelets/inflorescence	45.7	178.2	107	86	109
Male inflorescences at anthesis/hectare	0.6	3.9	2.7	2.1	3.3
Weevils/spikelet	5.7	78	57	76	59.1
Weevils/hectare	435.1	32758.6	16595.2	13934	21320.4
Fruit set (%)	48.5	88.5	73.6	49.4	71.9
Month			October	July	May

Figure 18 shows the relationship between the availability of anthesising male inflorescences and the number of weevils per hectare.

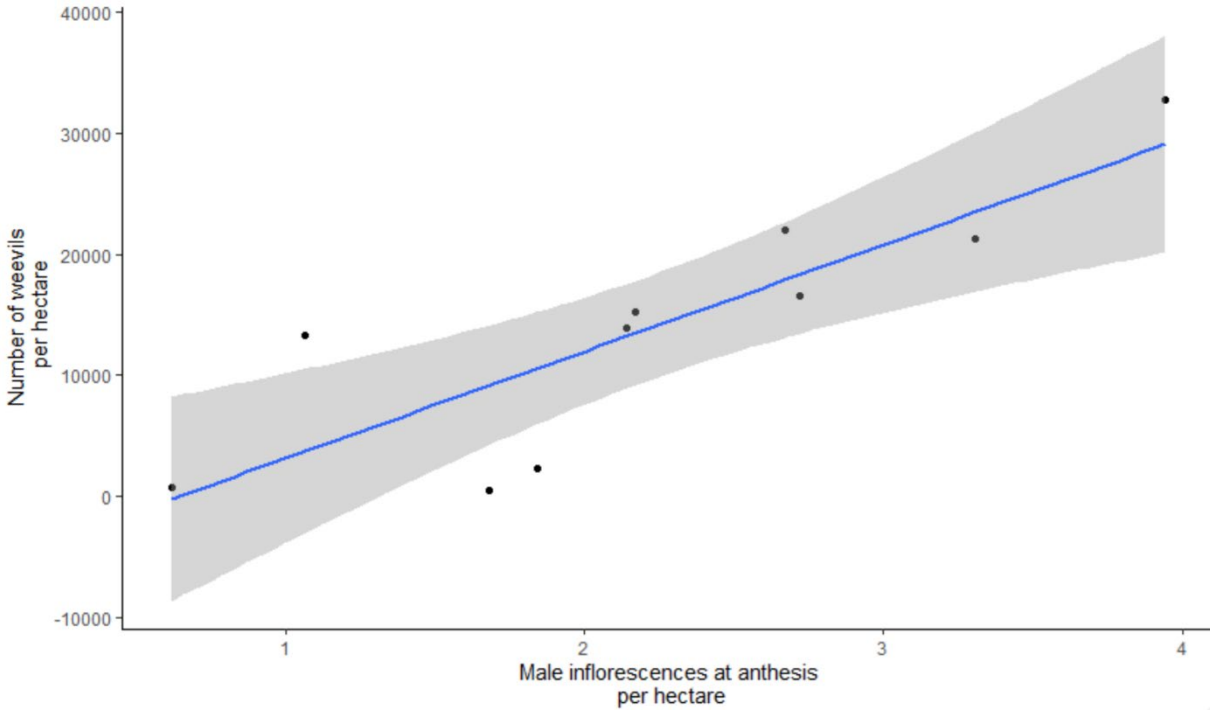

Figure 18: Effect of male inflorescences on weevil density.

Plot showing the relationship between the average number of male inflorescences at anthesis per hectare and the number of weevils per hectare. The grey band displays the 95% confidence level.

4 Discussion

4.1 Weevil density and the effect of pollination boxes

The aim of this study was to evaluate the effect of the newly introduced pollination boxes in PT KAL. The boxes were introduced with the intent to increase the local weevil populations and thereby facilitate pollination and ultimately increase fruit set and palm oil yields. At the time of this study, no assessment of the pollination boxes had yet been executed. As the technique required plantation workers to locate, harvest and change the male inflorescences in the pollination boxes every sixth day, and open and close the lids of the pollination boxes on a daily basis, it is a rather costly and time consuming enterprise. This study seeks to identify whether the pollination boxes are an efficient use of resources, or whether resources should be allocated elsewhere.

The analyses revealed that the relative density of weevils was not affected by distance to the nearest pollination box or the number of pollination boxes within a radius of 500 m giving no support to hypothesis 1 “The relative population density of *Elaeidobius kamerunicus* decreases at increasing distance to pollination boxes”. Detailed information on the flying and dispersal activity of *E. kamerunicus* is currently lacking. Prasetyo et al. (2014) described a technique very similar to pollination boxes, where six post-anthesis male inflorescences are placed in “hatch and carry” boxes to increase the local populations of *E. kamerunicus*. They found an increase in fruit set within a radius of 200 m from the hatch and carry boxes, while at longer distances (up to 400m) no increase in fruit set was registered. They also found fruit bunches to be smaller at a 400m distance as compared to those sampled within 200 m of the boxes. These results indicate that under the conditions of that study weevils might not disperse much further than 200 m. The pollination boxes in my study area are distanced roughly 300–800m from each other. These results might suggest that the pollination boxes in PT KAL could preferably be placed out with shorter distances (up to 400m apart for a radius of 200m)

Prasetyo et al. (2014) observed an average of 0.75 anthesising male inflorescences per hectare. This number is very low, considering that I found at least one anthesising male inflorescence within each sampling location of 5x5 palms (see below), and also compared to other studies which have reported considerably higher numbers, ranging from five to >60

male inflorescences at anthesis per hectare (Dhileepan 1992, Donough et al. 1996, Nurul Fatihah et al. 2019, Siswanto and Soetopo 2020). Prasetyo et al. (2014) reported a 20-fold increase in weevil density (from 2571 weevils/ha to 51 908 weevils/ha) after the addition of hatch and carry boxes. The initial low number of anthesising male inflorescences per hectare may not have been sufficient to support a large weevil population. The introduction of hatch and carry boxes may therefore have contributed greatly to the weevil population through the addition of six extra post-anthesising male inflorescences per box.

