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Oil Palm Pollinator Dynamics and Their Behavior on Flowers of Different Oil Palm Species *Elaeis guineensis*, *Elaeis oleifera* and the *oleifera* x *guineensis* Hybrid in Ecuador

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ABSTRACT

The entomofauna and the behavioral patterns of potential pollinators were studied on female and male flowers of the oil palms *Elaeis guineensis*, *Elaeis oleifera* and *oleifera* x *guineenis* (OxG) hybrids in the Pacific coast and Amazon basin productive regions in Ecuador. Insect population studies were performed using a stratified sampling method and the determination of insect activity by monitoring insect arrivals to female flowers in anthesis. Additionally, insect pollinator pollen-transport capacity and life cycles were determined for *Elaeidobius kamerunicus*, *Grasidius hybridus*, *Couturierius constrictirostris* and *Mystrops costaricensis*. *Elaeis guineensis* female flowers were visited only by *Elaeidobius kamerunicus*, in both locations, at the Amazon basin plantation and at the Pacific coast plantation. *Elaeidobius kamerunicus* was the most abundant species (1,960 individuals) on *E. guineensis* during the dry season in Amazonia. *Elaeis oleifera* and OxG hybrids showed high numbers of *G. hybridus* (771 and 194 individuals,

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respectively). *Couturierius constrictirostris* and *M. costaricensis* visited the flowers in lesser numbers. The activity studies showed that *E. kamerunicus* had diurnal behavior, while *G. hybridus* was active in the morning in the Amazon region and at dusk on the Pacific coast. *Elaeidobius kamerunicus* was the pollinator with the highest pollen loading capacity (8,273 grains/individual). The life cycle of *C. constrictirostris* was the longest (41.7 days in the Amazon region and 30.3 days on the Pacific coast), followed by *E. kamerunicus,* with 36.7 days in Amazonia and 30.3 days on the Pacific coast.

Keywords: *Couturierius*, *Elaeidobius*, *Elaeis guineensis*, *Elaeis oleifera*, hybrids, *Mystrops*

INTRODUCTION

Oil palm crops provide high revenue, foreign exchange and working places in tropical South America that present limited employment opportunities. Ecuador reported 263,840 ha of oil palm in 2016 (Salazar et al., 2016) and 257,120.93 ha in 2017 (Asociación Nacional de Cultivadores de Palma Aceitera [ANCUPA], 2018), and approximately 87% of the national production units belong to small farmers (Fomento de Exportaciones de Aceite de Palma y sus derivados [FEDAPAL], 2017). Oil palm is one of the most efficient oleaginous crops per hectare, covering the whole internal demand for vegetal oil for human consumption in many countries such as Indonesia, Malaysia, Venezuela, Ecuador, among others (Labarca & Narváez, 2009; Pacheco et al., 2017; Salazar et al., 2016; Turner & Gillbanks, 1974).

The expansion of "bud rot", known as "PC" disease, in Ecuador during the 1970s has forced growers to use the interspecific hybrids of *Elaeis oleifera* x *Elaeis guineensis* (OxG), which is tolerant to this disease and has therefore been considered as an alternative for developing new vegetal material suitable for production (Burgos, 2013; Louise et al., 2007). Research institutes and private organizations in Brazil, Costa Rica, Colombia, Venezuela and Ecuador have assessed interspecific hybrids (OxG) to increase production levels free from "bud rot" disease with promising results (Alvarado et al., 2010; Barba & Baquero, 2012; Bravo & Bernal, 2015; Teixeira Souza Júnior, 2013). However, these interspecific hybrids present a critical agronomical disadvantage in terms of low pollination levels in comparison with *Elaeis guineensis* (Alvarado et al., 2000, 2013). Assisted pollination is a common agronomic practice used to obtain good fruit set levels in commercial crops. However, this practice increases production costs and entails logistic limitations (Hacienda La Cabaña, 2009; Rosero & Santacruz, 2014). Most pollination studies have been performed on *Elaeis guineensis*, but very few have focused on *Elaeis oleifera* or the OxG hybrids. In the last few years, there has been an important increase in OxG hybrid planting areas in Ecuador. Plantations will have to renew the vegetal materials in at least 30,000 ha/year (ANCUPA, 2018), but there is a lack of information about the

OxG hybrid agronomic behavior, pollination mechanisms and pollinator adaptation to monoculture.

Two families of Coleoptera, namely Curculionidae (Baford et al., 2011; Mondragón & Roa, 1985) and Nitidulidae (*Mystrops costaricensis*) have been reported to be pollinators of oil palms (Baford et al., 2011; Syed, 1979, 1984). Curculionidae beetles, such as *Elaeidobius kamerunicus*, *Elaeidobius subvittatus*, *Couturierius* sp., and *Grasidius* sp., have been considered to be the most efficient pollinators in commercial oil palm plantations (Tuo et al., 2011) in Côte D´Ivoire, Western Africa. Further studies conducted by Syed (1984) showed that pollination by *E. kamerunicus* had increased the fruit set in *E. guineensis*. Several studies have been conducted since 1980 that introduce *E. kamerunicus* to commercial plantations to increase fruit set (Caudwell, 2002; Meléndez & Ponce, 2016; Syed, 1982). Artificial introduction of *E. kamerunicus* populations in *E. guineensis* crops the fruit set increased from 15% to 26% and resulted in a 60% increase in crop yield (Harun & Noor, 2002; Prasetyo et al., 2014; Syed, 1979; Syed & Saleh, 1988). However, there are some reports of poor fruit set apparently caused by a combination of environmental factors and poor-quality pollen that may be affecting the performance of *E. kamerunicus* (Teo, 2015).

There is high interdependence between insect pollinators and plants; male flowers are essential for pollinators to complete their life cycle, since these flowers are used for oviposition and as a food source for larvae and adults, and the leaf bracts are used to protect the pupae (Caudwell, 2002; Labarca & Narváez, 2009; Syed, 1984). Curculionidae and Nitidulidae beetles feed on the pollen grains in male flowers and transport pollen from male to female flowers (Henderson, 1986; Labarca & Narváez, 2009). The insect affinity for oil palm flowers is essential for the survival of the species since insects are attracted to the flowers only during anthesis because they respond to specific flower chemical changes during anthesis (Baford et al., 2011). Mystropinae beetles have shown diurnal visitation patterns to flowers (Núñez et al., 2005). However, other studies showed that these insects can still be active late in the afternoon, between 18:00 and 20:00 (Genty, 1985).

Due to the expansion of hybrid material, there is a need to understand the pollination mechanisms and pollinator dynamics in *E. oleifera* and the OxG hybrid in Ecuador. The present work focused on evaluating the insect diversity associated with the inflorescences of *E. guineensis*, *E. oleifera* and hybrid oil palms, the life cycles and activity of the potential pollinators and the capacity of insects to carry pollen to establish their potential as pollinators.

