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The insects of the inflorescences of neotropical palms (Arecaceae): diversity and coevolution

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ABSTRACT

Introduction: Palms hold a significant position in the Amazonian flora. This study examines the insects associated with the inflorescences of various genera and species of neotropical palms, with a focus on those of local or national economic significance in the countries studied (Brazil, Ecuador, Peru).

Objective: To characterize the entomological community and analyze the diversity of insects in several species and genera of neotropical palm trees, and to demonstrate the coevolutionary relationships between insects and palm trees.

Methods: The study was conducted between 1990 and 2020, in the Brazilian, Ecuadorian, and Peruvian Amazon, in the Atlantic Forest of Brazil, and in the Peruvian Andes. Several thousand insects were collected in plastic bags or with an entomological net on the inflorescences of selected palm trees and anesthetized with insecticides. The insects were classified into families. A significant part was prepared on entomological pins, referenced, and sent to specialists for identification. Species new to science were described whenever possible.

Results: Consistent with previous studies, it is confirmed that the Nitidulidae (Mystropini) and Curculionidae (Derelomini) families are specialists in palm inflorescences. Additionally, among hemipterans, the families Miridae (Phylini) and Thaumastocoridae (*Discocoris*), as well as Staphylinidae beetles, exhibit a high degree of specialization. In contrast, the Dynastidae (Cyclocephala genus) and Apidae (Trigoninae), frequently cited as palm pollinators, are not specialized and should be considered as opportunistic.

Conclusion: The specific-level analysis presented here shows that a close coevolutionary relationship exists between certain insect species and specific genera or species of palms.

Key words: Amazonia; Atlantic Forest; Andes; pollinators.

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RESUMEN

Los insectos de las inflorescencias de palmas neotropicales (Arecaceae): diversidad y coevolución

Introducción: Las palmas ocupan un lugar destacado en la flora amazónica. Este estudio examina los insectos asociados con las inflorescencias de varios géneros y especies de palmas neotropicales, centrándose en aquellos de importancia económica local o nacional.
Objetivo: Caracterizar la comunidad entomológica y analizar la diversidad de insectos en varias especies y géneros de palmeras neotropicales, y demostrar las relaciones coevolutivas entre insectos y palmeras.
Métodos: El estudio fue conducido entre los años 1990 y 2020, en la Amazonía brasileña, ecuatoriana y peruana, en la Mata Atlántica de Brasil y en los Andes peruanos. Varios miles de insectos fueron recolectados en bolsas de plástico o con red entomológica en las inflorescencias de las palmeras seleccionadas y anestesiados con insecticidas. Los insectos fueron separados por familias. Una parte significativa fue preparada en alfileres entomológicos, referenciada y enviada a especialistas para su identificación. Las especies nuevas para la ciencia fueron descritas, cada vez que fue posible.
Resultados: Concordante con estudios previos, las familias Nitidulidae (Mystropini) y Curculionidae (Derelomini) son especialistas en inflorescencias de palmeras. Además, entre los hemípteros, las familias Miridae (Phylini) y Thaumastocoridae (*Discocoris*), así como los escarabajos Staphylinidae, exhiben un alto grado de especialización. En contraste, los Dynastidae (género *Cyclocephala*) y Apidae (Trigoninae), frecuentemente citados como polinizadores de palmeras, no están especializados y deben considerarse como oportunistas.
Conclusión: El análisis a nivel específico presentado aquí muestra que existe una estrecha relación coevolutiva entre ciertas especies de insectos y los géneros o especies de palmeras estudiados.

Palabras clave: Amazonía; Mata Atlántica; Andes; polinizadores.

INTRODUCTION

Palms hold a significant position in the Amazonian flora and have been studied by various authors (Bernal & Galeano, 2006; Dransfield & Beentje, 1996; Henderson et al., 1995; Kahn & de Granville, 1992; Kahn & Mejia, 1988; Kahn & Mejía, 1990; Lima et al., 1986; Uhl & Moore, 1977). It is estimated that there are currently 39 genera and 180 described species native to the Amazon, with the *Ceroxylon* genus, found beyond the western boundary of the Amazon (Kahn & de Granville, 1992), along with the palm *Attalea funifera* from the Brazilian Atlantic Forest (Voecks, 2002). Since the synthesis conducted by Henderson (1986), insects associated with palm inflorescences have been the subject of numerous publications due to their relevance to pollination. Barfod et al. (2011) provide a critical review of studies published over the past 25 years, particularly mentioning the negative role of certain insects in the reproductive success of palms. Additionally, Howard et al. (2001) as, more recently, Henderson (2024) published a synthesis of our knowledge on palm-associated insects.

The objective of this work is to characterize the populations of different insect species in relation to the various species and genera of the most common neotropical palms to demostrate an evident coevolution. Insects that clearly attack inflorescences before they open, such as *Foveolus* spp. (Curculionidae), *Dynamis* spp. (Dryophthoridae), and *Hemiphileurus* sp. (Dynastidae), are not covered in this study.

These results were obtained from over 20 years of observations by the authors in the Brazilian, Ecuadorian, and Peruvian Amazon. The palm species selected for the monitoring were those used by humans for food and medicine, as well as for various domestic purposes (Balick, 1984; Balslev et al., 2008; Brañas & Horna, 2011; Brokamp et al., 2011; Collazos & Mejía, 1988; Didonet & Ferraz, 2014; Graefe et al., 2013; Instituto de Investigaciones de la Amazonía Peruana [IIAP], 2005; Lima et al., 1986; Kahn, 1988; Mejía & Kahn, 1996; Moussa & Kahn, 1997; Moussa et al., 1996; Paniagua-Zambrana et al., 2017). Some of these are of great economic importance in local and national markets (Clement & Mora-Urpí, 1987; Delgado et al., 2007; Mejía, 1992; Barboza da

Silva et al., 2021). These results, many of which had not been previously published, are complemented by those of other authors published in the last 30 years.

MATERIALS AND METHODS

Study areas: The study was primarily conducted in the Amazon region: in Brazil, in the states of Pará, at Empresa Brasileira Agropecuaria (Embrapa) (Belém, 1°08'34" S & 48°43'16" W) and Amazonas (Manaus, Rio Urubu, 02°06' S & 60°02' W, Rio Negro community Terra Preta, 02°30'40" S & 60°52'34" W); in Ecuador, in the provinces of Sucumbíos (Shushufindi, 0°03'15" S & 77°06'58" W), Morona Santiago (San Rafael, l0°09'82" S & 77°16'71" W), Santo Domingo (Quinindé, Palmeras de Los Andes, 00°13'11" S & 79°06'58" W), and Cotopaxi (Otonga Reserve, 02°02'08" S & 78°51'04" W); in Peru, in the departments of Loreto (Iquitos, El Dorado research station of the National Agricultural Research Institute (INIA), 03°57'16" S & 73°24'41" W, Jenaro Herrera, Instituto de Investigaciones de la Amazonía Peruana (IIAP) research station, 04°54'14" S & 73°40'50" W (IIAP), Iquitos-Nauta road 04°32' S & 73°33' W, Allpahuayo Reserve, 03°97'89" S & 73°42'19" W, Yanapuma site, 04°23'44" S & 73°34'23" W, Nauta city (la Circular, 04°39' S & 73°35' W), Maniti(Santa María, 03°36" S & 72°57' W) and Rio Yarapa near Puerto Miguel 73°23'13" W & 04°29'21" S, in the department of Madre de Dios, Puerto Maldonado 12°50' S & 59°20' W, and in the department of San Martín, Uchiza (Palmas del Espino plantation 08°27'33" S & 76°27'48" W). Outside the Amazon, sampling was conducted in the Atlantic Forest, in the state of Bahia (Brazil: Ilheus-Itabuna 14°47' S & 39°21' W), and in the Peruvian Andes, department of Amazonas (Ocol, 2 370 m altitude 06°15'48"S & 77°34'41" W).