4.2 Weevil density and the effect of inflorescences at anthesis

Hypothesis 2 "The relative population density of *Elaeidobius kamerunicus* is affected by the number of anthesising inflorescences" is supported by the model without the control transect (model 1) but not by the model including the control transect (model 2). In model 1, the number of weevils per spikelet per cm flower development was negatively correlated to the total number of male and female inflorescences at anthesis. The expected number of weevils per spikelet per cm flower development decreased from approximately three weevils per spikelet when two anthesising inflorescences were available to right under two per spikelet when ten anthesising inflorescences were available.

The average number of anthesising male and female inflorescences was 2.4 and 3.9 inflorescences, respectively, per sampling location of 5x5 palms (1123.2 m^2). This corresponds to ~21.4 male and ~34.7 female inflorescences at anthesis per hectare. The number of weevils found per spikelet (mean = 22.8) in this study is similar to that found in other studies (ranging between 5 - 99.2 weevils per spikelet) (Dhileepan 1992, 1994, Wahid and Kamarudin 1997, Yue et al. 2015, Daud and Abd Ghani 2016). The anthesising male inflorescences may be exposed to a dilution effect, where a high number of anthesising inflorescences cause lower levels of flower visitation because the limited local weevil population has plenty of resources (flowers) to choose between (Dauber et al. 2010). This may be part of the reason why a high number of inflorescences at anthesis cause decrease in the number of weevils per spikelet. The weevil population in PT KAL may have been scattered across many available anthesising male inflorescences or visiting anthesising female

inflorescences at the time of sampling. Even though the addition of six post-anthesised inflorescences in the pollination boxes add more weevils to the area, this effect may not be recognised by sampling random spikelets if a dilution effect causes the weevils to disperse across the many available inflorescences (Hegland 2014). This effect is also visible in the plantation data from 2018, as the number of spikelets per inflorescence and the number of anthesising male inflorescences per hectare were lower in block F45 compared to block F50 and E50, but the number of weevils per spikelet are highest in block F45. At the time of my study, I also noticed that the anthesising male inflorescences were generally much smaller in block F45 compared to the other blocks, which was the reason why less spikelets were gathered from transect D on block F45.

Adding the variables male and female inflorescences at anthesis separately did not improve the model. The plantation data from 2018 provided by PT KAL, however, shows a positive correlation between the number of anthesising male inflorescences and weevil density, with an increase from <5000 to >25 000 weevils per hectare as the number of anthesising male inflorescence increases from one to four per hectare. The number of anthesising female inflorescences is not known from this data. Many studies have likewise found a positive correlation between weevil densities and the availability of male inflorescences at anthesis (Dhileepan 1994, Donough et al. 1996, Nurul Fatihah et al. 2018, Nurul Fatihah et al. 2019). At least one study did, however, not detect a relationship between the number of anthesising male inflorescences and weevil densities, but rather found that increasing numbers of anthesising female inflorescences increased the number of weevils sampled per male spikelets, resulting in a positive relationship between female anthesis and weevil density (Wahid and Kamarudin 1997). Presumably, this effect is caused by weevils remaining on the male inflorescences as this provides an assured supply of resources. Daud and Abd Ghani (2016) also found a positive relationship between the availability of anthesising female inflorescences and weevil density.

In the plantation data collected by PT KAL, the ten blocks included had <4 male inflorescences at anthesis per hectare. PT KAL considers >4 anthesising male inflorescences per hectare to be sufficient to maintain acceptable levels of weevil populations for sufficient pollination. This number is considerably lower than the number of anthesising male inflorescences registered in my study from 2017, where an average of 21.4 per hectare were found across the focal blocks (F45, F50, E46, K29). Maleness in *E. guineensis* is determined

by climatic conditions approximately two years prior to flowering (Adam et al. 2005), and the palms may have gone through a male phase during October 2017 when I did my sampling. Still, the plantation data was obtained throughout the year and is consistently on the low side. The results from the plantation were calculated by counting all anthesising male inflorescences within six rows per block. The average number of anthesising male inflorescences was then divided by the number of observed palm trees and multiplied with the number of palms in one hectare. In my study in 2017, anthesising male inflorescences were counted in 37 unique sampling locations of 5x5 palms and many of these locations were sampled twice. This technique is similar to the one used by Nurul Fatihah et al. (2019), where male anthesis was counted in sites of 25 palms, reporting between eight to >60 male inflorescences at anthesis per hectare in their study site in Malaysia. Perhaps the pollination boxes of PT KAL had a larger effect in 2018 when the availability of anthesising male inflorescences was much lower compared to 2017.