MATERIALS AND METHODS

Sites Description and Plant Materials

Oil palm pollinator studies were performed in two oil palm plantations, one in the Pacific coast lowlands and one in the Amazon basin lowlands in Ecuador. The first location was the Palmar del Río plantation (0°19´ S, 77°04´ W) at 290 m.a.s.l. and with annual precipitation of 3,392 mm. This plantation has 10,000 ha of oil palm crops and is located in Francisco de Orellana province (Site 1). The studies at this location were performed during the rainy and dry seasons in 2014. The second study location was the Energy and Palma plantation (1° 07´ N, 78° 45´ 50" W) in the province of Esmeraldas, which was 13,000 ha in size and located on the Pacific coast of the country (Site 2). It is located at 500 m.a.s.l., with an annual precipitation of 1,500-1,800 mm. The studies were performed during the dry season in 2015 and the rainy season in 2016 (Table 1).

The cultivated area of the plantations was divided into strata that included *E. guineensis*, *E. oleifera* and hybrid material (OxG). The insects were collected in each stratum using a randomized sampling method (Galindo, 2008).

The pollinators of flowers (male and female) of *E. guineensis and E. oleifera* and interspecific (OxG) hybrids in anthesis were studied at both localities using the same method. The hybrids (OxG) evaluated at Palmar del Río were Taisha x Avros, Taisha x LaMé and Cuarí x LaMé. At Energy and Palma, the evaluated hybrids were Unipalma (OxG) and Cuarí x LaMé. *Elaeis guineensis* and *E. oleifera* (Taisha) were evaluated at both sites. *Elaeis guineensis* was taken as the genetic material of reference because it has been the most commonly cultivated palm.

Table 1

Number of oil palm flower samples in anthesis at the two study sites: The Amazonia basin lowlands (Site 1) and the Pacific coast (Site 2)

Palm species	Female flowers		Male flowers	
	Season			
	Dry	Rainy	Dry	Rainy
Site 1 (Amazonia)				
Elaeis guineensis (Papúa)	2	2	2	2
Elaeis oleifera (Taisha)	2	2	2	2
Hybrid Taisha x Avros	17	17	17	17
Hybrid Cuarí x LaMé	24	24	24	24
Hybrid Taisha x LaMé	3	3	3	3
Site 2 (Pacific coast)				
Elaeis guineensis (Papúa)	10	10	8	8
Elaeis oleifera (Taisha)	1	1	1	1
Hybrid Unipalma	36	36	21	21
Hybrid Cuarí x LaMé	14	14	14	14

Insects Associated with Oil Palm Inflorescences

Insects were collected from male flowers during anthesis described by Hormaza et al. (2010), and 20 spikes were shaken over a white paper to gather the specimens. Insects were identified using taxonomic keys (Borror et al., 1989; Hala et al., 2012; O'Brien et al., 2004).

Diurnal and nocturnal insect activity was observed among the female inflorescences. Observations were executed every 20 minutes from 5:00 until 0:00 (midnight). Visiting insects were collected and later identified. Observations were repeated three times for four different female inflorescences (12 samples per species). The insects visiting female flowers in anthesis were trapped using a 40 x 50 cm^2 plastic sheet smeared with BIOTAC glue (IUPAC number: polybutene polymer; exporter: Marketing ARM, International, Inc., USA) combined with odorless vegetable oil to facilitate the application of the glue. The plastic film was fixed over the female inflorescences and left in place for a period of 24 hours starting at 6:00.

Life Cycle of the Insects

Eggs and immature stages of *E. kamerunicus*, *G. hybridus*, *C. constrictirostris* and *M. costaricensis* were collected from male flowers and kept in small plastic boxes (6 cm diameter) with a wet paper towel. Developmental changes were recorded daily. The working area and materials were sanitized with 0.02% formaldehyde. Insects were kept under natural light conditions at a temperature of approximately 20°C.

Pollen Carried by Potential Insect Pollinators

Elaeidobius kamerunicus, *G. hybridus*, *C. constrictirostris* and *M. costaricensis* were selected to evaluate their capacity for carrying pollen grains. Twenty specimens were collected from male inflorescences during anthesis and placed in Eppendorf tubes. Distilled water and Tween 20 were added (0.5 ml each), along with four drops of 7% safranin staining solution (Prada et al., 1998). The pollen grains were counted using a Neubauer chamber of 0.1 mm depth and 0.0025 mm^2 area (Marienfeld, Germany; Model: Fuchs-Rosenthal bright line) according to the methods described by Chinchilla and Richardson (1991) and Prada et al. (1998).

Data Analysis

Insect population percentages were calculated, and descriptive statistical analysis were used. Simpson's diversity index (D) was calculated to determine the diversity level and predominance of species associated with each oil palm type. This index was expressed as 1-D to facilitate analysis and to interpret the lowest values as indicating the dominance of one species and a value near 1.0 as indicating high diversity.

Analysis of similarities (ANOSIM) was performed in the software PAST, version 3.26, to compare insect species composition between different oil palm species in the Amazon basin (Site 1) and Pacific coast (Site 2).

For statistical analysis in pollen transport potential, an ANOVA was conducted to compare the different capacities of the insects to carry pollen. Furthermore, a Tukey test ($p<0.05$) was performed on the obtained data.

RESULTS AND DISCUSSION

The results regarding the insect pollinators found and their percentage incidence in female flowers are shown in Table 2.

Elaeis guineensis and *E. oleifera* showed a higher specificity of insects visiting the female flowers (Table 2). *Elaeis guineensis* flowers were visited by *E. kamerunicus* (a total of 2,576 specimens at the Amazon plantation and 1,429 at the Pacific coast plantation). This insect represented 100.0% of the whole pollinator population sampled among these palms. The insect diversity on palms was evaluated using Simpson's index, and the results showed that *E. guineensis* presented index values of 0.00 and 0.001 at all sampled locations and during the two seasons. These values indicate that female flowers are associated mostly with a unique pollinator species, i.e. *E. kamerunicus*. The fact that *E. kamerunicus* was introduced to the continent to pollinate *E. guineensis* might explain the affinity of this pollinator for the palm (Chinchilla et al., 1990; Syed, 1979). *Elaeis guineensis* was not visited by other Curculionidae species in high numbers, and during the dry season, this palm received a very limited number of *M. costaricensis* visits (16 specimens).