Collection methods and preservation of entomological material: Inflorescences in anthesis were collected in transparent plastic bags, whose dimensions were adapted to those of the inflorescences. In some cases, only part of the inflorescence was collected due to its large size (e.g., *Mauritia flexuosa*), or directly with an entomological net. This allowed for the collection of most insects present in the targeted part of the plant. Sometimes it was necessary to climb the stipe to reach the inflorescence. Insects were quickly anesthetized with insecticidal spray and placed in the shade to avoid tissue swelling. In the laboratory or a suitable location, the insects were separated from the plant material present in the sample (anthers and other plant debris) and placed in 70 % alcohol with proper references. Later, insects were sorted by families, and representative samples were sent to specialists for specific identification. New species for science were described. It should be noted that in the case of the Curculionidae Derelomini, which are difficult to identify, not all specimens were identified at the species level; some even require a revision of several genera (O'Brien, pers. comm., 2014). In these cases, they were labelled with a letter for identification purposes.

Identifications and material deposits: The identified species are housed in the collections of the following museums and laboratories: Museum of Entomology at the National Agrarian University La Molina (Peru), Peruvian Amazon Research Institute, Iquitos (Peru), National Museum of Natural History (Paris), entomological collection of the Empresa Brasileira de Pesquisa Agropecuaria (Embrapa, Belém, Brazil), entomological collection of the National Institute for Amazonian Research (INPA, Manaus, Brazil), Museum of Natural History of Rio de Janeiro (Brazil), the collection was destroyed due to the fire of 2 September 2018, private collection of Roberto Pace (Verona, Italy), private collection of Charles O'Brien (Green Valley, Arizona, United States of America) now in the collection of the Arizona State University, (Tempe, United States of America), Museum of Natural History of Saint Petersburg (Russia). Some genus and species names of palms have been modified during this work. The names mentioned are those from the time of collection. Synonyms are provided

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in parentheses. The palms were identified by F. Kahn and K. Mejia, botanists and specialists in neotropical palms.

RESULTS

The results are organized by palm genera and species, followed by notable insects. Given that the taxonomy of palms has been modified, we found it preferable to maintain the identifications as they appear on the collection labels, indicating synonyms here. The *Astrocaryum* genus has been extensively reviewed by Kahn (2008) and Kahn and Millán (1992). The *Attalea* genus has been reviewed by Zona (2002) and Pintaud (2008). Balick (1986) reviewed the *Oenocarpus* or *Jessenia* complex.

The palms

***Attalea* spp. (= *Scheelea*, *Orbignya*, *Maximiliana*):** The genus was reviewed by Pintaud (2008) and Zona (2002). Two species were studied: *A. funifera* Mart. Ex Spreng. in the Atlantic Forest (Brazil) and *Attalea plowmanii* (Glassman) in the Allpahuayo Reserve area (Iquitos, Peru).

***Astrocaryum* subgender, *Monogynanthus* and *A. subg. Pleiogynanthus*:** The genus was reviewed by Kahn and Millán (1992), and we sampled the following species:

- Subgenus *Monogynanthus*: *Astrocaryum gratum* Kahn & Millan, *Astrocaryum javarense* Trail ex Drude, Mart., *Astrocaryum macrocalyx* and *Astrocaryum urostachys* Burrett.
- Subgenus *Pleiogynanthus*: *Astrocaryum aculeatum* Meyer, *Astrocaryum jauari* Martius, *Astrocaryum chambira* Burrett, *Astrocaryum vulgare* Martius. Consiglio and Bourne (2001) reported about a single inflorescence of *A. vulgare* in Guyana, with nearly 30 000 Nitidulidae (possibly Mystropini).

Padilha de Oliveira et al. (2003) studied the pollination biology of *A. vulgare* in Brazil (Belém), and T. Peyret (nov. 2000, unpublished) studied *A. urostachys* in Ecuador. Several species of the genus *Celetes* develop in young fruits: in a count on *A. javarense* in Iquitos and *A. gratum* in Puerto Maldonado, we found between 95 and 100 % of fruits parasitized (Table 1).

Table 1

Parasitism of the female flowers of *Astrocaryum javarense* and *Astrocaryum gratum* by the genus *Celetes* sp. (Derelomini) in three locations in Peru.

Palm Locality	Total number of female flowers	Number of parasitized flowers	Formed fruits	*Celetes* spp.
A. javarense (Loreto, Tamshiyacu) Inflorescence				
A	342	322	20	sp. 1
B	301	301	0	sp. 1
C	367	367	0	sp. 1
A. javarense (Loreto, Santa Cecilia) Inflorescence				
A	377	303 + 74 (*)	0	sp. 1
B	111	98 + 13 (*)	0	sp. 1
A. gratum (Madre de Dios, Puerto Maldonado Inflorescence				
A	414	414	0	sp. 1
				sp. 2
				sp. 3

(*) second number: undeveloped fruits, but with doubts about parasitism.

***Bactris gasipaes* Kunth:** From an economic perspective, *B. gasipaes* is the most studied species (Beach, 1984; Clement & Mora-Urpí, 1987; Essig, 1971; Graefe et al., 2013; Mora-Urpí & Mexzon, 1996; Mora-Urpí & Solís, 1980; Oviedo et al., 2020). We sampled it in several locations in Brazil, Ecuador, and Peru.

B. gasipaes is characterized by the presence of *Anomalocornis couturieri* (Miridae) (see Heteroptera below), *Mystrops bactrii* (Nitidulidae), *Phyllotrox* spp., and several other species of Derelomini (Listabarth, 1996). Mora-Urpí and Solís (1980) reported *Andranthobius* (= *Derelomus*) *palmarum*.

Ceroxylon quindiuense (H. Karst.) H. Wendl., an Andean palm, has been reviewed by Galeano et al. (2008), Sanín and Galeano (2011), and Sanín et al. (2013). The entomological fauna of *C. quindiuense* presents significant particularities, including the presence of the Derelomini *Terioltes mejiai* (Perrin & Couturier, 2024), six species of Mystropini (Kirejtshuk & Couturier, 2009) (Table 2), and the Cyclocephalinae *Ancognatha vulgaris* Arrow. In a sampled male inflorescence, we estimated a total of around 250 000 insects. Carreño-Barrera et al. (2019) and Carreño-Barrera (2020) studied the entomological fauna of *Ceroxylon parvifrons* (Engel.) H. Wendl., *Ceroxylon ventricosum* Burret, and *Ceroxylon vogelianum* (Engel.) H. Wendl. in Colombia. They reported *A. vulgaris* and seven unidentified species of Staphylinidae Aloeocharinae. Regarding the Nitidulidae Mystropini, they found the same species as we did on *C. quindiuense*, confirming the specialization of these insects in the *Ceroxylon* genus. Balhara et al. (2013) studied the floral structure of *Ceroxylon ceriferum* in Venezuela.