4.3 Weevil density and the effect of flower development and position of spikelet

"Flower development on spikelets" was, in addition to serving as an offset variable in my analyses, also included as an explanatory variable. This variable was included in both models and explained most of the variation in model 1 (not considering the random effect palm ID). . Since the offset variable was cancelled in model 1, according to this model the expected number of weevils per cm flower development per spikelet is independent of the length of flower development on spikelets, making it difficult to interpret the variance contribution of this model. According to model 2, relatively less weevils per cm flower development per spikelets are present with increasing length of flower development.

"Percentage flower development on spikelets" also contributed to the explained variation in weevil densities in both models. The variable was included as a quadratic term, showing a strong positive correlation for the linear term and a negative correlation for the quadratic term. This shows that the number of weevils per cm flower development on spikelets increased until an optimum was reached and subsequently decreased. Other studies (Dhileepan 1992, 1994, Yue et al. 2015) have divided anthesis into "day of anthesis" and have produced similar results showing that the number of weevils per spikelet increases to a peak as the percentage flower development on spikelets progresses, before the weevil numbers start declining

towards the end of anthesis (Dhileepan 1992, 1994, Yue et al. 2015). This suggests that weevils seek alternative male inflorescences when most staminate flowers already have eggs deposited inside them or most anther filaments have been consumed leaving less pollen to attract weevils. High intraspecific competition when the number of weevils per spikelet are bountiful, may also cause weevils to depart to look for other male inflorescences, and in the process transfer pollen to female inflorescences (Dhileepan 1992). These results indicate that anthesising male inflorescences are an important factor in attracting (Siswanto and Soetopo 2020) and retaining weevils on the inflorescences.

The explanatory variables "flower development per spikelet" and "percentage development of flowers per spikelet" are highly correlated ($r = 0.72$). This does not pose a problem as the AICc model selection criterion was used to pick the variables that best explain the observed variation. While "percentage development per spikelet" was included to describe how far anthesis had progressed on individual spikelets, "flower development per spikelet" rather indicates how much habitat is available to weevils. Small spikelets completely covered in flowers (end of anthesis) might have the same measure of flower development (in cm) as larger spikelets that only have a relatively small proportion covered by flowers.

In model 1, slightly more weevils were found on spikelets located in the middle of the inflorescence. Several predators, like rats, ants, spiders and mites are known to prey on weevils in all life stages (Prasetyo et al. 2014, Yue et al. 2015, Li et al. 2019), and rats may cause high levels of mortality of larvae in the field (Hussein et al. 1991). Spikelets positioned in the middle of an inflorescence may provide a higher degree of protection to the weevils, which may preferentially aggregate there. The managers at PT KAL tried to minimise the effect of predation on weevils developing in the inflorescences stored inside the pollination boxes by closing the mesh covered lid every day at sundown and reopening them in the morning. This probably serves as an effective protection against rat predation, but they still reported problems regarding ants crawling inside the boxes and were unsure how to solve the problem. Ants are known to feed on both the larvae and adults of *E. kamerunicus* (Yue et al. 2015, Hakim et al. 2018) and could therefore affect weevil densities within inflorescences. Ants were observed entering the pollination boxes during this study, and also seen capturing adult weevils on live inflorescences (*pers. obs.*).

4.4 Weevil density and the effect of palm age

Much of the variation in model 2 was explained by the planting year of the palms. A significantly higher proportion of weevils were observed per cm flower development on spikelets in the planting year 2012 compared to year 2011. The variable "planting year" did not have interactions with the other variables in model 2, indicating that the underlying dynamics influencing the system in the areas planted in 2011 are the same as those influencing the area planted in 2012.

The palms in my study were five and six years old at the time of sampling. Daud and Abd Ghani (2016) also found higher numbers of weevils per spikelet in younger palms when they compared five and eight year old palms. The five year old palms had an average of 13.5–54.1 weevils per spikelet throughout the study period, while the corresponding numbers for the eight year old palms were 21.2–26.1 weevils per spikelet. On the opposite, Nurul Fatihah et al. (2019) compared four and six year old palms and found that the average weevil population per hectare to be higher for the older palms. The average population per hectare for the six year old palms was 25 712 weevils compared to 21 086 weevils in the area with four year old palms. The difference was not reported as significant between the two areas. In the study of Nurul Fatihah et al. (2019), the area with the four year old palms was specifically chosen because fruit set was poor in this area. However, the study found both areas to have sufficiently large weevil populations to ensure good fruit set (Nurul Fatihah et al. 2019). The study reported a significant and strong positive correlation between the number of male inflorescences at anthesis and the population abundance of weevils. The authors mention that the average number of spikelets per inflorescence is higher in the older palms (Nurul Fatihah et al. 2019), a factor that may contribute to a slightly larger weevil population in this area as compared to the area with the four year old palms.

Daud and Abd Ghani (2016) mentioned that the higher number of weevils among the young palms in their study might be due to the palms being shorter in that area, and that it perhaps is easier for the weevils to reach anthesising inflorescences in short palms, or that the weevils may simply prefer young, smaller palms.