Elaeis oleifera attracted three individuals of *E. kamerunicus* (3.7%) at the Amazon basin plantation. The most common insect associated with its female flowers was *G. hybridus* at both sampling sites. Among the palms at the Pacific coast site, 404 specimens (31.5%) were collected during the rainy season, and 771 specimens (68%) were collected from the palms in the Amazonian basin during the dry season. This American native palm showed that *G. hybridus*, *C. constrictirostris* and *M. costaricensis* were associated with its female flowers in both locations, the Amazon basin and on the Pacific coast. The presence of *C. constrictirostris* was more common among the Amazon basin palms (362 specimens; 32%) during the dry season. Another species associated with *E. oleifera* was *M. costaricensis*: higher numbers were observed among the palms on the Pacific coast during the rainy season (734; 57.2%), but lower numbers were observed during the dry season (13; 28.3%). The presence of this species increased the values of Simpson's diversity index (1-D) in the coastal region. The higher variety of insects on *E. oleifera* might be explained by the coevolution between native insects and palms from America (Mondragón & Roa, 1985). *Elaeis oleifera* in comparison with *E. guineensis* and the OxG hybrids, achieved the highest 1-D index value in the Amazonian basin during the rainy season

Table 2

Pollinator population occurrence and Simpson's index (D) calculated for female flowers during anthesis

Season/ Site/ Palm species	Insect species									
	Eleidobius kamerunicus		*Grasidius hybridus*		*Couturierius constrictirostris*		*Mystrops costaricensis*		Total	Simpson's index (1-D)
Rainy season	n	(%)	n	(%)	n	(%)	n	(%)		
Amazonia										
Elaeis guineensis	152	(99.3)	1	(0.0)	0	(0.0)	0	(0.0)	153	0.01
Elaeis oleifera	3	(3.7)	59	(72.0)	20	(24.4)	0	(0.0)	82	0.74
TxA	99	(70.2)	42	(29.8)	0	(0.0)	0	(0.0)	141	0.42
CxL	253	(87.8)	34	(11.8)	1	(0.3)	0	(0.0)	288	0.21
TxL	213	(91.0)	19	(8.1)	2	(0.9)	0	(0.0)	234	0.17
Pacific coast										
Elaeis guineensis	1429	(100.0)	0	(0.0)	0	(0.0)	0	(0.0)	1429	0.00
Elaeis oleifera	0	(0.0)	404	(31.5)	144	(11.2)	734	(57.2)	1282	0.56
Unipalma	0	(0.0)	194	(100.0)	0	(0.0)	0	(0.0)	194	0.00
CxL	1	(5.9)	16	(94.1)	0	(0.0)	0	(0.0)	17	0.12
Dry season										
Amazonia										
Elaeis guineensis	2576	(100.0)	0	(0.0)	0	(0.0)	0	(0.0)	2576	0.00
Elaeis oleifera	0	(0.0)	771	(68.0)	362	(32.0)	0	(0.0)	1133	0.44
TxA	334	(85.4)	57	(14.6)	0	(0.0)	0	(0.00)	391	0.25
CxL	721	(86.6)	112	(13.4)	0	(0.0)	0	(0.00)	833	0.23
TxL	137	(92.6)	11	(7.4)	0	(0.0)	0	(0.00)	148	0.14

Table 2 *(Continued)*

Season/ Site/ Palm species	Insect species								Total	Simpson's index (1-D)
	Eleidobius kamerunicus		*Grasidius hybridus*		*Couturierius constrictirostris*		*Mystrops costaricensis*			
Pacific coast										
Elaeis guineensis	188	(92.2)	0	(0.0)	0	(0.0)	16	(7.8)	204	0.15
Elaeis oleifera	0	(0.0)	21	(45.7)	12	(26.1)	13	(28.3)	46	0.66
Unipalma	37	(34.3)	70	(64.8)	0	(0.0)	1	(0.9)	108	0.66
CxL	46	(38.3)	44	(36.7)	0	(0.0)	30	(25.0)	120	0.66

Note. TxA: Taisha x Avros; TxL: Taisha x LaMé; and CxL: Cuarí x LaMé
n: Number of specimens

(1-D = 0.74). The coevolution of native pollinators with this American palm may explain the choice of different insect species for this palm, as stated previously.

All female flowers from oil palm OxG hybrids received fewer insect visits than *E. guineensis* and *E. oleifera* flowers during anthesis. In general, hybrids present well-developed bracts that completely cover the female flowers, possibly hindering access to insects. These morphological characteristics might reduce the attraction of pollinator species (Syed, 1984).

Elaeidobius kamerunicus was the most numerous insects associated with OxG hybrid female flowers during anthesis in the Amazonian basin. The lowest percentage of *E. kamerunicus* among hybrids was 70.2% (99 specimens) for Taisha x Avros (TxA). In the Ecuadorian coastal region, hybrids such as Unipalma and CxL had a higher presence of *G. hybridus*, accounting for up to 100% of the sample, with 194 individuals on Unipalma during the rainy season. These observations could indicate that for this hybrid, the presence of *E. kamerunicus* is more strongly affected by its cultivation in areas that experience high rainfall than *G. hybridus* (Prada et al. 1998). Populations of the native insect *G. hybridus* on hybrids were similar in both studied regions, showing similar numbers during the two seasons. Female oil palm flowers in the Amazonian basin presented high quantities of associated insects during the rainy season (898 individuals) and dry season (5,081), but at the Pacific coastal plantation, there were more insects during the rainy season (2,922) and very few insects during the dry season (478). These results suggest that this insect could be used all year long as a pollinator of hybrids in commercial plantations. In fact, *E. kamerunicus* and *G. hybridus* seem to successfully coexist on OxG hybrids, although *E. kamerunicus* populations are higher. The female flowers of the hybrids do not attract *C. constrictirostris* or *M. costaricensis* in high numbers; consequently, these pollinator species remain less important for commercial plantations. Moreover, a study conducted by Labarca and Narváez (2009) mentioned that high numbers of *M. costaricensis* are detrimental for pollination because this species did not visit female flowers in large numbers; moreover, it fed on pollen from male flowers.

The CxL hybrid was studied in both sampling areas during the two seasons, and it hosted more insects than the other hybrids. *E. kamerunicus* showed a maximum of 721 (86.6%) specimens in the Amazon basin and *G. hybridus* showed a maximum of 112 specimens (13.4%) on the Pacific coast during the dry season. The higher number of insects during the dry season is apparently due to the presence of a higher number of male flowers during the dry season, which serve as food source (Appiah & Agyei, 2013; Teo, 2015). The highest numbers of *E. kamerunicus* on the CxL hybrid were recorded in the Amazon region (87.8 and 86.6% during the rainy and dry seasons, respectively), whereas on the coast, the percentages were 5.9 and 38.3% during the rainy and dry seasons, respectively. The second most common pollinator associated with the CxL hybrid was *G. hybridus*. Even though it was not as numerous as *E. kamerunicus*, it contributed to pollen dissemination among the female flowers. This pollinator is more abundant during the rainy season in the coastal region (94.1%), which contrasts with the pattern observed for *E. kamerunicus* (5.9%). This pattern of seasonal changes in population numbers may suggest that the pollination process could occur all year long. Simpson diversity values for the CxL hybrid were low (0.21 and 0.12) at the Amazon plantation, while on the Pacific coast, during the dry season, the diversity value reached 0.66, which was similar to that for *E. oleifera*. These numbers might indicate that anthesis and the chemical composition of the attractants of female flowers of CxL are closer to those of *E. oleifera* than *E. guineensis*. The TxL hybrid presented the lowest diversity value (1-D = 0.17 and 0.14), while Unipalma achieved a relatively high diversity value during the dry season (1-D = 0.66) but a very low value in the rainy season because only *G. hybridus* was recorded among the flowers. The OxG hybrid flowers showed high diversity values due to the presence of *E. kamerunicus* and *G. hybridus* on the female flowers during anthesis.