- In *Oenocarpus bataua* in Ecuador and Perú (Pace, 2010).
- Amazoncharis: 3 unidentified species in *Phytelephas seemanni* in Colombia (Bernal & Ervik, 1996).
- In *Orbignya polysticha* (Attalea) (Pace, 2010).

***Elaeis oleifera* (Kunth) Cortés and *Elaeis guineensis* Jacq.:** *E. guineensis*, the African oil palm, was included in this study due to its close relationship with *E. oleifera*. Three species of Derelomini native to Africa *Elaeidobius kamerunicus* Faust, *Elaeidobius singularis* Faust, and *Elaeidobius plagiatus* F. were intentionally introduced to this palm to improve pollination and, thus, productivity (Genty et al., 1986; Auffray et al., 2017). A fourth species, *Elaeidobius subvittatus* Faust, like the other three, is found on *E. guineensis*. It was likely introduced much earlier, possibly during the slave trade. The species was described by Bondar as *Elaeisae* in 1942 (O'Brien & Woodruff, 1986). Haran et al. (2023) also recently reviewed the genus and described two new species of African *Elaeidobius*. *E. oleifera* has its own fauna and does not host any *Elaeidobius* species, with the Derelomini *Grasidius hybridus*, *Grasidius* sp., *Couturierius carinifrons*, and *Couturierius constrictirostris* being strictly dependent on *E. oleifera* (O'Brien et al., 2004; Beaudoin-Ollivier et al., 2017).

Regarding the hybrid *E. guineensis* × *E. oleifera*, Meléndez and Ponce (2016) demonstrated that the first-generation hybrid attracts Derelomini from both species. However, the backcross *E. guineensis* × *E. oleifera* × *E. guineensis* loses its appeal to Derelomini associated with *E. oleifera* (Couturier et al., 1996) (Table 3).

***Euterpe oleracea* Engel. and *Euterpe precatoria* Mart.:** Campbell et al. (2018) and Bezerra et al. (2020) show that 90 % of pollination is carried out by native bees (Table 4).

Different species of *Cyclocephalini* known in palm inflorescences:

- *A. vulgaris* arrow on *C. quindiuense*.
- *Cyclocephala amazona* L. on *A. macrocalyx*, *B. gasipaes*, *O. bataua*, *M. flexuosa*, *Phytelephas tenuicaulis*, and *E. oleifera*.
- *Cyclocephala boulardii* Dechambre on *Bactris hirta* (Küchmeister et al., 1998).
- *Cyclocephala collaris* Burmeister on *E. oleifera*.

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Table 2
Presence of different species of beetles: Curculionidae, Nitidulidae, and Staphylinidae in the inflorescences of palm trees.

	Astrocaryum subgenera *Monogynanthus*	*Astrocaryum* subgenera *Pleiogynanthus*	*Attalea* spp.	*Bactris gasipaes*	*Bactris maraja, B. monticola*	*Ceroxylon quindiuense*	*Elaeis oleifera*	*Elaeis guineensis*	*Euterpe oleracea, E. precatoria*	*Mauritia flexuosa, M. carana*	*Oenocarpus* spp.	*Phytelephas tenuicaulis*	*Socratea* sp. *Iriartea* sp.	*Syagrus* spp.
Curculionidae														
Anchylorhynchus spp.	0	0	0	0	0	0	0	0	0	0	++	0	0	++
Celetes spp. AA	+++											0		
Celetes spp. BB		+++										0		
Couturierius spp.	0	0	0	0	0	0	+++	0	0	0	0	0	0	0
Grasidius spp.	0	0	0	0	0	0	+++	0	0	0	0	0	0	0
Elaeidobius spp.	0	0	0	0	0	0	0	+++	0	0	0	0	0	0
Terires sp.									0					
Terires minusculus	++	++	0	0	0	0	0	0	0	0	0	0	0	0
Phyllotrox spp.	+	0							0					
Nitidulidae														
Anthepurops depressa	0	0	0	0	0	0	0	0	0	0	0	+++	0	0
Anthocorcina subcalva	0	0	0	0	0	0	0	0	0	0	0	0	+++	0
Mystrops astrocaryi	+++	0	0	0	0	0	0	+	0	0	0	0	0	0
M. atrata	0	0	0	0	0	0	0	0	0	0	0	+++	0	0
M. bactrii	0	0	0	+++	0	0	0	0	0	0	0	0	0	0
M. beserrai	0	0	0	0	0	0	+	0	0	0	+++	0	0	0
M. costaricensis	0	0	0	0	0	0	+++	+++	0	0	0	0	0	0
M. dalmasi	0	0	0	0	0	0	0	0	0	+++	0	0	0	0
M. debilis (1)	0	0	+++	0	0	0	0	0	0	0	0	0	0	0
M. delgadoi	0	0	0	0	0	+++	0	0	0	0	0	0	0	0
M. discoidea	0	0	0	0	0	0	0	0	0	0	0	0	0	0
M. gigas	0	0	0	0	0	++	0	0	0	0	0	0	0	0
M. hisamatsui	0	0	0	0	0	++	0	0	0	0	0	0	0	0
M. kahni	+++								0					
M. komissari	0	0	0	0	++	0	0	0	0	0	0	0	0	0
M. lobanovi	0	0	0	0	0	0	0	0	0	0	0	0	+++	0
M. neli	0	0	0	0	0	+++	0	0	0	0	0	0	0	0
M. pectoralis	0	+++	0	0	0	0	0	0	0	0	0	0	0	0
M. pulchra	0	0	0	0	0	+++	0	0	0	0	0	0	0	0
M. rotundula	0	0	0	0	0	+++	0	0	0	0	0	0	0	0

	Astrocaryum subgenera *Monogynanthus*	*Astrocaryum* subgenera *Pleiogynanthus*	*Attalea* spp.	*Bactris gasipaes*	*Bactris maraja, B. monticola*	*Ceroxylon quindiuense*	*Elaeis oleifera*	*Elaeis guineensis*	*Euterpe oleracea, E. precatoria*	*Mauritia flexuosa, M. carana*	*Oenocarpus* spp.	*Phytelephas tenuicaulis*	*Socratea* sp. *Iriartea* sp.	*Syagrus* spp.
M. squamae	+++	0	0	0	0	0	0	0	0	0	0	0	0	0
M. vasquezi	0	0	0	0	0	0	0	0	0	0	+++	0	0	0
Platychorodes adentatus	0	0	0	0	0	0	0	0	0	0	0	+++	0	0
Staphylinidae														
Delgadobius amazonensis	0	0	0	0	0	0	0	0	+	+++	+	0	0	0
Amazoncharis spp.	-	-	-	-	-	0	-	-	0	-	-	+++(2)	-	-
Plesiomalota palmarum	-	-	++(3)	-	-	-	-	-	0	-	-		-	
Arecaceopora spp.	0	0	0	0	0	0	0	0	0	0	0	+++	0	0
Oussipaliaglossa couturieri	0	0	+++	0	0	0	0	0	0	0	0	0	0	0
Atheta chunitayensis									0		++			
Atheta couturieri	-	-	-	-	-	-	-	-	0	-	-	++	-	-
Phoinixiusa ecuadorensis	-	-	-	-	-	-	-	-	0	-	++(1)	-	-	-
Feluva pichinchaensis	-	-	++(3)	-	-	--	-	-	-	-	-	-	-	-

0 Absence, + Less than 10 in an inflorescence, they are considered erratic, ++ Between 10 and 100 in an inflorescence, +++ More than 100 in an inflorescence, - Not confirmed.