Even though in my study more weevils were present per cm flower development on spikelets in the control area with five year old palms (planting year 2012), this will not necessarily translate into higher fruit set. The microclimate between the areas likely differ, as the young

area consisted of much smaller palm trees, most of them <1.5 m. The areas with six year old palms (planting year 2011), on the other hand, had a considerable larger variation in palm sizes, ranging from mostly >1.5 m to several meters tall. The canopy was relatively closed in these areas, offering some degree of protection to rainfall. Rainfall can reduce fruit set by decreasing pollen viability and pollen load carried by weevils (Dhileepan 1992).

Palm age, size, environmental and microclimatic differences may separately or combined contribute to the higher number of weevils found in the area with the younger palms and may be more important regulators of weevil numbers than the presence or lack of pollination boxes. Consideration should be taken when comparing the palms planted in 2011 with the palms planted in 2012 in this study though as, in addition to the differences between the areas mentioned above, only 42 spikelets were sampled for the planting year 2012 as compared to 323 spikelets for the planting year 2011.

4.5 The use of an offset variable to count weevil densities

Most studies calculate the number of weevils per spikelet by removing 3–15 spikelets per inflorescence (Dhileepan 1992, 1994, Prasetyo et al. 2014, Yue et al. 2015, Nurul Fatihah et al. 2019, Siswanto and Soetopo 2020) and counting all weevils present. Some studies focus on adult weevils per spikelet, other studies count emerging weevils from post-anthesised inflorescences. The average number of weevils/spikelet is then multiplied by the number of spikelets per inflorescence to obtain an estimate of the number of weevils per inflorescence. This number can subsequently be multiplied by the number of anthesising male inflorescences per hectare to get an idea of the population abundance per hectare.

Counting all spikelets in a bunch was not feasible in this study, as it was not possible to cut down the entire male inflorescence. An alternative approach was used instead, where the flower development on spikelets was measured in cm. Since the flowers serve as a feeding and breeding site for weevils (Henderson 1988), the measure can be used as an indication of habitat available to the weevils. The total number of weevils per spikelet was subsequently corrected, by use of an offset variable in the statistical models (Reitan and Nielsen 2016), for the amount of available habitat per spikelet at the time of sampling, as this measure changes during the duration of anthesis (Dhileepan 1992, Tandon et al. 2001). This may be a better

way of calculating the number of weevils per spikelet, as it corrects the number of weevils found to the available habitat on individual spikelets. This may also make it easier to compare results when sampling palms of different ages, as spikelets are known to increase in size with palm age (Corley and Tinker 2016), i.e. older palms provide more habitat per spikelet compared to younger palms.

Using "flower development on spikelets" as an offset is preferable if the number of spikelets per inflorescence is difficult to obtain. When the number of spikelets per inflorescence is not known, looking at only visitation frequencies (weevils per spikelet) causes loss of information, as the number of spikelets in male inflorescences, and therefore the available habitat and amount of weevil-attracting pollen, can vary greatly. By using the offset variable (amount of cm flowers available), the variability in numbers of flowers observed is accounted for in the statistical analyses (Reitan and Nielsen 2016).

Careful consideration should be taken if the offset variable is also incorporated into the model as an explanatory variable, as this may lead to cancelation of the effect of the offset variable and make it difficult to interpret model output.

4.6 Trapping methods

I tested several trapping techniques with the initial intention of using the traps to obtain data on weevil visits to both anthesising male and female inflorescences along the transects, in addition to data on the possible presence of weevils in native palms in the forest areas surrounding PT KAL. Unfortunately, the traps did not provide satisfactory results, and further use of the traps was terminated after the initial phase. Several factors may have caused the low capture rates. The fly glue proved insufficiently adhesive to trap the weevils. The movement of weevils was merely impaired by the glue, and many would eventually escape. None of the traps were waterproof enough to keep the sheets of glue dry during rainy days, also causing loss of adhesiveness. A small amount of pollen was deposited in the traps to attract weevils, but it is likely that the large pollen production by the male inflorescence, and the related anis-scent, overshadowed this effect. Still, incoming and departing weevils to anthesising male inflorescences might have landed on the traps by mistake and gotten stuck, if a stronger glue had been used. The traps are unlikely to have been attractive enough to capture weevils visiting anthesising female inflorescences. Yue et al. (2015) also used sticky traps,

but with larger and presumably more adhesive sheets folded as cylinders surrounding entire male and female inflorescences, providing greater success. Somewhat better capture rates might have been obtained if the traps had been left out for a shorter time, as it took a little while for weevils that had landed on the glue to free themselves. Counting weevils on selected spikelets was used as an alternative approach to monitor visits to anthesising male inflorescences, which turned out as better choice under the prevailing conditions. However, without traps I was not able to obtain data on weevil visits to anthesising female inflorescences or potential visits to native palms.

4.7 The effect of weevil density on fruit set

Fruit set is dependent on pollination efficiency, which in turn depends on the weevil pollen carrying capacity, the pollen load carried to anthesising female inflorescences, and the pollen transferred to the receptive female inflorescence (Dhileepan 1992). Kevan (1986) coined the term “pollinator force”, referring to the number of weevils necessary to ensure good fruit set. Several studies have made efforts to quantify this concept with different results. Donough et al. (1996) reported that 20 000–85 000 weevils per hectare would be required to achieve a fruit set of 55% in their studied plantations in Sabah, Malaysia. Dhileepan (1992), on the other hand, found that fruit set was higher when the average number of weevils per spikelet was low compared to higher number of weevils per spikelet. In the study by Dhileepan (1992), a fruit set of 84.9% was reached when there was an average of 18.7 weevils per spikelet, while fruit set dropped to 72.1% when the average number of weevils per spikelets was 99.2. The number of weevils per hectare was not calculated in my study, since the number of spikelets per inflorescence was not known.