The ANOSIM test for insect composition on female flowers showed that most of R values were between 0 and 1 and were significant (Table 3). The analysis indicated that the insect species

Table 3

Analysis of similarities (ANOSIM) of insects on oil palm species female flowers, (Permutation N: 9999; p-*value <0.0001 and R=0.2732). Pairwise comparison according to the occurrence of* Elaeidobius kamerunicus*,* Grasidius hybridus*,* Couturierius constrictirostris *and* Mystrops costaricensis

Palm species (Groups)	TxA	CxL (Site 1)	TxL	*Elaeis guineensis* (Site 1)	*Elaeis oleifera* (Site 1)	Unipalma	CxL (Site 2)	*Elaeis guineensis* (Site 2)
CxL (Site 1)	0.042 (0.0685)							
TxL	-0.04892 (0.6202)	-0.02036 (0.5076)						
Elaeis guineensis (Site 1)	0.2543 (0.0468*)	0.4461 (0.0116*)	0.3016 (0.0696)					
Elaeis oleífera (Site 1)	0.4073 (0.0054*)	0.6857 (0.0008*)	0.8492 (0.0055*)	1 (0.0294*)				
Unipalma	0.238 (0.0001*)	0.3901 (0.0001*)	0.3266 (0.0004*)	0.3988 (0.0001*)	0.3264 (0.0033*)			
CxL (Site 2)	0.1197 (0.0033*)	0.3236 (0.0001*)	-0.002726 (0.4670)	0.1735 (0.0348*)	0.1109 (0.0848)	0.1528 (0.0005*)		
Elaeis guineensis (Site 2)	0.1364 (0.0141*)	0.162 (0.0068*)	-0.01154 (0.4691)	0.2802 (0.0492*)	0.9863 (0.0004*)	0.4547 (0.0001*)	0.3778 (0.0001*)	
Elaeis oleífera (Site 2)	0.4331 (0.0046*)	0.6993 (0.0008*)	0.8056 (0.0039*)	1 (0.0296*)	0.09375 (0.2868)	0.3311 (0.0015*)	0.1164 (0.0675)	0.9685 (0.0001*)

Note. The table shows the R value and the *p*-value (in brackets)
* Statistical significance between groups

composition in each of the female flower palm species and hybrids are more similar within each group than to insect species in the other palm species. The insect communities between *E. guineensis* and *E. oleifera* are different ($p \leq 0.05$) in both study sites. There are also differences in *E. guineensis* insect composition between the study sites, however, there were not differences in *E. oleifera* when comparing both study sites. The insect composition in the hybrid CxL in the Amazon basin (Site 1) did not show significant differences when compared with the hybrids TxA, TxL and *E. guineensis*. While the difference of CxL and TxL hybrids and *E. oleifera* is high. The difference of insect composition of *E. guineensis* and *E. oleifera* is high (R=1, p=0.0294). The insect composition in the hybrid CxL at the Pacific coast (Site 2) was not different from the hybrid TxL and *E. oleifera* (Table 3).

Male flowers of *E. guineensis* and *E. oleifera* in both sampling regions showed higher numbers of pollinator insects than the OxG hybrids. The highest numbers of total counted insects were 97,749 (100%) of *E. kamerunicus* on *E. guineensis* and 4,750 of *G. hybridus* (21.1%), 3,080 of *C. constrictirostris* (13.7%) and 14,678 of *M. costaricensis* (65.2%) on *E. oleifera* on the Pacific coast during the rainy season.

Male flowers of *E. guineensis* in the Amazon region showed a very high specificity, attracting *E. kamerunicus*, with a total of 8368 specimens during the rainy season (Table 4). The size of the population was similar during the dry season (8,517), with a diversity value of 0.00, showing that *E. kamerunicus* was the only insect that visited these flowers. In contrast, the pure *E. oleifera* material did not attract individuals of *E. kamerunicus* during the study. The massive populations of *E. kamerunicus* on *E. guineensis* could be limiting the arrivals of other pollinator species to this palm (Appiah & Agyei, 2013; Genty, 1985). *Grasidius hybridus* is present in high numbers on *E. oleifera* throughout the year in eastern Ecuador; however, this species duplicated its population during the dry season. There were 1,877 individuals in Amazonia during the rainy season and 3,519 individuals during the dry season. On the coast, the opposite pattern was observed: 2,560 insects were observed during the dry season and 4,750 were observed during the rainy season. The diversity values for this palm remained between 0.49 and 0.78, indicating that the insect populations are balanced on these oil palm species, perhaps due to species coevolution (Labarca & Narváez, 2009; Meléndez & Ponce, 2016).

The high affinity of each pollinator species for pure materials implies that in small commercial plantation fields, the numbers of male flowers should be high enough to replace manually assisted pollination with entomophilous pollination. Despite these facts, *E. kamerunicus* showed a lower affinity to male flowers of Unipalma, TxA and CxL hybrids, with maximum values of 890 (69.4%), 552 (94.4%) and 848 (31.6%) recorded insects, respectively. More studies of the morphological structures and chemical composition of male flowers

Table 4
Pollinator population occurrence on male oil palm flowers during anthesis. Simpson's index (D) of diversity calculated according to the insect population sampled

Season/ Site/ Palm species	Insect species: Elaeidobius kamerunicus		Grasidius hybridus		Couturierius constrictirostris		Mystrops costaricensis		Total	Simpson's index (1-D)
Rainy season	n	(%)	n	(%)	n	(%)	n	(%)		
Amazonia										
Elaeis guineensis	8368	(100.0)	1	(0.0)	0	(0.0)	0	(0.0)	8369	0.00
Elaeis oleifera	1	(0.0)	1877	(73.7)	669	(26.3)	0	(0.0)	2547	0.78
TxA	552	(94.4)	33	(7.1)	0	(0.0)	0	(0.0)	585	0.11
CxL	694	(92.9)	53	(5.6)	0	(0.0)	0	(0.0)	747	0.14
TxL	117	(94.4)	7	(5.6)	0	(0.0)	0	(0.0)	124	0.11
Pacific coast										
Elaeis guineensis	97749	(100.0)	0	(0.0)	0	(0.0)	0	(0.0)	97749	0.00
Elaeis oleifera	0	(0.0)	4750	(21.1)	3080	(13.7)	14678	(65.2)	27258	0.51
Unipalma	890	(69.4)	393	(30.6)	0	(0.0)	0	(0.0)	1283	0.43
CxL	458	(56.2)	357	(43.8)	0	(0.0)	0	(0.0)	815	0.49
Dry season										
Amazonia										
Elaeis guineensis	8517	(100.0)	2	(0.0)	0	(0.0)	0	0.00	8519	0.00
Elaeis oleifera	2	(0.0)	3519	(58.6)	2489	(41.4)	0	(0.0)	6010	0.49
TxA	94	(16.4)	369	(64.3)	111	(19.3)	0	(0.0)	574	0.52
CxL	848	(31.6)	1594	(59.3)	244	(9.1)	0	(0.0)	2686	0.55
TxL	35	(21.6)	122	(75.3)	5	(3.1)	0	(0.0)	162	0.39