- *Cyclocephala couturieri* Dechambre on *Astrocaryum* sp. aff. *murumuru*.
- *Cyclocephala decolorata* Herbst on *A. urostachys*, *O. bataua*, and *M. flexuosa*.
- *Cyclocephala distincta* Burmeister on *B. gasipaes*, *E. oleifera*, and *Oenocarpus mapora*.
- *Cyclocephala forsteri* Endrödi on *Acrocomia aculeata* (Scariot et al., 1991).
- *Cyclocephala goetzi* Endrödi 1966 on *A. urostachys*.
- *Cyclocephala guianae* Endrödi 1969 on *M. flexuosa*.
- *Cyclocephala lunulata* Burmeister on *A.* sp. aff. *murumuru*.
- *Cyclocephala marginalis* Kirsch on *A. urostachys*, *O. bataua*, and *Attalea microcarpa* (Küchmeister et al., 1998).
- *Cyclocephala rondoniana* Ratcliffe on *Astrocaryum* sp. and *Attalea attaleoides* (Küchmeister et al., 1998).
- *Cyclocephala stictica* Burmeister on *A. urostachys*.
- *Cyclocephala undata* Olivier on *B. hirta* (Küchmeister et al., 1998).
- *Cyclocephala variipenis* Miki on *A. urostachys*.
- *Mimeoma signatoides* Höhne on *A. urostachys*, *O. bataua*, and *O. mapora*.

Lepidocaryum tenue Mart., a small understory palm with very inconspicuous inflorescences, does not host any specialized and generalist fauna in the different places where it has been monitored.

***M. flexuosa* L. f. and *Mauritia carana* Wallace:** *M. flexuosa* is a dioecious palm abundant in the Amazonian floodplains (aguajales). We sampled *M. flexuosa* in Brazil, Ecuador, and Peru. Exploited for its fruits (Delgado et al., 2007), the "aguaje" hosts a very specific fauna, primarily the Miridae: Phylini: *Alvarengamiris alvarengai*, *Alvarengamiris kemberi*, *Alvarengamiris margaridae* (Peyret et al., 2005), the Staphylinidae *Delgadobius amazonensis* (Chani-Posse & Couturier, 2012), the Thaumastocoridae *Discocoris drakei* (Couturier et al., 1998),

Table 3
Number of individuals collected per inflorescence of different pollinating Derelomini species in *E. guineensis*, *E. oleifera*, the hybrid *E. guineensis* × *E. oleifera*, and the backcross *E. guineensis* × (*E. oleifera* × *E. guineensis*) at the 'Urubu River' plantation, Embrapa, Manaus, Brazil, October 1994.

Male inflorescence of	*Elaeidobius kamerunicus*	*Elaeidobius Subvittatus*	*Grasidius hybridus*	*Couturierius carinifrons y Couturierius constrictirostris*
Elaeis guineensis	515	17		
Elaeis oleifera			1 465	194
Elaeis oleifera			280	29
Elaeis oleifera			180	385
Elaeis oleifera. (end of anthesis)			7	1
Elaeis oleifera			648	4
Elaeis oleifera			937	319
E. guineensis x E. oleífera	1 567		2 250	3
E. guineensis x E. oleífera	3 521	1	940	20
E. guineensis x E. oleifera x guineensis	234			
E. guineensis x E. oleifera x guineensis	8 661			

Table 4
Presence of different species of Apidae in the sampled palm trees.

Genus, species	Host plant	Country, province, department or state, locality (Collectors, Authors)
Apis mellifera L	*Mauritia flexuosa*	Perú, Loreto, Santa Cecilia, (KM, 1991)
Melipona ebúrnea Friese	*Mauritia flexuosa*	Perú, Loreto, Santa Cecilia, (KM, 1991)
Melipona fasciata Cockerell	*Phytelephas seemanni*	Ecuador
Partamonia epiphytophila Pedro & Camargo	*Mauritia flexuosa*	Perú, Loreto, Santa Cecilia (KM, 1991)
Partamona vicina Camargo	*Euterpe oleracea*	Brasil, Para, Belem Abaetetuba (GC, FK, 1996)
Ptilotrigona lurida Smith	*Astrocaryum acaule*	(Küchmeister et al., 1998)
Tetragona clavipes Fab.	*Mauritia flexuosa*	Perú, Loreto, Santa Cecilia (KM, 1991)
Trigona amalthea Olivier	*Mauritia flexuosa*	Perú, Loreto, Iquitos (KM, 1991, 1992)
Trigona amalthea Olivier	*Phytelephas seemanni*	Ecuador Bernal & Ervik
Trigona amazonensis Ducke	*Ceroxylon quindiuense*	Perú, Amazonas, Ocol (GC, CD, KM, 2007)
Trigona amazonensis Ducke	*Attalea funifera*	Brasil, Para, Ilheus (GC, JD, 1993)
Trigona amazonensis Ducke	*Maximiliana maripa (Oenocarpus)*	Brasil, Amazonas, Manaus (GC, 1997)
Trigona cf. *brauneri* Cockerell	*Astrocaryum gynacanthum*	Brasil, Amazonas, Manaus, Küchmeister et al., 1998)
Trigona cf. *brauneri* Cockerell	*Attalea attaleoides*	Brasil, Amazonas, Manaus Küchmeister et al., 1998)
T. chanchamayoensis Schwarz	*Phytelephas seemanni*	Ecuador (Bernal & Ervik, 1996)
Trigona dellatorreana Friese	*Euterpe oleracea*	Brasil, Para, Belem Abaetetuba (GC, FK, 1996)
Trigona dellatorreana Friese	*Mauritia flexuosa*	Perú, Loreto, Santa Cecilia (KM, 1991)
T. ferricaudata Cockerell	*Phytelephas seemanni*	Ecuador (Bernal & Ervik,1996)
Trigona fuscipennis Friese	Unidentified palm	Brasil, Para, Manacaparamirim (GC, FK 1996)
Trigona hyalinata Lepeletier	*Elaeis oleífera*	Brasil, Bahia, Ilheus (GC, JD, 1993)
T. hyalinata Lepeletier	*Phytelephas seemanni*	Ecuador (Bernal & Ervik, 1996)
T. nigerrima Cresson,	*Phytelephas seemanni*	Ecuador (Bernal & Ervik, 1996)
T. schultesii Friese	*Phytelephas seemanni*	Ecuador (Bernal & Ervik, 1996)
T. spinipes Fab.,	*Phytelephas seemanni*	Ecuador (Bernal & Ervik, 1996)
T. williana Friese,	*Phytelephas seemanni*	Ecuador (Bernal & Ervik, 1996)
Trigona williana Friese	*Attalea microcarpa*	(Küchmeister et al., 1998)
T. fulviventris Guérin-Menneville	*Attalea microcarpa*	(Küchmeister et al., 1998)

Collectores: GC: G. Couturier, MJC: M. J. Cravo, JD: J. Delabie, FK: F. Kahn, KM: K. Mejía.

and the Nitidulidae *Mystrops dalmasi*. All of these species reproduce on the male inflorescence where they are very abundant. The Derelomini have not been identified by us, but Núñez-Avellaneda and Carreño-Barrera (2013) studied them in greater detail.