Pollination efficiency may be affected by intraspecific competition for resources when weevil populations increase in size, causing individual weevils to carry and transfer less pollen (Dhileepan 1992). The high level of weevils per spikelet in the study of Dhileepan (1992) in India, coincided with the wet season, which is generally considered favourable for population build-ups of *E. kamerunicus* (Dhileepan 1994), but high rainfall and number of rainy days may simultaneously have an adverse effect on pollen viability and pollen load carried by weevils (Dhileepan 1992). Decrease in fruit set may therefore be caused by high rainfall, rather than high weevil population levels (Dhileepan 1994). Nonetheless, fruit set was higher when weevil population levels were lower (Dhileepan 1992). Wahid and Kamarudin (1997)

measured an average pollinator force of 47 558 weevils per hectare in a plantation in Malaysia but found no relationship between the number of weevils per hectare and fruit set. The level of fruit set remained >60% throughout their four year study, even though estimated weevil densities ranged between 4711 and 141 577 per hectare.

The purpose of examining the effect of pollination boxes on weevil densities was to see what implications they might have on fruit set. The duration of this study was too short to observe development of fruit but, fortunately, PT KAL provided fruit set data from 2018. Since the pollination box project started in May 2017, and fruit set takes approximately 5–6 months after pollination, it is safe to assume that the potential effect of the pollination boxes on fruit set should have been operating when plantation workers gathered data from different blocks between January and December 2018. PT KAL aims for a fruit set of >70%. When looking at the three blocks that were included in my study (E50, F45, F50), block E50 had the highest fruit set of 73.6% as compared to 49.4% in block F45 and 71.9% in block F50. The variation in fruit set among all the blocks give room for doubt about the effect of the pollination boxes and begs to question whether other factors are at play.

Although no effect of pollination boxes was observed on weevil counts in my study, it is difficult to judge the actual effect of pollination boxes on palm oil yields as I do not have fruit set data or palm oil yields from the plantation from the years prior to the use of the pollination boxes. A comparison of fruit set data and oil yields before and after pollination boxes would to a larger degree highlight the actual effect of the pollination boxes.

4.8 Conclusion

Pollination boxes seem not to affect relative weevil densities in male inflorescences. Number of inflorescences in surrounding palm trees negatively affected weevil counts suggesting a dilution effect where inflorescences in the vicinity competed for weevils.

An alternative approach to pollination boxes might be to store and hatch weevils in a confined system in a storage warehouse, spray the weevils with viable pollen, and releasing them into high density areas of anthesising female inflorescences. This approach could have three possible benefits: (i) protect the weevils against predation, (ii) require less labour by eliminating daily maintenance of pollination boxes in the field, and (iii) increase the chances

of weevils first visiting an anthesising female inflorescence. More research would be required to confirm these statements.

5. Future studies

More long-term studies are needed to evaluate the interactions between climatic conditions, the spatial variation in availability of anthesising inflorescences, weevil populations, fruit set and oil yields, as these processes seem to be highly integrated. Studies of this integrate system should be performed at varying scales as the mechanisms influencing the system may be operating at different levels and in turn influence what is observed (Levin 1992, Dauber et al. 2010).

Any influence the pollination boxes had at weevil populations could not be observed at the scale of this study, but Prasetyo et al. (2014) reported an effect of hatch and carry boxes within a 200 m radius. Most of the geolocated pollination boxes in this study were distanced between 300 - 800 m apart. Future research should seek to uncover typical forage and dispersal behaviour of *E. kamerunicus*, as this might give an indication of the potential benefit of pollination boxes or similar techniques and at what scales these might be effective.

Future studies on pollination boxes (and hatch and carry boxes) also should focus on comparing high and low density areas of anthesising inflorescences, different palm ages, and have more/larger control areas to get a more accurate picture of the factors influencing fruit set and oil yield. These studies can preferably be performed in a plantation where pollination boxes are introduced for the first time, allowing comparison of weevil populations, fruit set, and oil yields before and after the introduction of the boxes.

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Appendix A: Traps

Trap design

Table A.1: Overview of traps, materials, size, shape and trapping method. **Trap** = trap ID. **Material** = material from which the trap was made. **Shape** = shape of trap. **Size** = size of trap. **Trapping method** = method of capturing weevils.

Sticky traps	Material	Shape	Size	Trapping method
A	Metallic mesh	Cylinderical	Rectangle: 17 x 31.4 cm	Rectangular sheet with fly glue along length of cylinder. Small amount of pollen
B	Metallic mesh	Cylinderical	Rectangle: 17 x 31.4 cm	Circular sheet of fly glue in middle of cylinder. Small amount of pollen
F	Bendable plastic, yellow	Equilateral triangle	Width 16 cm sides 17 cm	Sheet with fly glue. Small amount of pollen
G	Bendable plastic, yellow	Equilateral triangle	Width 11.5 cm sides 17 cm	Sheet with fly glue. Small amount of pollen
Funnel traps				
C	Plastic bottle	Bottle - shaped	0.5 litre	Bottle top turned upside down (funnel). Pollen in trap
E	Plastic container	Rectangular	9 x 9 x 12 cm	Funnel in top of container. Pollen in trap

Table A.2: Traps and number of weevils caught between the 5th and 14th of September, 2017. **Trap** = trap ID. **Male anthesis** = number of weevils caught in palm tree with an anthesising male inflorescence. **Control** = weevils caught in palm tree without anthesising male inflorescence. **Min** = minimum number of weevils caught in trap. **Mean** = mean number of weevils caught in trap. **Max** = maximum number of weevils caught in trap. **Traps emptied** = number of traps emptied. Double set of traps tested simultaneously on palm with and without anthesising male inflorescence.