Table 4 *(Continued)*

Season/ Site/ Palm species	Insect species								Total	Simpson's index (1-D)
	Elaeidobius kamerunicus		Grasidius hybridus		Couturierius constrictirostris		Mystrops costaricensis			
Pacific coast										
Elaeis guieensis	47760	(100.0)	0	(0.0)	0	(0.0)	0	(0.0)	47760	0.00
E.laeis oleifera	0	(0.0)	2560	(22.0)	1871	(16.1)	7183	(61.8)	11614	0.54
Unipalma	734	(39.2)	785	(41.9)	0	(0.0)	354	(18.9)	1873	0.64
CxL	334	(36.9)	570	(63.1)	0	(0.0)	0	(0.0)	904	0.47

Note. TxA: Taisha x Avros; TxL: Taisha x LaMé; and CxL: Cuarí x LaMé
n: Number of specimens

and pollen production in OxG hybrids are needed to explain their impact on insect populations during the rainy season.

In general, OxG hybrids showed similar quantities of *E. kamerunicus* at Site 2 (Pacific coast), CxL presented 458 individuals, and Unipalma was visited by 890 insects. These numbers suffered a reduction of 30.2% during the dry season for Unipalma and 19.3% for CxL. This pattern is very similar to that in the Amazonian region, where a reduction in *E. kamerunicus* during the dry season was observed on the CxL hybrids, from 92.9% (1-D=0.14) to 31.6% (1-D=0.55) for this pollinator. The reduction in the *E. kamerunicus* population seems to allow other species to occupy the flowers because the value 1-D= 0.55 indicates an increase in diversity on CxL.

Grasidius hybridus was assessed on OxG hybrids, and its population increased during the dry season on these plants. The population of this pollinator increased from 33 (7.1%) individuals to 369 (64.3%) on TxA, and from 53 (5.6%) to 1594 (59.3%) individuals on CxL in the Amazonian region. Likewise, on the coast, on the Unipalma hybrid, the population of this insect increased from 393 (30.6%) individuals to 785 (41.9%). These observations could be useful for the future management of pollinator populations and therefore increase production levels. It can be stated that *E. kamerunicus* proliferates during the rainy season, while *G. hybridus* proliferates during the dry season. This pattern is consistent with the findings described by Ponnamma (1999), Sánchez et al. (2004) and Syed (1984). Therefore, this information should be considered in commercial plantations where entomophiles pollination practices are used.

Couturierius constrictirostris is a pollinator restricted to *E. oleifera* materials and OxG hybrids. It increased in terms of its presence among male flowers during the dry season. This insect always remained less numerous than *G. hybridus*. In the Amazonian region, *C. constrictirostris* was not present on OxG hybrids during winter, but during the dry season, 111 (19.3%), 244 (9.1%) and 5 (3.1%) individuals were found on TxA, CxL and TxL, respectively. On *E. guineensis,* this pollinator was not observed during the collection procedures, and its populations on pure *E. oleifera* materials remained lower than those on *G. hybridus*. Its absence during the rainy season and its low numbers on OxG hybrids indicate that this insect as not a good candidate for use in assisted pollination programs on commercial plantations. In other works (Appiah & Agyei, 2013; Prasetyo et al., 2014; Teo, 2015; Yue et al., 2015), it was shown that populations of *E. kamerunicus* change with the weather conditions, suggesting that native insects could also be affected by this natural factor. The calculated diversity was higher on OxG hybrids than on *E. guineensis*, and this information suggests that hybrid male flowers have characteristics similar to their *E. oleifera* parents.

A fourth insect species was found in male inflorescences, i.e. *M. costaricensis*. The presence of this insect is restricted solely to the coastal region. It was present in high numbers in pure *E. oleifera* materials during the two sampling periods. Its presence was not recorded among the CxL hybrids, causing a decrease in their diversity index values (0.14 and 0.47). On Unipalma, the insect was not present during the rainy season, but it appeared during the dry season, with 354 specimens, and increased the diversity index value for this hybrid (0.64).

It is remarkable that male flowers provide a refuge for greater quantities of insects than female flowers; these insects are pollen feeders, and male flowers are their food source all year long.

The ANOSIM test for insect composition on male flowers showed that most of R values were between 0 and 1 and were significant (Table 5). The analysis indicated that the insect species composition in each of the male flower palm species and hybrids are more similar within each group than to insect species in the other palm species. The insect composition in the hybrid CxL in the Amazon basin (Site 1) did not show significant differences when compared with the hybrids TxL, TxA and *E. guineensis*. The insect composition on hybrid TxL did not show a significant difference with *E. oleifera*. The insect communities of *E. guineensis* in the Amazon basin (Site 1) and the Pacific coast (Site 2) were different ($p \leq 0.05$). While the insect composition in *E. oleifera* did not show significant differences between the two study sites (Table 5). The insect composition shows that *E. guineensis* is predominantly associated with *E. kamerunicus*, while *E. oleifera* is associated

Table 5

Analysis of similarities (ANOSIM) of insects on oil palm species male flowers (Permutation N: 9999; p-*value <0.0001 and R= 0.3308). Pairwise comparison according to the occurrence of* Elaeidobius kamerunicus, Grasidius hybridus, Couturierius constrictirostris *and* Mystrops costaricensis

Palm species (Groups)	TxA	CxL (Site 1)	TxL	*Elaeis guineensis* (Site 1)	*Elaeis oleifera* (Site 1)	Unipalma	CxL (Site 2)	*Elaeis guineensis* (Site 2)
CxL (Site 1)	-0.06291 (0.4873)							
TxL	-0.004842 (0.4137)	0.02949 (0.2284)						
Elaeis guineensis (Site 1)	0.2165 (0.0001*)	0.2343 (0.0001*)	0.3651 (0.0545)					
Elaeis oleífera (Site1)	0.2225 (0.0001*)	0.2336 (0.0001*)	0.3571 (0.039*)	1 (0.0268*)				
Unipalma	0.4278 (0.0001*)	0.3614 (0.0001*)	0.6496 (0.0001*)	1 (0.0001*	1 (0.0001*)			
CxL (Site 2)	0.3304 (0.0001*)	0.2693 (0.0001*)	0.7812 (0.0001*)	1 (0.0003*)	1 (0.0002*)	0.07399 (0.0321*)		
Elaeis guineensis (Site 2)	0.3476 (0.0002*)	0.306 (0.0001*)	0.9012 (0.0002*)	0.4529 (0.0085*)	1 (0.0005*)	1 (0.0001*)	1 (0.0001*)	
Elaeis oleifera (Site 2)	0.2393 (0.001*)	0.2653 (0.0016*)	0.1667) 0.144	1 (0.0636)	1 (0.0644)	1 (0.0011*)	1 (0.0018*)	1 (0.007*)

Note. The table shows the R value and the *p*-value (in brackets)
* Statistical significance between groups

with *G. hybridus*, *C. constrictirostris* and *M. costaricensis*. These results suggest that the insect composition on the hybrids have mixed characteristics from *E. guineensis* and *E. oleifera*, since the hybrid oil palm flowers attract insects that visit exclusively any of these two species. This may be due to mixed flower chemical attractant composition in the hybrids (Gomes et al., 2011).