***Oenocarpus* (= *Jessenia*):** The species considered are *O. bataua* Mart., *Oenocarpus bacaba* Mart., *Oenocarpus balickii* Kahn, *Oenocarpus distichus* Mart., *O. mapora* H. Karst., and *Oenocarpus multicaulis* Spruce. All the sampled species exhibit the same characteristics with a highly specialized fauna (Tables 2, Table 5). The characteristic insects include the Thaumastocoridae *D. drakei* Slater & Ashlock, present in all the species considered, as well as various species of *Anchylorhynchus* (*Anchylorhynchus bicarinatus* O'Brien on *O. mapora* in Belém, Brazil, Embrapa). The latter are also present in different species of *Syagrus* studied by other authors (see "Curculionidae" below). Núñez-Avellaneda et al. (2015) on three species of *Oenocarpus*, Núñez-Avellaneda and Rojas-Robles (2008) on *O. bataua*, Valente & Madeiros (2013), Silberbauer-Gottsberger et al. (2013) and de Melo-Valente and Souza de Medeiros (2013), report various species of *Anchylorhynchus* in several species of *Syagrus* (see below). We found different species of *Anchylorhynchus* in all the sampled species of *Oenocarpus*.

***Phytelephas seemannii* O.F. Cook, *P. tenuicaulis* (Barfod) A. J. Hend.:** *P. seemannii* has been studied in Ecuador by Bernal & Ervik (1996), Barfod et al. (1987), Ervik et al. (1999), while *P. tenuicaulis* was studied by us in Peru. *P. tenuicaulis* is a multi-stemmed dioecious palm of the lowlands (Costa et al., 2009). The male inflorescences exhibit a great diversity of insects (Table 2, Table 5), most of which develop on them. In *P. tenuicaulis*, we found Mystropini with three species, (Kirejtshuk & Couturier, 2010), an unidentified species of Derelomini, not found on other palms, as well as Drosophilidae larvae and Ptiliidae adults during inflorescence decay. It is noteworthy that we did not observe any insects on the female

Table 5

Presence of different species of heteropterans in the inflorescences of palm trees.

	Astrocaryum subgénero *Monogynanthus*	*Astrocaryum* Subgénero *Pleiognanthus*	*Attalea* spp.	*Bactris gasipaes*	*Bactris maraja* *B. monticola*	*Ceroxylon quindiuense*	*Elaeis oleifera*	*Elaeis guineensis*	*Mauritia flexuosa*, *M. carana* *Mauritiella* sp.	*Oenocarpus* spp.	*Phytelephas tenuicaulis*	*Socratea* spp.	*Syagrus* spp.
Miridae Fulvini													
Anomalocornis spp.	+++	+++	0	+++	-	0	0	0	0	0	0	0	0
Alvarengamiris spp.	0	0	0	0	0	0	0	0	+++	0	0	0	0
Fulvius sp.	++	0	0	0	0	0	0	0	0	0	0	0	0
Thaumastocoridae													
Discocoris drakei	0	0	0	0	0	0	0	0	0	+++	0	0	0
D. fernandezi	0	0	0	0	0	0	0	0	+++	0	0	0	0
Pentatomidae													
Lincus spp.	++	-	0	0	0	0	+++	+++	+	0	0	-	-

0 absence, + less than 10 in an inflorescence, they are considered erratic, ++ between 10 and 100 in an inflorescence, +++ more than 100 in an inflorescence, - not confirmed.

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inflorescences, either during the day or at night. However, Bernal and Ervik (1996) report several species visiting the female inflorescences of *P. seemannii* in Ecuador, but in much lower numbers compared to the male inflorescences.

***Syagrus* spp.:** This genus was not sampled by us. We mention it here because it is the exclusive host, along with the genus *Oenocarpus*, of the Derelomini *Anchylorhynchus*. In *Syagrus cocoides* Mart., *Syagrus vermicularis* Noblick, and *Syagrus sancona* (Kunth) H. Karsten, Costa et al. (2009), de Melo-Valente and Souza de Medeiros (2013), and Valente and Madeiros, (2013) report many species of Curculionidae Derelomini, including various species of *Anchylorhynchus* (see below). Costa et al. (2009), Silberbauer-Gottsberger et al. (2013), de Melo-Valente and Souza de Medeiros (2013), report different species in several species of *Syagrus* (see below, insects). We found different species of *Anchylorhynchus* in all the sampd species of *Oenocarpus*. Therefore, this genus of Derelomini is clearly dependent on *Syagrus* and *Oenocarpus*.

The insects

Dynastidae (Coleoptera): Unlike other common insect groups in neotropical palm inflorescences that are highly specialized, such as Curculionidae Derelomini, Nitidulidae Mystropini, or Miridae Phylini, Dynastidae shows no apparent specialization (Table 6). Adult insects are attracted to palm inflorescences from the moment the bract opens and anthesis begins. Several authors have demonstrated that they contribute to pollination, however, Mora-Urpí and Solís (1980), Scariot et al. (1991), as cited by Barfod et al. (2011), consider their role to be secondary, with a limited function in pollen transfer. Moore and Jameson (2013) report various unidentified *Cyclocephala* species on several Arecaceae species. Aguiar-Gonçalves (2018) studied the spatial distribution of *Cyclocephala* in Brazil. Therefore, the role of *Cyclocephalini* in pollination seems limited, and they should be considered opportunists, similar to Hymenoptera, Apidae (Table 6), which are very common in palm inflorescences (Barfod et al., 2011; Ervik et al., 1999).

- *Ancognatha vulgaris* in *C. quindiuense*
- *C. amazona* in *B. gasipaes, O. bataua*, and *M. flexuosa*.
- *P. macrocarpa* ssp. *P. tenuicaulis, E. oleifera*.
- *C. collaris* in *E.oleifera*,
- *C. couturieri* on *A.* sp. *aff. murumuru*.
- *C. discolor* in *A. urostachys, O. bataua,* and *M. flexuosa*
- *C. distincta* in *E. oleifera, B. gasipaes, O. mapora*.
- *C. goetzi* in *A. urostachys*.
- *C. guianae* in *M. flexuosa*
- *C. lunulata* in *A.* sp. *aff. murumuru.*
- *C. marginalis* in *A. urostachys*, *O. bataua* and *Attalea microcarpa*
- *C. stictica* in *A. urostachys*,
- *C. variipenis* in *A. urostachys*.
- *M. signatoides* in *A. urostachys*, *O. bataua*, and *O. mapora*.

Some species are rare or observed in small quantities: *Caladenia marginata* on *A. urostachys* in Ecuador, associated with *C. distincta* and *C. couturieri* on *A. aff. murumuru* in Uchiza, Peru (Dechambre, 1998).