	Weevils captured					
Trap*	Male anthesis	Control	Min	Mean	Max	Traps emptied
A	5	0	0	0.4	2	14
B	8	2	0	0.7	4	14
F	8	1	0	0.6	6	14
G	2	1	0	0.3	2	12

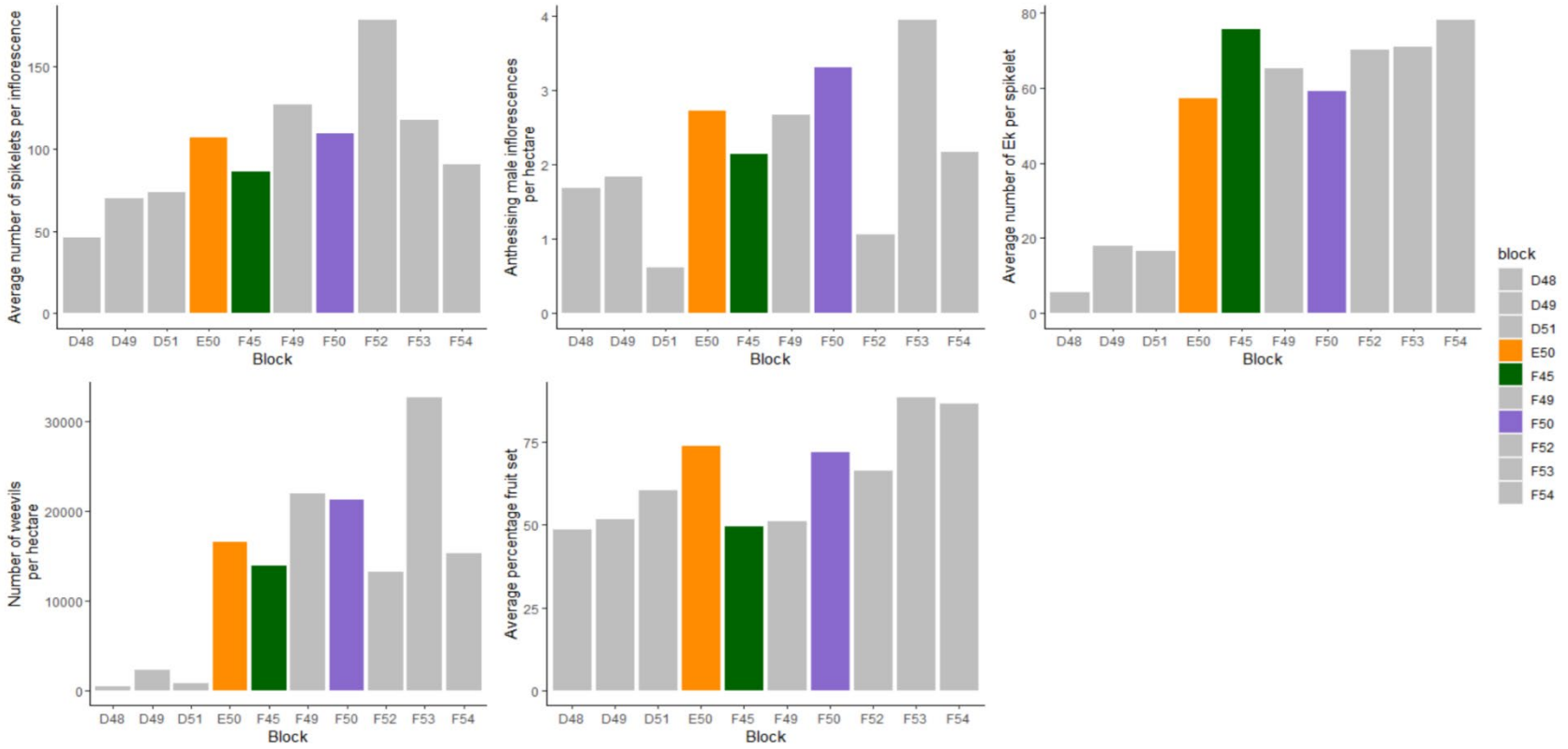
*Trap C and E were omitted from table x.x because only zero values were obtained.

Figure A.1: Examples of trap design. Top panel shows trap G. The middle panel shows trap E (left) and trap C (right). The bottom panel shows trap A. Information about traps in table x.x

Figure A.2: Traps in palm trees. The left panel shows trap G in control palm. The left panel shows trap B hanging above an anthesising male inflorescence.