Diurnal and Nocturnal Insect Behavior on Female Flowers

The results of observations of pollinator arrivals to female *E. oleifera* flowers are shown in Figure 1.

The curves show that *E. kamerunicus* is practically absent during the whole day on this palm regardless of the region. The opposite phenomenon was observed in the case of *G. hybridus*, which emerged in the morning and stopped moving before 17:00 in the afternoon, showing diurnal activity in the Amazonian region. A different behavior of this insect was observed on the coast, where *G. hybridus* showed crepuscular activity beginning at 17:00 and stopping before 20:00 during twilight. During its peak visiting time (18:40), visits surpassed 350 individuals; this is in contrast to the mobility observed at the Amazonian location, where the highest peak of arrivals accounted for approximately 150 individuals.

The behavior of *C. constrictirostris* was similar to that of *G. hybridus* on these *E. oleifera* palms, with the difference being that the populations were significantly reduced in comparison to those of *G. hybridus*. The highest population peaks were 53 individuals in the Amazonian region and 89 in the coastal region.

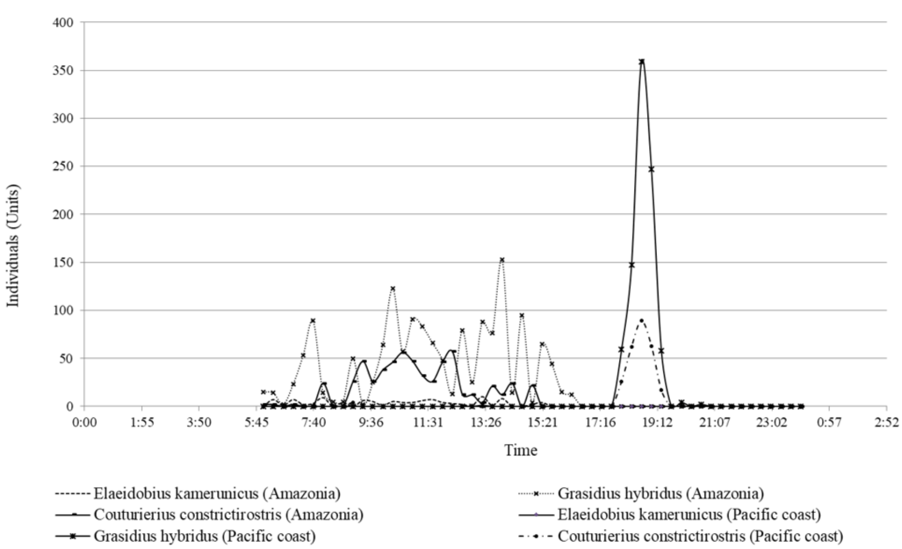

Figure 1. Diurnal and nocturnal insect activity on female *Elaeis oleifera* palm flowers

In Figure 2, the three pollinator insects show a diurnal activity pattern, and a certain temperature level (warm) is needed for their activity and mobility, since environmental factors and insect metabolism affect the mobility of pollinators that are active fliers and visit flowers at a specific time of the day ("daily activity window") (Herrera, 1990; Stone et al., 1999). In fact, Genty (1985) and Sánchez et al. (2004), in their studies showed that in moderate temperatures 22.3 and 30.1°C *E. kamerunicus* population proliferated and during the day, between 10:00 and 11:00 insects visit in high numbers the oil palm flowers. The reduced activity of *E. kamerunicus* on *E. oleifera* in comparison to *E. guineensis* could be further proof of an affinity for oil palm genetic characteristics. According to Jianjun et al. (2015), insects are linked to flowers according to anthesis phases and palm species. Figure 2 shows that *E. kamerunicus* was recorded in both geographical regions during the day.

The highest activity of *E. kamerunicus* was observed after 07:00 in the morning and before 16:00 in the afternoon. This insect showed a peak of activity, with a high number of insects (379 specimens), at 10:40 in the morning. These results are similar to those obtained by Hala et al. (2012), in studies done in Côte d´Ivoire (West Africa).

An oil palm hybrid (CxL) was observed in both the Amazonian and coastal regions. As shown in Figure 3, female flowers in anthesis are able to attract exotic (*E. kamerunicus*) and native pollinators (*G. hybridus* and *C. constrictirostris*). Nevertheless, in contrast to *E. guineensis*

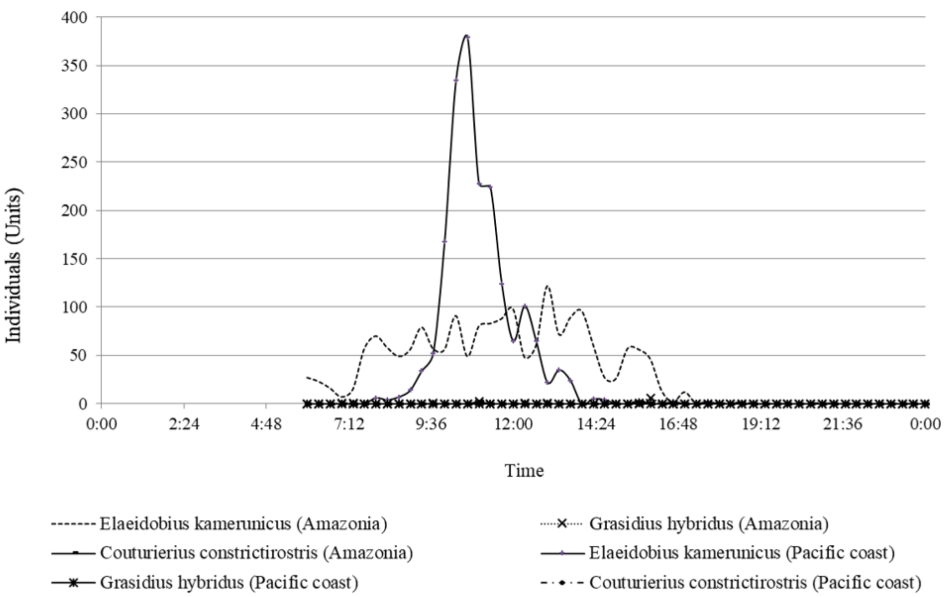

Figure 2. Diurnal and nocturnal insect activity on female *Elaeis guineensis* palm flowers

and *E. oleifera* (shown in Figures 1 and 2), the CxL hybrid flowers presented a limited number of insects. *E. kamerunicus* oscillated between 15 and 20 individuals during the highest peaks of activity (between 8:00 and 17:00). *Grasidius hybridus* was the most numerous insects during the twilight peak, reaching 86 specimens. The other native pollinator, *C. constrictirostris,* has a very similar behavior but is present in small numbers.