Curculionidae (Coleoptera) (Table 2). Many species are attracted to the anthesis of most palm species. Most belong to the subfamily Curculioninae, tribe Derelomini. The phylogeny of Derelomini was established by Franz (2006). In a recent study, Haran et al. (2023) proposed a synthesis on pollinating Curculionidae.

Not all genera and species mentioned in the literature will be discussed here, only those with confirmed generic and specific identification. In Table 2, we report the most notable genera observed by us, including references from other authors. The genus *Anchylorhynchus* seems specialized in the genera *Oenocarpus*, *Syagrus*, and *Butia*. We personally found it in all the sampled species of *Oenocarpus*, including *A. bicarinatus* O'Brien and *Anchylorhynchus* spp. (identification in progress). Küchmeister et al. (1998)

Table 6
Presence of the Dynastidae: Cyclocephalinae: *Ancognatha*, *Cyclocephala* and *Mimeoma* in the inflorescences of palm trees.

Authors Collectors	Genus, species	Host plant	Country, province, department or state, locality
GC/CD/KM	*Ancognatha vulgaris* Arrow	*Ceroxylon quindiuense*	Peru, San Martin, Ocol
Ervik et al. 1999	*Cyclocephala aequatoria* Endrödi	*Phytelephas seemannii*	Ecuador
KM/FK 1986 GC/FK 1992 FK/KM 10.1996 GC/FK 29.01.1994	*C. amazona* L.	*Astrocaryum macrocalyx*	Perú, Loreto, Jenaro Herrera, Iquitos, Quistococha
FK 10.1985	*C. amazona* L	*Oenocarpus (Jessenia) bataua*	Perú, Loreto Iquitos
GC 13.10.1991	*C. amazona* L.	*Bactris gasipaes*	Perú, Loreto, Jenaro Herrera
GC/JV 13.4.91	*C. amazona* L.	*Mauritia flexuosa*	Perú, Loreto, Quistococha
GC/PB 18.10.2002 GC/FK 29.01.1992	*C. amazona* L.	*Elaeis oleifera* *Astrocaryum macrocalyx*	Ecuador, Quinindé Perú, Iquitos
Bernal & Ervik,1996 Ervik et al. 1999,	*C. amazonica* L.	*Phytelephas seemannii*	Ecuador
GC/JD 10.1993	C. *collaris* Burm.	*Elaeis oleífera*	Brasil, Bahia, Ilheus
GC/JLl10.1988	*C. couturieri* Dech.	*Astrocaryum aff. murumuru*	Perú, San Martin. Uchiza
GC/JLl 10.1988	*C. dilatata* Prell	*Astrocaryum macrocalyx*	Perú San Martin. Uchiza
LR/IS 02.09.1999	*C. discolor* Herbst	*Oenocarpus bataua*	Ecuador, Napo, Tena
LR/IS 02.11.1999	*C. discolor* Herbst	*Astrocaryum urostachys*	Ecuador, Napo, Tena
FK 10.04.1987	*C. discolor* Herbst	*Phytelephas macrocarpa*	Perú, San Martin, Uchiza
GC/JV 13.04.1991	*C. discolor* Herbst	*Mauritia flexuosa*	Perú, Loreto, Quistococha
Ervik et al. 1999	*C. discolor* Herbst	*Aphandra natalia*	Ecuador
Ponchel Y. http:// consult. 2015	*C. discolor* Herbst	No identificado	Perú
GC/FK 19.08.87	*C. discolor* Herbst	No identificado	Perú, San Martin Uchiza
LR 02.09.1999	*C. discolor* Herbst	*Jessenia bataua (=Oenocarpus)*	Ecuador, Napo, Tena
GC/JD 06.11.1993	*C. distincta* Burmeister	*Elaeis oleifera*	Brasil, Bahia Ilheus
GC/MSP 15.07.1997	*C. distincta* Burmeister	*Oenocarpus mapora*	Brasil, Belem Embrapa
GC/JD 06.02.1993	*C. distincta* Burmeister	*Bactris gasipaes*	Brasil, Bahia Ilheus
Bezerra de Souza et al. 2014	*C. distincta* Burmeister	No identificado	Brasil
GC/JD 11.1993	*C. distincta* Burmeister	*Attalea funifera*	Brasil, Bahia Ilheus
Moron *et al.* 2014	*C. fasciolata* Bates	*Astrocaryum mexicanum*	Mexico, Vera Cruz
Oliveira & Avila 2011	*C. forsteri* Endrödi	*Acronomia aculeata*	Brasil, Mato Grosso
T.P 19.11.2000	*C. goetzi* Endrödi	*Astrocaryum urostachys*	Ecuador, Remolino
GC/FK 05.1996	*C. guyanae* Dechambre	*Mauritia flexuosa*	Brasil, Amazonas, Manaus
GC/FK 05.1996	*C. guyanae* Dechambre	*Oenocarpus bacaba*	Brasil, Amazonas, Manaus
GC 09.1988	*C. lunulate* Burmeister	*Astrocaryum murumuru*	Perú, San Martin, Uchiza
TP 01.09.1999	*C. marginalis* Kirsch	*Oenocarpus bataua*	Ecuador, Tena
GC/FK 29.09.1991	*C. marginalis* Kirsch	*Phytelephas tenuicaulis*	Perú, San Martin, Uchiza
GC/FK 18.08.1987	*C. peruana* Endrödi	*Phytelephas tenuicaulis*	Perú, San Martin, Uchiza
Ervik et al. 1999	*C. quadripunctata* Hohne	*Phytephas macrocarpa*	Ecuador
TP 12.12.2000	*C stictica* Burm.	*Astrocaryum urostachys*	Ecuador, Alto Pastaza
TP 19.09.2000	*C. variipenis* Miki	*Astrocaryum urostachys*	Ecuador, Pastaza Remolino
TP 05.11.2000	*Mimeoma signatoides* Höhne	*Oenocarpus bataua*	Ecuador, Pastaza Chunitayo
GC/FK 05.1996	*Mimeoma maculata* Burmeister.	*Oenocarpus bacaba*	Brasil, Amazonas, Manaus
TP 12.12.2000	*Mimeoma signatoides* Höhne	*Astrocaryum urostachys*	Ecuador, rio Pastaza
TP 09.09.2000	*Mimeoma signatoides* Höhne	*Oenocarpus bataua*	Ecuador, Chunitayo
CD/GC 06.10.2006	*Mimeoma signatoides* Höhne	*O. mapora*	Perú, rio Maniti, Villa Maria
GC/FK 05.1996	*Mimeoma signatoides* Höhne	*O. vacaba*	Brasil, Amazonas, Manaus
GC/PB/MSP 06.1997	*Phileurus couturieri* Dechambre	*O. mapora*	Brasil, Belem, Embrapa
GC 11.06.1992	*Phileurus excavatus* Prell	*Mauritia flexuosa*	Perú, Loreto, Jenaro Herrera, Fierrocaño

Collectors: PB: P. Beserra, GC: G. Couturier, JD: J. Delabie, CD: C. Delgado, FK: F. Kahn, KM: K. Mejía, MSP: M. Padilha, TP: T. Peyret, LRL: L. Reynaud, and IS: I. Suarez.