Appendix B: Plantation data

Plantation data from PT KAL 2018. Row 1: average number of spikelets per inflorescence (left panel, average number of anthesising male inflorescences per hectare (middle), average number of weevils hatched per spikelet (right). Row 2: average number of weevils per hectare (left panel), and the average percentage fruit set (right panel). The legend shows from which block the data is gathered. The blocks included in my study are marked in orange (E50), green (F45), and purple (F50). The other blocks included are shown with grey bars for comparison



Appendix C: Covariates

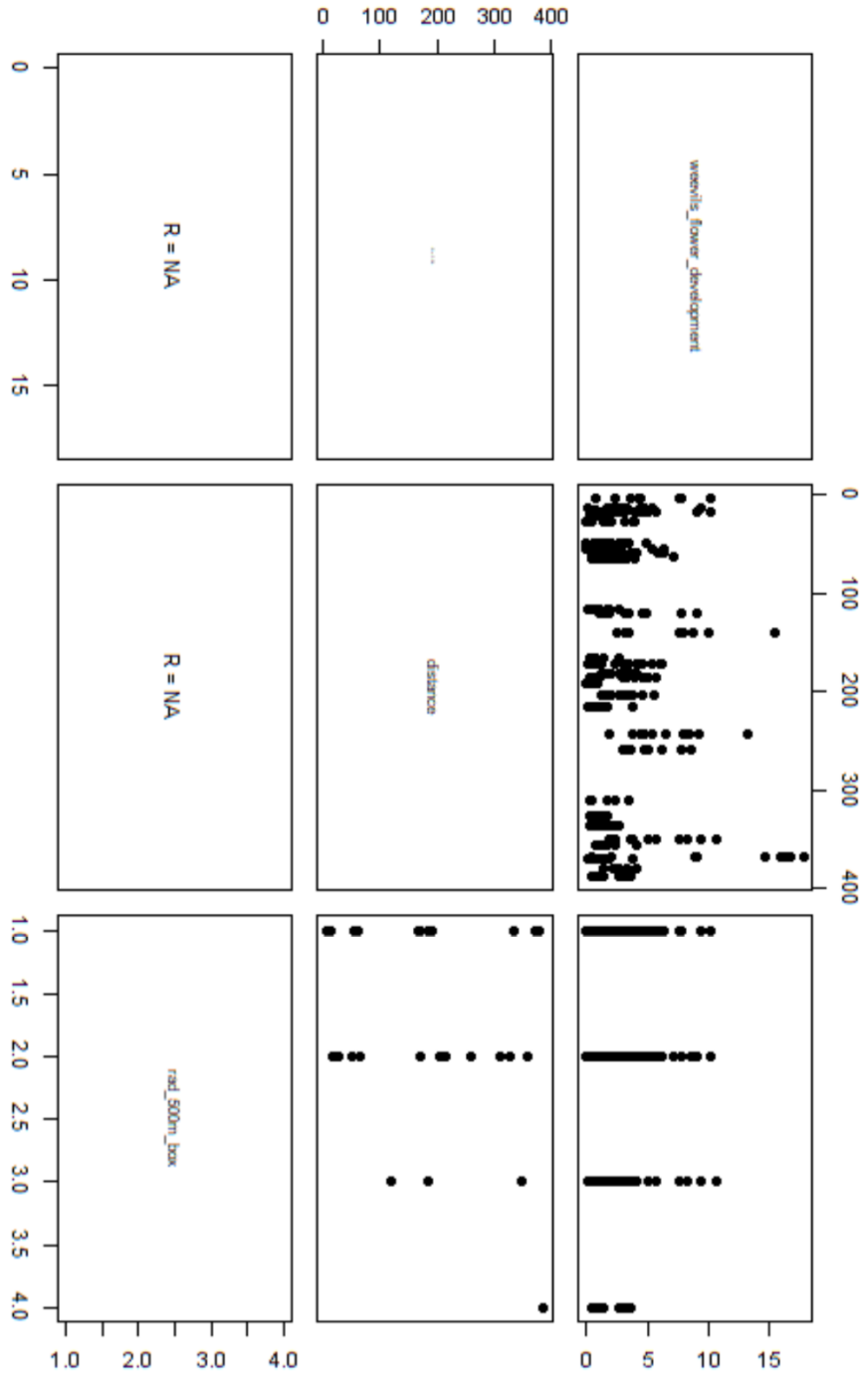
Table C.1: List of covariates included in model selection to find the best GLMM to explain the relative weevil density recorded from 9th – 28th October 2017.

	Covariate	Description
	FIXED EFFECTS	
Distance variables	Distance	Continuous variable (4.8 - 386.8 m) measuring distance to pollination box in the transect. Log transformed.
	Box within 500m radius	Number of available pollination boxes within 500m radius
Availability of inflorescences	Male inflorescences	Number of available male inflorescences at anthesis at sampling location
	Female inflorescences	Number of available female inflorescences at anthesis at sampling location.
	Total anthesis	Sum of male and female inflorescences at anthesis at sampling location.
Inflorescence measures	Flower development	Continuous variable. Amount of spikelet covered in flowers (cm). Available weevil habitat. Log transformed.
	Percentage development	Continuous variable. Percentage of spikelet covered in flowers. Log transformed.
	Non-floral	Continuous variable. Amount of

	development		spikelet not covered in flowers (cm)
	Spikelet position		Factor variable with 3 levels (1 = base, 2 = middle, 3 = top) Position of spikelet within inflorescence.
	Stage anthesis		Factor variable with 5 levels (1 = 0-20%, 2 = 21-40%, 3 = 41 - 60%, 4 = 61 - 80%, 5 = 81 - 100%) Describes percentage of spikelets covered in flowers in stages.
Quadratic term	Percentage development		Test for non-linear effect of percentage development of flowers on spikelet. Log transformed.
Statistical interaction	Male and female inflorescences		Test for interaction between male and female inflorescences at anthesis.
		RANDOM EFFFECTS	
Spatial variables	Palm ID		Factor variable with 33 levels (model 1) and 37 levels (model 2) ID of sampled palm trees.
	Block		Factor variable with 4 levels (model 1) and 5 levels (model 2) ID of block where sample was taken.
	Transect		Factor variable with 6 levels (model 1) and 7 levels (model 2) ID of transect where sample was taken.
Temporal variable	Day of year		Continuous predictor (282 - 301). 1 = 1st of January 2017.