The presence of the three pollinator insects suggests that the genetic composition of hybrids could influence the production of certain compounds of chemicals created by the plant to attract pollinators to the flowers (Kirejtshuk & Couturier, 2010). Other hybrids were assessed: TxA and UNIPALMA. TxA was studied in the Amazonia region, and the other hybrid, UNIPALMA, was observed only on the coast. Hybrid TxA flowers attracted the three pollinator species in small numbers. On the one hand, the highest peak of *E. kamerunicus* was 16 individuals at approximately 09:30 in the morning. The maximal population of *G. hybridus* was 6 specimens presenting diurnal behavior. On the other hand, *C. constrictirostris* is even less numerous, with 4 individuals observed at 11:00 in the morning. The limited presence of pollinators during the whole day showed

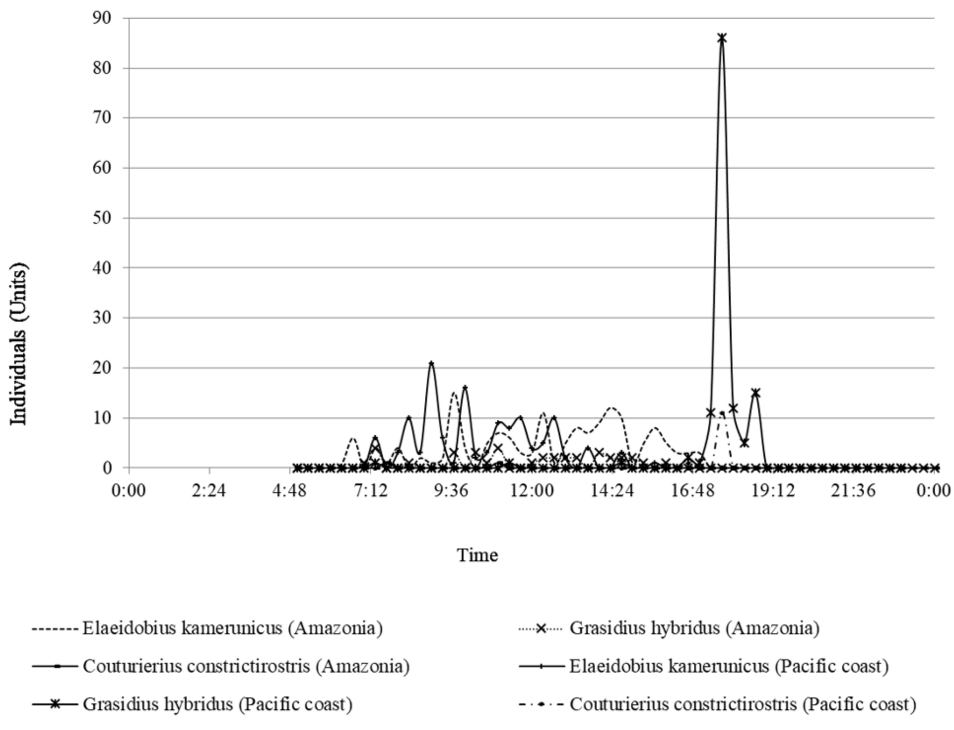

Figure 3. Diurnal and nocturnal insect activity on female flowers of CxL hybrid palms

shorter durations of insect activity on these flowers in comparison to that observed on *E. guineensis* and *E. oleifera* or CxL hybrids. The Unipalma hybrid presented a low number of insects (8 specimens) on female flowers arriving at twilight, between 18:20 and 19:20.

Pollen Transport Capacity of Pollinator Insects

The pollination capacity of each insect was assessed and is shown in Figure 4.

Elaeidobius kamerunicus was the pollinator that showed the highest pollen loading capacity per individual (8,273 pollen grains). This species is significantly different from the other three species studied in terms of the pollen loading capacity. This study presented a high standard deviation of the data, which is assumed to be a result of the fact that male and female insects were not analyzed separately. Male specimens present a high number of corporeal setae, which could increase the amount of pollen that is collected from male flowers (Syed, 1984). The second group of pollinators that showed a high capacity to transport pollen grains from male to female flowers was *G. hybridus* (3,517 grains) and *C. constrictirostris* (2,623 grains). Nevertheless, considering the population results, as *G. hybridus* numbers surpassed those of C. *constrictirostris* on female flowers, *G. hybridus* could be considered a better pollen carrier in oil palm plantations. A third statistical group appeared in this study corresponding to *M. costaricensis*, which was the insect that carried the least

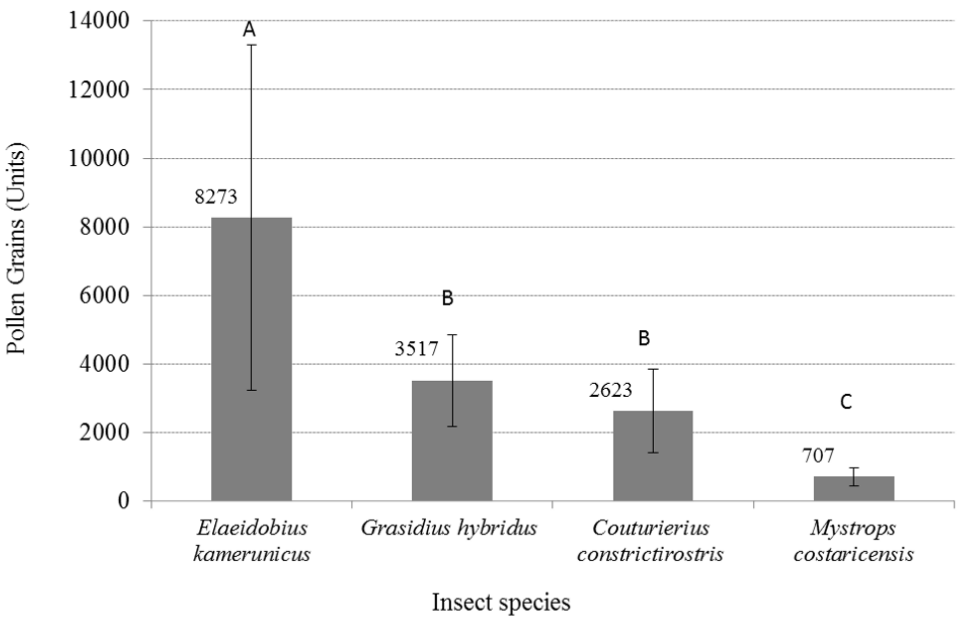

Figure 4. Pollen transport capacity per insect of four pollinator species associated with female flowers on oil palm. ANOVA comparing insects (*p*=0.000) and Tukey's test at a 95% confidence level

amount of pollen grains (707). The results could be influenced by several factors, including pollinator size, the presence of insect setae and population size (Ågren, 1996; Núñez et al., 2005; Prada et al. 1998; Teo, 2015). As is known, this insect is not a good pollen carrier (Labarca & Narváez , 2009) because of its size and body structure (Kirejtshuk & Couturier, 2010).