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reported *Anchylorhynchus tricarinatus* Vaurie on *O. bataua*. Souza de Medeiros and Núñez-Avellaneda (2013) described three new species: *Anchylorhynchus pinocchio* and *Anchylorhynchus luteobrunneus* on *S. sancona* H. Karst., *Anchylorhynchus centrosquamatus* Medeiros & Núñez on *Syagrus orinocensis* (Spruce) Burret and reported that adults are pollinators while the larvae develop in the endosperm, preventing fruit development. Costa et al. (2009) reported *A. amazonicus* Voss on *S. cocoides* Mart., and *S. vermicularis* Noblick. Silberbauer- Gottsberger et al. (2013) reported *Anchylorhynchus camposi* Bondar on *Syagrus petraea* (Mart.) Becc., and *Anchylorhynchus bicolor* Voss on *Butia paraguayensis* (Barb.Rodr.) L.H.Bailey.

Guerrero-Oyala et al. (2018) reported several unidentified species of Curculionidae on *S. sancona* (Kunth) H. Karst., where the genus *Anchylorhynchus* is undoubtedly found. Souza de Medeiros and Núñez-Avellaneda (2013) cited *Anchylorhynchus elongatus* on *S. sancona*, and Souza de Medeiros and Vanin (2020) described *Anchylorhynchus multisquamis* on *Syagrus* sp. Souza de Medeiros et al. (2019) reported *Anchylorhynchus trapezicollis* on *Syagrus coronata*, and de Melo-Valente and Souza de Medeiros (2013) described *Anchylorhynchus vanini* on *S. vermicularis* Noblick. Guerrero-Oyala and Núñez-Avellaneda (2017) reported *A. luteobrunneus* on *S. sancona* (Kunth) H. Karst., Souza de Medeiros and Nuñez-Avellaneda (2013) reported *A. elongatus* also on *S. sancona*, and Medeiros and Farrell (2019) described *A. trapezicollis* on *S. coronata*. Souza de Medeiros and Vanin (2020) described *A. multisquamis* on *Syagrus* sp. Souza de Medeiros et al. (2019) and Haran et al. (2023) reported that females lay their eggs in the female flowers, thereby limiting their role in fruit production (Silberbauer-Gottsberger et al., 2013).

The genus *Andranthobius*: de Melo-Valente and Lima da Silva (2014) reported *Andranthobius setirostris* on *S. cocoides*, and Mora-Urpí and Mexzon (1996) on *A. palmarum* in *B. gasipaes*.

The genus *Phyllotrox* is cited by most authors, including ourselves (six different species separated in our collections, (O'Brien, pers. comm.), on most palm genera and species. Listabarth (1996) considers them to be pollinators (Table 2) The specific identification of this genus is extremely difficult, but Küchmeister et al. (1998) cited ten species, and Voisin (1989) described *Phyllotrox lamottei* in Venezuela without specifying the host plant.

We found an undetermined species of Derelomini with red larvae, which was very abundant in all the sampled *P. tenuicaulis* and entirely absent from other palms.

The genus *Celetes* includes several species considered to be pollinators; however, they should also be regarded as parasites of young fruits (Table 1). An unidentified species was found exclusively on *A. funifera* in the Atlantic Forest (Ilheus, Brazil).

The genus *Terires*, with *Terires minusculus*, was found only on *Astrocaryum* of the subgenus *Pleiogynanthus*. It develops in young fruits, and in a count of 200 fruits, a parasitization rate of 35 % was revealed.

Nitidulidae (Coleoptera): The tribe Mystropini (Table 2) was revised by Kirejtshuk & Couturier (2010), where ten new species were described. They are considered the most effective pollinators, alongside Curculionidae Derelomini. Núñez-Avellaneda et al. (2005) studied the role of climate in pollination by Mystropini. Scariot et al. (1991) reported *Mystrops cf. minusculus* on *A. aculeata* (not studied by us). Restrepo-Correa et al. (2016) reported a very high degree of specialization between *Mystrops* and *Wettinia* spp. in Colombia.
Since the *Mystrops* were not identified at the species level, the relationship with other palm genera and species cannot be established. However, these results confirm a high level of specialization, as seen in the review by Kirejtshuk & Couturier (2010).

Staphylinidae (Coleoptera): The genus *Arecaceopora* Pace appears to depend on *P. tenuicaulis*, with three species: *A. couturieri*, *Arecaceopora delgadoi*, and *Arecaceopora perlifera* (Pace, 2010) (Table 2). Interestingly, in

Ecuador, it is the genus *Amazoncharis* that is found on *P. seemanni* (Bernal & Ervik, 1996; Ervik et al., 1999). *Oussipaliaglossa couturieri* Pace was found only on *A. funifera* (outside the Amazon), and *D. amazonensis*, a unique species on *M. flexuosa*, was very abundant on all male inflorescences of the sampled individuals (Chani-Posse & Couturier, 2012).

Heteroptera (Table 5) are characterized by three main families. The Miridae Phylini, with the genera *Alvarengamiris* (*A. alvarengai* Carvalho, *A. kemberi* Costa & Couturier, *A. margaridae* Costa & Couturier, are found only in the male inflorescences of *M. flexuosa* and *M. carana*, where they are highly abundant and reproduce. The *Anomalocornis* genus includes six known species in palms: *A. couturieri* Carvalho & Costa, *Anomalocornis geijskesi* Carvalho & Wygodzinsky, *Anomalocornis gentyi* Costa & Couturier, *Anomalocornis peyreti* Couturier & Costa, *Anomalocornis rondoniensis* Carvalho, and *Anomalocornis tucuruiensis* Carvalho, which are associated with *Astrocaryum* spp. and *B. gasipaes* (Carvalho & Costa, 1999; Couturier et al., 2003; Costa & Couturier, 2002; Costa & Couturier, 2012). The host plant for *Astrocaryum ariasi* Carvalho from Manaus (Brazil) is unknown, though it is likely a palm that remains to be identified. *Parafulvius henryi* Costa & Couturier is found on *A. urostachys* (Costa & Couturier, 2000), and *Fulvius chaquenus* Carvalho & Costa on *A. javarense*. Listabarth (1996) reported the presence of an unidentified Miridae on *B. gasipaes*.

The Thaumastocoridae (Heteroptera) family includes two highly specialized species of *Discocoris*: *D. drakei* Slater & Ashlock on *Oenocarpus* spp. (Couturier et al., 2002; Núñez-Avellaneda et al., 2015) and *Discocoris fernandezi* Slater & Brailowsky on *M. flexuosa* and *M. carana* (Couturier et al., 1998; Couturier, et al., 2002).

The Pentatomidae (Heteroptera) family includes the genus *Lincus*, which has been found on *Astrocaryum* spp. and *E. guineensis*, where they are known to transmit wilt disease (Couturier & Kahn, 1989a; Couturier & Kahn, 1989b; Llosa et al., 1990; Rolston, 1983; Rolston, 1989), as well as *Antiteuchus kerzhneri* Rider (2006) on *M. flexuosa*.