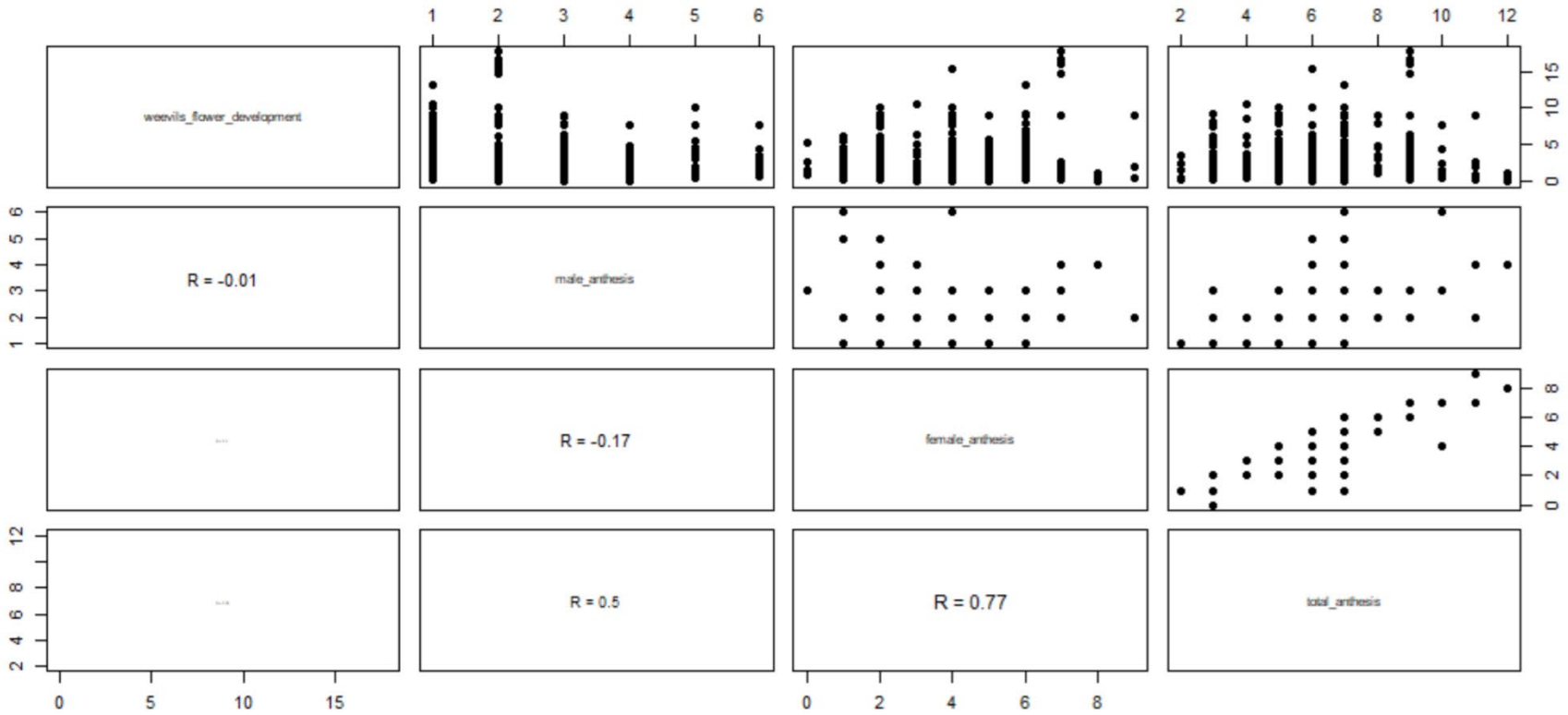
		OFFSET VARIABLE	
Inflorescence measure	Flower development		Continuous variable. Amount of spikelet covered in flowers (cm). Available weevil habitat. Log transformed.

Appendix D: Correlation plots



Correlation plots for weevils per cm flower development and distance variables. **Distance** = distance to pollination box. **Rad_500m_box** = pollination boxes within radius of 500m.

Correlation plots showing correlations between the number of weevils per cm flower development and availability of inflorescences variables.
Male_anthesis = male inflorescences at anthesis at sampling location. **Female_anthesis =** anthesising female inflorescences at sampling location.
Total anthesis = total number of anthesising inflorescences at sampling location.



Correlation plots showing correlation between weevils per cm flower development and inflorescence measure variables. **Flower_development =** the amount of spikelets covered in flowers (cm). **Percentage_development =** the percentage of spikelets covered in flowers. Indicates how far anthesis has progressed. **Spikelet_length =** length of spikelet. **Spikelet position =** position of spikelet within inflorescence.