These studies were conducted in the Ecuadorian Amazonian and coastal regions, and no significant difference was found among the different insect transport capacities analyzed in each region (Figure 4). These results suggest that the insects are subjected to similar conditions among the male flowers in both regions.

Pollinator Life Cycle

The pollinator life cycles presented some variations among species. These results appear in Table 6.

Eggs and adults were collected from male flowers of oil palm species. The four pollinator species showed 3 larval stages, which were variable according to species. The longest life expectancy corresponded to *C. constrictirostris*, which presented 41.2±4.7 and 36.0±1.8 days in the Amazonia and coastal regions, respectively. *E. kamerunicus* and *G. hybridus* were similar in longevity in the different regions; the former pollinator showed 36.7±4.1 (Amazonia) and 30.3±2.8 days (Pacific coast). In the same way, *G. hybridus* showed

Table 6

Average pollinator life cycle values in the Ecuadorian Amazonia and coastal regions

Insect species	Developmental stages (days)						
	Egg	Larva 1	Larva 2	Larva 3	Pupa	Developmental cycle	Life span
Amazonia							
Elaeidobius kamerunicus	1.3±0.8	1.7±0.9	2.4±0.8	2.3±1.2	3.2±1.0	21.0±4.1	36.7±4.1
Grasidius hybridus	2.3±0.7	1.3±0.8	2.0±1.0	3.9±0.9	5.0±0.9	17.6±2.6	36.4±3.1
Couturierius constrictirostris	2.9±1.3	1.4±0.5	3.1±1.1	2.8±1.1	4.7±1.0	21.3±4.0	41.2±4.7
Pacific coast							
Elaeidobius kamerunicus	1.5±0.5	1.5±0.5	2.7±0.6	2.5±0.5	2.7±0.5	19.3±2.5	30.3±2.8
Grasidius hybridus	2.3±0.5	2.6±0.5	2.6± 0.5	3.6±0.5	3.5±0.5	17.3±1.1	31.8±0.8
Couturierius constrictirostris	2.6±0.5	2.7±0.5	2.7± 0.5	3.4±0.5	3.5±0.5	21.1±1.8	36.0±1.8
Mystrops costaricensis	2.7±0.4	1.6±0.5	2.4±0.5	3.5±0.5	2.6±0.5	13.8±1.2	26.5±1.2

a life expectancy of 36.4±3.1 and 31.8±0.8 in the two studied regions, respectively. The data obtained from the observations of *E. kamerunicus* are different from the results presented by Tuo et al. (2011), who found a life span of 59.18±8.53 days for this insect.

Mystrops costaricensis, a relatively small species of Coleoptera (Nitidulidae), presented the shortest life expectancy among oil palm pollinators (26.5±1.2 days). In the present study, the most numerous insects were *E. kamerunicus* and *G. hybridus*, which coexist and share their ecological niches in the male flowers of OxG hybrids and present good pollen grain transport capacity. The developmental cycles of both species were longer than 15 days. *E. kamerunicus* had a developmental cycle of 21.0±4.1 days in Amazonia and 19.3±2.5 on the coast; these results are within the range presented by Syed (1982) and Tuo et al. (2011). During this life cycle period, the pollinator is able to visit female flowers, pollinating them. In the same way, *G. hybridus* showed a developmental cycle of 17.6±2.6 days in Amazonia and 17.3±1.1 on the coast. According to Greenberg et al. (2005), warm temperatures can positively affect the female oviposition level or longevity in other Curculionidae species.

CONCLUSIONS

Oil palm species are associated with specific pollinator insects. *Elaeis guineensis*, material introduced from Africa, presented high affinity for hosting *E. kamerunicus* on its male flowers, and this insect was present in lesser quantities on female flowers. Only one species of pollinator was observed on flowers of *E. guineensis*, which was *E. kamerunicus*. On *E. oleifera*, the diversity of pollinators was higher, although the pollinator most associated with its flowers was *G. hybridus*, native to tropical America, suggesting coevolution between the palms and their pollinators. OxG hybrids are palms that are associated with high numbers of *E. kamerunicus* and moderate numbers of *G. hybridus*. These results should be considered in agronomic practices on commercial plantations because both insects could be useful for entomophilous pollination. The release of pollinators on plantations must consider population fluctuations during the rainy and dry seasons. In general, in Amazonia during the dry season, pollinators on female flowers are more numerous than they are during the rainy season, and the opposite was registered on the Pacific coast. An increase in the number of male flowers should permit the avoidance of agronomic practices such as manually assisted pollination, particularly in small production units, where the cost of such practices is high.

OxG hybrids offer refuge and food to three species established as their potential pollinators (*E. kamerunicus*, *G. hybridus* and *C. constrictirostris*) that seem to coexist successfully on oil palm plantations. Nevertheless, *E. kamerunicus* and *G. hybridus* are more numerous on hybrid palms, and they maintain their population numbers during the rainy and dry seasons. This pollinator diversity in hybrids could be related to their genetic origin, as they originate from African and American palms. However, more studies regarding this hypothesis are needed.

Regarding the evaluation of the mobility patterns of pollinators among female flowers, it can be stated that regarding *E. oleifera*, more activity of insects was observed during the day in Amazonia and during twilight on the coast, i.e. *G. hybridus* and *C. constrictirostris*, respectively. For *E. guineensis*, *E. kamerunicus* showed its highest peak of activity on the coast at 10:40, and in Amazonia, the insect maintains its activity the whole morning. This pattern shows the preference of this insect for diurnal activity.

The mobility behavior of insects on CxL hybrid female flowers showed moderated arrivals of the two species (*E. kamerunicus* and *G. hybridus*) all day long. However, the high frequency of arrival of *G. hybridus* on the coast showed that this insect prefers twilight conditions for shifting plants.

The life cycle results from the present work were very similar in Amazonia and on the coast. The good pollen-transport capacity of *E. kamerunicus* and *G. hybridus* (8,273 and 3,517 pollen grains, respectively) as well as the long life expectancy of *E. kamerunicus* (36.7 days in Amazonia and 30.3 days on the coast) and *G. hybridus* (36.4 days in Amazonia and 31.8 days on the Coast) indicate that these two species have potentially useful roles as pollinators on commercial plantations. It is also important to mention that these two insect species are able to coexist on the same oil palm OxG hybrids.

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