Apidae (Hymenoptera): Several species of Apidae visit palm inflorescences without any particular specialization (Table 4). These are primarily Trigoninae and *Apis mellifera*. Campbell et al. (2018) and Bezerra et al. (2020) observed that Apidae are the most important pollinators for *E. oleracea*.

On *P. seemanni* in Ecuador: *Melipona fasciata* Cockerell, *Trigona amalthea* Olivier, *Trigona chanchamayoensis* Schwarz, *Trigona ferricauda* Cockerell, *Trigona hyalinata* Lepeletier, *Trigona nigerrima* Cresson, *Trigona schultesii* Friese, *Trigona spinipes* Fab, *Trigona williana* Friese, and *Trigona* sp. (Bernal & Ervik, 1996).

Küchmeister et al. (1998) report *Ptilotrigona lurida* Smith on *Astrocaryum acaule*, *Trigona branneri* Cockerell cf. on *Astrocaryum gynacanthum* and *A. attaleoides*, as well as *T. williana* Friese and *Trigona fulviventris guianae* on *A. microcarpa*.

Other insects: There are many other insects. Núñez-Avellaneda (2014) found 79 species as occasional or permanent visitors to *O. bataua*, *O. balickii*, and *Oenocarpus minor*, contributing to pollination or participating in the degradation (e.g., Ptiliidae in *P. tenuicaulis*, Couturier G and Delgado C, pers. obs.) of the inflorescences. For example, unidentified larvae of Drosophilidae develop in the male inflorescences of *P. tenuicaulis*. The Drosophilidae *Palmophila ecuadoriensis* and *Palmomyia incerta* were described by Grimaldi et al. (2003) on *Wettinia maynensis* (P.e.), *Chamaedorea linearis*, and *P. seemannii* (P.i.). Many species of Hymenoptera (Formicidae, Vespidae), Diptera, and Chrysomelidae beetles have been reported in various palm inflorescences (Küchmeister et al., 1998).

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DISCUSSION

The detailed analysis of the fauna associated with various genera and species of neotropical palms, particularly regarding the fauna of their inflorescences, reveals different levels of specialization or coevolution. It goes without saying that only precise species identification allows the linkage between insect species and the relevant genera and species of palms. This has not always been possible.

Samples were taken outside the Amazonian region, in the Peruvian Andes at 2 300 m of altitude on *C. quindiuense*, as well as in the Brazilian Atlantic Forest on *A. funifera*. This demonstrates that geographic factors are not the primary drivers of species distribution; instead, the genera and species of palms determine the presence of different insect species.

One family (tribe) of insects and one genus or subfamily of palms (as in the case of *Astrocaryum* ssg., *Monogynanthus* and *Pleiogynanthus*).

One insect species is linked to one or two palm species (within the limits of our current knowledge). Therefore, we can consider this as coevolution. This specialization is strictly related to the specific genera and species of palms in question. In fact, the collections made outside the Amazon, both from *Ceroxylon* in the Peruvian Andes and from *A. funifera* in the Brazilian Atlantic Forest, have demonstrated that geography does not play a major role in the distribution of insect species. Godsoe et al. (2009) showed that the mutualism between insect and plant does not depend on climatic or geographical factors, but rather on the presence of the host plant species.

Some examples: The Curculionidae Derelomini *Couturierius* and *Grasidius* live exclusively on *E. oleifera* (O'Brien et al., 2004). They are replaced by several species of *Elaeidobius*, imported from Africa, on *E. guineensis*, which was also imported from Africa. *M. flexuosa* and *M. carana* host a highly specialized fauna, such as the Miridae of the genus *Alvarengamiris* (three species), the Mystropini *M. dalmasi*, the Thaumastocoridae *D. fernandezi*, and the Staphylinidae *D. amazonensis*. The Nitidulidae Mystropini *Mystrops nitidulus* is present in the genus *Attalea* (*A. funifera* in the Atlantic Forest of Brazil and *A. plowmanii* in the Iquitos region, Allpahuayo Reserve), as reported by Núñez-Avellaneda et al. (2005). However, it is also found in *Syagrus* but is completely absent from other studied palm genera.

The highest level of specialization is observed at the tribal level (Derelomini for Curculionidae, Mystropini for Nitidulidae, Philini for Miridae). It is highly likely that the chemical compounds emitted by palms, as shown by Knudsen (1999) for the palms *Geonomeae* and Lajis et al. (1985) for *E. guineensis*, as well as thermogenesis (Moore & Jameson, 2013), determine the selective attraction of palms to insects. Additionally, Godsoe et al. (2009) showed that the mutualism between insect and plant does not depend on climatic factors, but rather on the presence of the host plant.

The increase in the temperature of spathes before their opening has been noted by several authors: Schroeder (1978), Küchmeister et al. (1998), and more recently Pincebourde et al. (2016). This phenomenon contributes to the attraction of insects, as observed in *O. mapora*.

In this study, the role of insects in pollination is discussed. It is important to note that pollination is only confirmed if the insects in question actually move from the male to the female flowers and carry viable and compatible pollen (Beserra, 2002). For example, in the case of *M. flexuosa*, Khorsand-Rosa and Koptur (2013) demonstrated that insects play no role in its pollination, a fact we also observed: the abundant fauna found on the male inflorescences is absent from the female inflorescences. However, this observation is questioned by Mendes et al. (2016). In the female inflorescences, we only observed insects that were "predators" of the fruits, such as *Tyrannion* sp. (Curculionidae), several species of Baridinae, and *Leptoglossus hesperus* (Coreidae) (Vasquez et al., 2008). It should also be emphasized that Baridinae are generally rare or absent during anthesis and only approach the inflorescences when the young fruits are forming, as seen with *Palmelampius heinrichi* on *B. gasipaes* (O'Brien & Kovarik, 2000).

Some groups of insects considered to be pollinators are ubiquitous, such as *Cyclocephala* spp. (Dynastidae) and bees of the genus *Trigona* sensu lato, which visit various palm species indiscriminately during anthesis. However, Campbell (2018) consider native bees to be the main pollinators of *E. oleracea* in Brazil.

Thus, many studies leave uncertainty regarding pollination (Meekijjaroenroj & Anstett, 2003). Barfod et al. (2011) and Nuñez-Avellaneda et al. (2005) point out that experiments to control pollination have rarely been carried out, and that anemophily likely plays a more important role than previously anticipated (Rios et al., 2014). In fact, it should be considered that the insect in question must carry viable pollen and visit the female flowers. This point is highlighted by Núñez-Avellaneda et al. (2015), and it is also important that the insects do not develop on the young fruits (Beserra, 2002).

Regarding the close relationship between insects and their host plants, it will be necessary to better understand the volatile compounds of palm inflorescences, as demonstrated by Lajis et al. (1985) for *E. guineensis*, as well as advancements in the specific identification of insects. We encountered difficulty in identifying certain groups, such as Nitidulidae Mystropini and Curculionidae Derelomini. In fact, too often some authors label species as sp. A, B, etc., or sp. 1, 2, which only introduces confusion between different studies. All these examples confirm the close relationship between certain insect groups and their host palms, and these conclusions are consistent with those of Haran et al. (2023) for Curculionidae and Kergoat et al. (2006) which show the phylogenetic relationships between the genus *Acacia* (Fabaceae: Mimosoideae) and its associated seed predators.

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